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BLEACHING, UPPER THERMAL LIMITS AND TEMPERATURE ADAPTATION IN REEF CORALS

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THESIS DEDICATION

This thesis is dedicated to my loving wife Mary and my boys Daniel and Nicholas who did without me for so long while I was busy with this.

PUBLICATIONS ARISING FROM THIS THESIS

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ABSTRACT

The broad-scale ecology of coral bleaching and coral upper thermal limits were investigated to improve the basis for risk assessment and prediction of possible climate change effects on the Great Barrier Reef (GBR). Evidence from the spatial distribution of bleaching on the GBR in 1998, and a temporal study of physical variables at two reefs over a 10 – 12 year period, indicates that temperature is the single most important factor leading to coral bleaching. A novel empirical approach was developed to quantify the bleaching thresholds of reefs in terms of the magnitude and duration of thermal stress. Results from this study provide the first comprehensive synthesis of exposure times and temperatures involved in coral thermal stress, allowing more accurate predictions of the time-temperature thresholds that are likely to lead to bleaching for a variety of reefs throughout the GBR. Bleaching threshold curves indicate that both latitudinal and cross-shelf trends exist in the bleaching thresholds of reefs. These trends correlate with local temperature regimes and suggest that thermal adaptation has taken place over local and regional scales (10's – 1000's km). These bleaching curves provide the basis for the development of an early warning system for coral bleaching using near real-time automatic weather stations.

Experimental studies involving temperature manipulation show that three species of corals (*Pocillopora damicornis*, *Acropora elseyi* and *A. formosa*) from Orpheus Island on the inshore central GBR have sharply defined temperature tolerances and, like corals in other reef provinces, live precariously close to their upper thermal limits during most summers. Winter upper thermal limits of *P. damicornis* were 1°C lower than summer limits, raising the possibility that corals may be capable of short-term thermal acclimation. However, a short-term (10-day) acclimation study of two coral species (*P. damicornis and Porites cylindrica*) indicated that their thermal tolerance limits could not be extended beyond existing summer limits. Although these results indicate that the potential for development of short-term phenotypic tolerance to increasing temperatures

may be limited, they do not preclude the possibility that acclimation may take place over longer time periods.

Experimental studies also indicate that the breakdown of symbiosis between corals and zooxanthellae initiated by thermal stress continues for up to six weeks after removal of stress. Heat stress has a longer-term effect on coral health than can be accounted for by existing bleaching models, suggesting that an additional mechanism or process may be involved in coral bleaching. The delay in onset, or full development, of bleaching symptoms also has implications for the timing of bleaching surveys, namely, that to capture the full extent of bleaching, surveys need to be carried out 4-6 weeks after a stress event.

An aerial survey method was employed and evaluated to document the spatial extent and intensity of bleaching on the GBR during the severe 1998 event. This method provided a spatially comprehensive, cost-effective and conservative estimate of bleaching over large areas (>2000km). An equivalent overview of bleaching could not have been obtained from visitor-based reports or small-scale in-situ surveys. The aerial survey results, together with historical reports of bleaching covering six separate events since 1980, were used to detect spatial patterns in bleaching on the GBR. These results indicate that inshore reefs are more prone to bleaching than offshore reefs. Coupled with higher rates of temperature warming on the southern GBR compared to the northern GBR over the 20th century, inshore southern reefs may be at greater risk of climate change-related changes in sea temperature than other areas on the GBR.

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I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institution of tertiary education. Information derived from the published or unpublished work of others has been acknowledged in the text and a list of references is given.

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Chapter 1

General Introduction

Mortality of plate Acropora species at Otter Reef (18.05°E, 146.56°W) associated with coral bleaching, April 1998. Photo courtesy GBRMPA

1.1. Background

Our global atmosphere has changed since the pre-industrial era, with some of the changes due human-related emissions of greenhouse gases. Over the 20th century, the global average surface temperature has increased by 0.6 ± 0.2°C and is projected to increase by another 1.4 - 5.8°C over the next 100 years (IPCC 2001a). These climate changes have had discernable impacts on a wide range of biological systems, causing shifts in plant and animal ranges, declines in some plant and animal populations, earlier flowering of trees, and changes in the emergence of insects and egg-laying in birds (IPCC 2001b). The narrow thermal tolerance range of many coral species studied to date (reviewed in Brown 1997a, Hoegh-Guldberg 1999), also makes coral reefs vulnerable to climate change. Potential climate change impacts highlight the need for renewed research into the envelope of environmental conditions under which corals and coral reefs exist. This information is necessary to help us understand how corals and the reefs they build will be affected by predicted environmental changes.

1.2. Coral bleaching

Excessively high temperatures, coupled with high light intensities, cause corals to bleach (e.g. Yonge and Nicholls 1931a, Jokiel and Coles 1974, Coles and Jokiel 1978). This effect is manifested by a breakdown of the zooxanthella-coral symbiosis and a reduction in zooxanthellae density (Yonge and Nicholls 1931a). Other stresses such as low salinity, aerial exposure and pollutants (e.g. Coffroth et al. 1990, Jones 1997a, Jones et al. 1999) can also cause bleaching, but these tend to be local-scale influences. Thermal anomalies are generally large-scale regional influences and can cause widespread bleaching and, depending on the magnitude and duration of stress, also mortality (reviewed in Glynn 1993, Brown 1997b, Hoegh-Guldberg 1999). The first thermal bleaching event was reported in 1911 at Bird Key Reef in the Florida Keys when large numbers of corals were 'injured' during unusually hot and calm weather conditions, which also killed many fish, *Diadema* and molluscs (Mayer 1914). In 1929, a mass bleaching event was noted at Low Isles on the GBR, also during hot calm conditions which killed many corals on the reef flat (Yonge and Nicholls 1931a). No more bleaching events were recorded until 1961 when large scale bleaching was evident at Key Largo in the Florida Keys (Shinn 1966). Since 1979, the number of coral reported bleaching events has grown dramatically and this trend has been linked to climate change (Williams and Bunkley-Williams 1990, Glynn 1993, Brown 1997b, Hoegh-Guldberg 1999). Although the evidence for such a link is circumstantial, it is important to document large-scale bleaching events to understand the nature, dynamics and magnitude of such disturbances. This may in turn lead us to a better understanding of links between bleaching, weather and climate and thus assess future risk to reefs from climate change.

1.3. Mechanism of bleaching

The physiological and biochemical mechanism of coral bleaching is not fully understood. However, significant progress has recently been made with the use of pulse-amplitude modulation fluorometry and advances in biochemical techniques. Thermal stress in corals is thought to commence with inhibition of the dark reaction cycle in photosynthesis (Jones et al. 1998). Excitation energy, which would normally flow into photochemistry and the synthesis of sugars, is retained in the light reaction centres of the chloroplasts, causing the production of oxygen radicals. Oxygen radicals are highly corrosive and damage chloroplasts. This model explains the important (but secondary) role of light in coral bleaching (Hoegh-Guldberg 1999). Subsequent steps leading to the expulsion of zooxanthellae are not yet understood, but may involve certain active oxygen molecules entering the coral host (Downs et al. 2000). However, the coral hosts themselves also produce reactive oxygen species in the mitochondria as a result of heat stress (Downs et al. 2000). Impaired or compromised host membrane function as a result of thermal stress has also been noted (Downs et al. 2000), suggesting the biochemical mechanism of bleaching is complex and may involve more than just photoinhibition and expulsion of zooxanthellae.

1.4. Upper thermal limits

Upper thermal limits for any given species may not be fixed in time or in space. Intra-specific variation in tolerance limits in corals from widely separated geographical regions may be considerable. The upper lethal temperatures of Enewetak corals for example, are generally 1-2°C higher than Hawaiian corals (Coles et al. 1976). Similarly, *Porites porites* colonies from Florida are about 1°C more tolerant than their conspecifics from Hawaii (Marcus and Thorhaug 1981). *Pocillopora damicornis* from the Gulf of Panama have different tolerance limits to those of the Gulf of Chiriqui in the western Pacific (Glynn and D'Croz 1990). The most thermally tolerant corals are thought to occur in the Persian Gulf. Shallow water surface temperatures along the Trucial coast range from 16 to 40°C, and from 20-36°C at 4-5m depth (Kinsman 1964). Yet this area sustains coral reefs dominated by *Acropora spp.,* a genus generally regarded as thermally sensitive (Marshall and Baird 2000). How long it has taken for these regional differences in tolerance limits to arise is not known. Upper thermal limits of corals on the Great Barrier Reef (GBR) and their variation in space and time have received relatively little attention to date.

1.5. Acclimation and Acclimatisation

Little is known of thermal acclimation or acclimatization in corals. The term 'acclimation' is normally applied to experimentally controlled phenotypic responses to change, whereas 'acclimatization' to phenotypic responses under natural (field) conditions (Prosser 1973). In addition, two forms of thermal acclimation are generally recognized: 'capacity acclimation', which refers to the ability of organisms to undergo whole or partial compensation of metabolic function (eg in respiration rate) as temperatures change, and 'resistance acclimation', which refers to the ability of organisms to extend their normal thermal range (Precht, 1958). Resistance acclimation is often, but not necessarily, accompanied by capacity acclimation (Precht, 1958). The evidence for both forms of acclimation in corals is limited. Capacity acclimation has been demonstrated in the foliose hard coral *Echinopora gemmacea* which undergoes seasonal adjustment in respiration and photosynthesis (Al-Sofyani and Davies 1992). However, no capacity acclimation in respiration or photosynthesis was found in the pocilloporids

Stylophora pistillata and *Seriatopora hystrix*, or in the Caribbean massive coral, *Siderastrea siderea* (Munthiga and Szmant 1987, Hoegh-Guldberg and Smith 1989, Al-Sofyani and Davies 1992).

The only experimental evidence for resistance acclimation in hard corals comes from early work by Coles and Jokiel (1978) while conducting experiments on the interaction of light and temperature. Although acclimation was not the primary objective of these experiments, the authors found that colonies of *Montipora verrucosa,* acclimated for 56 days at 28°C, showed increased survivorship when exposed to 30°C for three days and 32°C for four days, compared to colonies incubated at 26°, 24° or 20°C. Circumstantial evidence for thermal acclimatisation was also found in the recovery of corals downstream of a thermal effluent stream of a power plant following a natural bleaching event (Meesters and Bak 1993). Regeneration of experimentally induced lesions in bleached *Porites astreoides* in the thermal effluent stream was faster than bleached colonies outside the effluent stream. In spite of the paucity of data on thermal acclimation in reef corals, it is a key issue in the climate change debate and research into the acclimation potential of coral is urgently needed.

1.6. Objectives

The research presented in this thesis addresses the broad-scale ecology of coral bleaching and coral upper thermal limits on the GBR. Valuable insights into physiological tolerances of corals are gleaned from an investigation of the scales and magnitudes of temperature variation on the GBR, anomalous temperatures associated with a bleaching event, as well as experimental investigations of bleaching thresholds and acclimation. The specific objectives of my research were:

1. **To document the occurrence of large-scale coral bleaching events on the Great Barrier Reef.** Documenting the scale and intensity of bleaching events on the GBR has proved challenging due in large part to its large size and the remoteness of many

of its reefs. Historical records of bleaching events are examined and a novel approach is trialled in documenting a large-scale bleaching event in 1998.

2. **To examine the magnitude and patterns of variation in sea temperature on the Great Barrier Reef.** As temperature is a dominant and pervasive influence on animal and plant populations everywhere, considerable insights could be gained into the physiological tolerances of corals from an examination of the thermal regimes experienced by coral populations.

3. **To investigate variation in the upper thermal limits of corals between seasons and over small spatial scales.** This study will set a benchmark for the upper tolerance limits of a number of coral species in the inshore central GBR against which spatial and temporal variation can be compared.

4. **To determine if the summer upper thermal limits of corals can be increased by short-term acclimation.** Determining and quantifying the ability of corals to acclimatize to increasing temperatures will assist in making more accurate predictions on the fate of coral reefs as a result of climate change. The experiments conducted here are a small, but important step towards this goal.

5. **To establish time-integrated thermal bleaching thresholds for selected reefs on the Great Barrier Reef.** Bleaching is not only a function of the size of the temperature anomaly, but also the exposure time at high temperatures. This study will attempt to define this time-temperature relationship using in-situ temperature data and historical bleaching records for a range of reefs on the GBR. Examination of spatial trends in these thresholds may provide insights into variation in tolerance limits over a wide geographic area.

Chapter 2

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Temporal and spatial patterns in coral bleaching on the Great Barrier Reef

Lorne Reef (foreground) showing extreme bleaching and Rattlesnake Island (background; 19.04°E, 146.61°W) during aerial surveys, March 1998. Photo courtesy GBRMPA

2.1. ABSTRACT

Documenting the scale and intensity of bleaching events is important for understanding the magnitude of bleaching disturbances, and for investigating spatial and temporal patterns that might help establish causal relationships. These data also help in assessing links to, and potential consequences of, climate change. Historical reports of bleaching based on observations by researchers and other reef-based professionals show that six bleaching events, of varying spatial extent and severity, have occurred on the Great Barrier Reef since 1980. As a general pattern, inshore reefs show a greater propensity to bleach than offshore reefs. However, despite considerable effort in soliciting bleaching reports, large spatial gaps exist in the data making it difficult to get a representative overview of the GBR during any one bleaching event. Broad-scale aerial surveys were successfully tested as a technique for gaining a more comprehensive overview of the scale and intensity of bleaching during a major bleaching event in 1998. Although the aerial survey technique generally underestimated the intensity of bleaching, they indicated that the GBR experienced its most intensive and extensive coral bleaching event on record in early 1998. The inshore-offshore pattern was again prominent with ~ 87% of inshore reefs bleached at least to some extent (>1% of coral cover affected) compared to 28% of offshore (mid- and outer-shelf) reefs. Approximately 25% of inshore reefs had extreme levels of bleaching (>60% of coral cover affected) while no offshore reefs showed this level of bleaching. Spatial patterns in bleaching intensity matched sea surface temperature (SST) patterns suggesting that temperature was the primary cause of the 1998 bleaching event. The temporal and spatial patterns in bleaching and the correlation of spatial bleaching patterns to SST suggest that inshore reefs are more vulnerable to climate change than offshore reefs. Despite high levels of bleaching, recovery was almost complete on most surveyed reefs 6-8 months later. Selected reefs in the Palm Island region were exceptions with relative declines in coral cover of up to 73%.

2.2. INTRODUCTION

Mass coral bleaching events in tropical ocean systems have been widely reported in the past two decades (Williams and Bunkley-Williams 1990, Glynn 1993, Brown 1997a). There have been repeated bleaching events in the 1980's and 90's on reefs in French Polynesia (5 events), Jamaica (4 events), the Bahamas (4 events), the Galapagos Islands (3 events), Thailand (2 events) and Panama (2 events) (Brown 1997b). The Great Barrier Reef (GBR) has also experienced repeated coral bleaching in recent years (Oliver 1985, Jones et al. 1997). Documenting the scale and intensity of bleaching events is important in understanding the magnitude of bleaching disturbances, studying spatial patterns, establishing causal relationships and assessing potential links to climate change. However, documenting bleaching events in a large coral reef province such as the GBR is problematic. The GBR consists of approximately 2900 reefs along its length of over 2000km, and is up to 300km wide in parts. Ground survey methods such as quadrats, line, belt, photo or manta tow transects (e.g. Cook et al. 1990, Hoegh-Guldberg and Salvat 1995, Davies et al. 1997) provide high quality information at local scales. However, the logistics and costs involved in obtaining a representative overview of a coral bleaching event using such small-scale methods would be huge and prohibitive. One way of improving the knowledge base of a bleaching event is to augment ground survey techniques with reports of coral bleaching from scientists and people employed in reef-based industries such as tourism and fishing. These reports can provide information on many more reefs affected by bleaching together with a qualitative indication of the intensity of bleaching at each reef. However, under-reporting, particularly in areas away from concentrated scientific and tourist activity, remain a problem. In addition, unbleached reefs also tend to be under-reported thus limiting the value of these data in documenting bleaching. Another broad-scale technique able to provide an overview of bleaching is aerial surveys. This technique has, to my knowledge, not been used before to document coral bleaching and its usefulness has thus not been assessed.

In this chapter, I collate and examine data covering six separate bleaching events on the GBR during the 1980's and 1990's. For the 1998 bleaching event, I also present data from a GBR-wide aerial survey to assess the scale and intensity of bleaching and compare these data to in-situ video survey data at a number of reefs. I also assess mortality at these reefs following the 1998 bleaching event.

2.3. METHODS

2.3.1. Bleaching observations

Observations of coral bleaching were collated by J. Oliver for bleaching events in 1980, 1982 and 1987, and by myself and J. Oliver for bleaching events in 1992 and 1994. Bleaching observations consisted of verbal reports, questionnaires, field notes and quantitative field data from scientists, staff from the Great Barrier Reef Marine Park Authority, Queensland Parks and Wildlife Service and reef tourism operators. The information collated included location, depth, time, species and percentage of living corals affected. However, because of the difficulty in standardising the percentage bleaching among observers, data are presented as 'bleached/unbleached' observations for reefs. An overall indication of the severity of bleaching in each year was inferred based on the reported percentages of coral cover affected on bleached reefs according to the categories: 'Moderate' (1 – 10%), 'High' (10 – 30%) or 'Very high' (>30%).

2.3.2. Aerial surveys

In 1998, a total of 654 reefs in the Great Barrier Reef Marine Park (i.e. 22.6% of reefs), were assessed for bleaching by visual aerial survey. The surveys were conducted from a fixed wing aircraft at a flying height of approximately 150m, at or around low tide over 10 days between 9 March and 10 April 1998. The survey period ranged from 4 to 6 weeks after bleaching was first reported on mid-shelf and inshore reefs (respectively) on the GBR. Reefs were classified into 5 bleaching categories based on the proportion of coral cover which appeared white in a zone covering the reef crest and upper reef slope. Coral cover was assumed to be in the range of 30 – 60% of ground surface in the area being surveyed, a figure generally representative of reefs on the GBR in 1998 (Sweatman et al. 2000, Fig 2.12 - 2.13). Local knowledge of coral cover assisted in estimating bleaching at a number of reefs. The categories were: 1 (extreme, > 60% bleached); 2 (very high, 30 – 60% bleached); 3 (high, 10 – 30% bleached); 4 (moderate, 1 – 10% bleached); and 5 (no or low bleaching, < 1% bleached). During non-bleaching periods, most reefs are considered to fall in the latter category.

Table 2.1. Dates and area covered by the aerial survey of bleaching in 1998.

Date	**Survey area**	**Latitude**
9 March 1998	Inshore Townsville to Cairns	19.2° – 17.0°S
10 March 1998	Inshore Townsville to Whitsundays	19.2° – 20.5°S
15 – 17 March 1998	Offshore Gladstone to Cairns	24.3° – 17.0°S
17 March 1998	Inshore Cairns to Lizard Island	17.0° – 14.7°S
6 – 7 April 1998	Inshore Whitsundays to Gladstone	20.5° – 24.3°S
8 April 1998	Offshore Cairns to Cape York	17.0° – 10.7°S
9 April 1998	Inshore Cape York to Lockhart River	10.7° – 12.9°S

2.3.3 Ground surveys

For the 1992 bleaching event, five x 20m line intercept transect surveys were conducted per site on the reef flat and slope in two bays at Magnetic Island. Surveys were conducted at Nelly Bay (two sites) and Geoffrey Bay (three sites) between 26 February and 26 March 1992. For each centimetre of intercept, corals were recorded to genus where possible, but later aggregated to total coral cover (hard and soft corals) for analysis. Based on a qualitative assessment of pigmentation, corals were also assigned to one of three bleaching categories: 'White bleached' – corals with little or no visible pigment, 'Partially bleached' – corals with pigment between or underneath branches/colonies, and 'Not bleached' – corals apparently normally pigmented.

For the 1998 event, video surveys were conducted during the bleaching event between 25 March and 23 April 1998, and again 6 - 7 months afterwards between 15 September and 27 November 1998. A total of 1105 transects were filmed, consisting of five x 5-min timed swims (~0.5m wide) in two reef zones (reef crest and slope), three sites (generally) and 20 reefs. The exact number of sites and habitats included at each reef are detailed in Table 2.2. Timed swims were used to maximize the number of transects that could be filmed in a short space of time (one month). Transects corresponded to approximately 50m and were standardized and verified between divers. Three divers were used for all transects and the maximum error, after training, was ± 5m. Transects were haphazardly chosen within fixed sites (GPS position; accuracy ± 50m) and swum end to end with a ~10m gap between them, following the reef crest (0-1m below datum) and a fixed depth contour on the reef slope (3-5m below datum). Reefs were chosen to represent the full range of bleaching categories reported in the aerial surveys. At one reef (NE Reef at Orpheus Island) an existing set of fixed transects were filmed. Data from this site are presented, but not included in statistical analyses. Video tapes were analyzed as per the methods detailed in Christi et al. (1996). Bleaching categories used in the video tape analysis are as detailed for the 1992 event.

Table 2.2. Summary of reefs and the number of zones (reef crest and slope), sites and transects surveyed by video during and after the bleaching event in 1998.

		March-April 1998			*September-November 1998*		
Region	**Reef**	**Zones**	**Sites**	**Transects**	**Zones**	**Sites**	**Transects**
Magnetic Is	Nelly Bay	2	3	5	2	3	5
	Geoffrey Bay	2	3	5	2	3	5
	Virago Shoal	2	3	5	2	3	5
	Middle Reef	1	3	5	1	3	5
Palm Is	Curacao Is	2	3	5	2	3	5
	Falcon Is	2	3	5	2	3	5
	Rattlesnake Is	2	3	5	2	3	5
	Northeast Rf	1	1	5	1	1	5
Whitsunday Is	Border Is	2	3	5	2	3	5
	Daydream Is	2	3	5	2	3	5
	Deloraine Is	2	3	5	2	3	5
	Hamilton Is	2	3	5	2	2	5
Offshore	Otter Rf	2	3	5	2	3	5
	Little Kelso Rf	2	3	5	2	3	5
	Trunk Rf	2	3	5	2	3	5
	Britomart Rf	2	3	5	2	3	5
	Duncan Rf	2	3	5	2	3	5
	Keeper Rf	2	3	5	2	3	5
	No Name 18-022	2	3	5	2	3	5
	No Name 18-017	2	3	5	2	3	5

2.3.4 Environmental parameters

Sea temperatures were recorded every 30 minutes on the reef slope at Nelly Bay on Magnetic Island using a data logger (Dataflow Systems, 905 semiconductor sensor). The data logger was calibrated before and after deployment against a NATA certified digital thermometer; the final accuracy of the sensor was approximately ± 0.1°C. Daily average temperatures were calculated and presented along with daily minima and maxima.

Salinity was measured at 30-minute intervals on the reef flat at Nelly Bay using a data logger with an inductance coil sensor (Dataflow Systems). The data logger was downloaded and cleaned weekly between 12 January and 7 March 1998. The sensor was calibrated before and after deployment against stock solutions of NaCl; the final accuracy of the sensor was approximately ± 1 ppt. Data were averaged for each day of the observation period.

Satellite sea surface temperatures (SSTs) were obtained from Dr. W. Skirving (Australian Institute of Marine Science) for the period 25 January – 30 March 1998. SST's derived from the NOAA-14 satellite and AVHRR sensor were collected at a spatial resolution of 1km and processed using the NOAA non-linear sea surface temperature algorithm (Skirving and Guinotte 2001). Data are shown for the period 4 – 6 February 1998 and are representative of the spatial distribution in SST's for the whole of February 1998.

2.3.5. Data analysis

The percent of coral cover that bleached (partial and white-bleached categories combined) was compared among zones and reefs using a 2-factor ANOVA. Reefs were grouped into geographic regions (Magnetic Island, Palm Islands, Whitsunday Islands, Offshore reefs). As reefs were chosen on the basis of bleaching intensity and bleaching intensity is correlated with region, the analysis could not be used to test for differences among regions. Instead, each region was considered in a separate analysis. Reefs were considered a fixed factor. Reefs with missing sites or zones (Middle Reef, NE Reef) were excluded from the analysis, thus yielding a balanced design ('Zone': 2 levels, 'Reefs': 3-8 levels depending on the region, 'Site': 3 replicates). Transects were aggregated to means of sites in the analyses because Site (nested in Reef) was the residual error term in the model. Homogeneity of variance was checked using spread vs level plots of predicted versus studentized residuals and normality was checked using QQ plots of studentized residuals. Where significant heteroscedacity or deviation from normality were evident in the data for any region (Magnetic Island, Whitsunday and Offshore regions), data were square root and arcsine transformed prior to analysis. Significant results involving the interaction of 'Zone' and 'Reef' were analysed further for differences among levels using custom hypothesis tests (e.g. difference between reef flat and slope at Border Island).

Variation in coral cover during and after the bleaching event, and among zones and reefs was investigated using a 3-factor split-plot ANOVA model with time as a repeated factor. The model can be represented as:

$$\left(\begin{pmatrix} R^f \\ \mid \\ S^r \end{pmatrix} xZ^f \right) xT^f$$

where, R = 'Reef', S = 'Site', Z = 'Zone' , T = 'Time', f = fixed and r = random.

Each region was considered in a separate analysis as above. Transects were again aggregated to means of sites. 'Site (nested in Reef)' was included as a factor in the model as it formed part of the error term for the factors 'Reef', 'Zone', 'Reef x Zone', 'Time' and 'Reef x Time' (refer Tables 2.8 – 2.11). Assumptions of normality and variance heterogeneity were checked as above and no transformation of the data was necessary for any region. Significant results involving the main factor of interest, 'Time' or its interaction with 'Zone' or 'Reef' for any region are presented in tables and, where appropriate, further analysed for differences among levels using custom hypothesis tests (e.g. difference between time 1 and 2 on reef flat).

2.4. RESULTS

2.4.1. Bleaching observations: 1980 -1998

Six coral bleaching events occurred on the Great Barrier Reef (GBR) in the 1980s and 1990s. The first of these was in early 1980 when eight reefs were reported to be bleaching, including inshore reefs at Turtle Island, south of Mackay and Magnetic Island near Townsville (Fig 2.1). Reports of bleaching were also received for several reefs near Cairns and Decapolis Reef north of Cooktown (Appendix A; refer Fig 2.3 for a map showing place names). The overall severity of bleaching in 1980 was considered moderate, based on the relatively low proportions of coral cover affected. No observations were reported for reefs that did not bleach.

In mid-January 1982, bleaching reports were received for 14 reefs between Turtle Island and Lizard Island (Fig 2.1, Appendix A). Although the geographic spread of this bleaching event is similar to the 1980 event, the severity of bleaching was much higher. At least 25 taxa of hard coral were noted as bleached, with inshore reefs such as Magnetic Island suffering bleaching levels of 30 – 60% among acroporids and 50 – 80% among pocilloporids (Oliver 1985). Similar levels of bleaching were also noted on an offshore reef at Myrmidon among acroporids, although no data were collected for pocilloporids (Oliver 1985). The severity of the 1982 event is thus estimated to have been very high.

Another bleaching event occurred in 1987. Bleaching reports were received for 23 reefs spread from Lady Musgrave Reef (latitude 23.9°S) in the southern GBR to May Reef in the northern GBR (latitude 12.8°S). For the first time, data were also collected on reefs which did not bleach. Bleaching was prominent on inshore reefs whereas most mid- and outer-shelf reefs near Townsville, including Myrmidon Reef, remained unbleached (Fig 2.1). Although the spread of bleached reefs was large and many more reefs were reported to have bleached in 1987 compared to previous events, the severity of bleaching at affected reefs was less than in 1982. The 1987 event is thus considered high in severity.

Bleaching was also reported at isolated reefs in 1992 and 1994. Most of the bleached reefs were inshore reefs, with only one report received from an offshore reef in 1992 (Agincourt No. 4). Inshore reefs affected in 1992 included the Keppel Island area in the southern GBR, Dingo Beach near the Whitsunday Islands, Magnetic Island, and the Palm and Brook Island groups north of Townsville (Fig 2.1, Appendix A). Offshore reefs near Cairns were mostly unaffected. In 1994, bleaching reports were restricted to Magnetic Island and the Palm Island group (Fig 2.2, Appendix A). Offshore reefs from Cairns to Mackay were unaffected in 1994. Both events are considered moderate in severity.

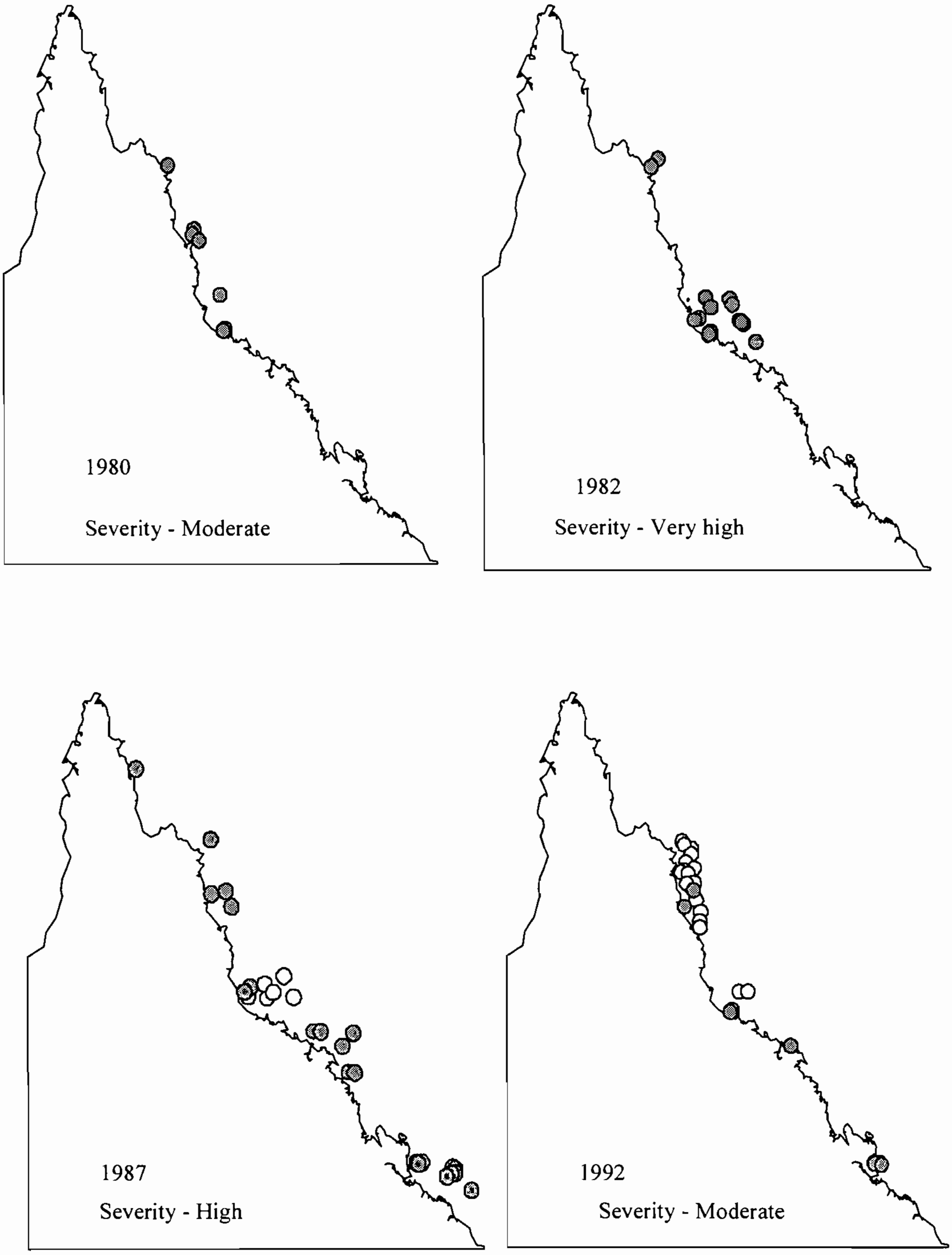


Fig 2.1. Records of bleaching on the GBR from 1980 to 1992. Grey circles are reports of bleached reefs, white circles are reports of unbleached reefs. Approximate overall severity of bleaching on affected reefs is indicated on a three-point scale: 'Moderate', 'High' and 'Very high'. Names and locations of reefs are as per Appendix A.

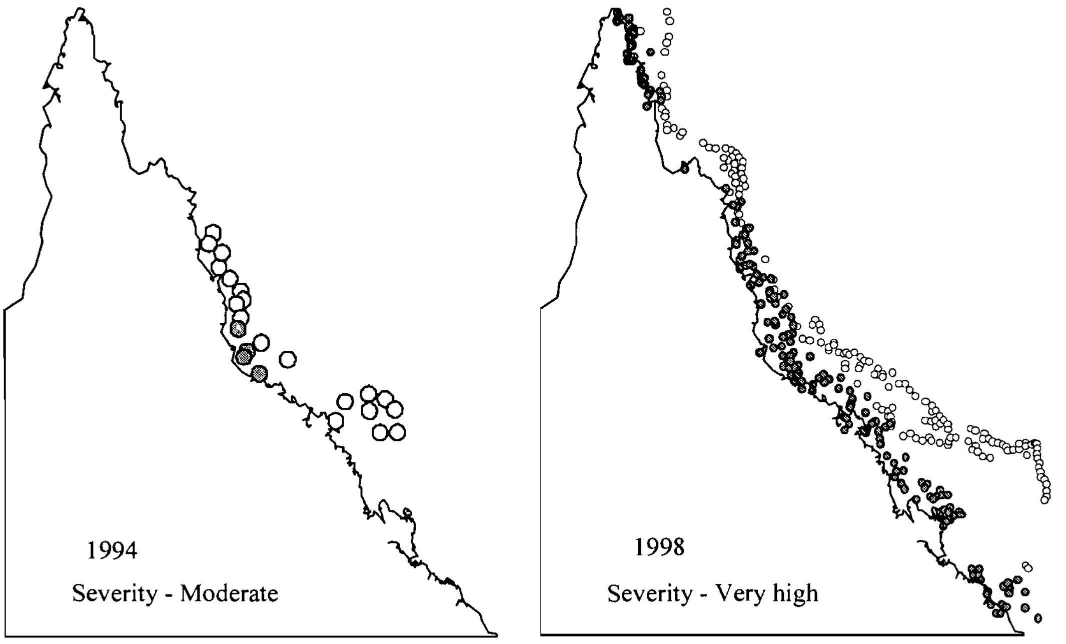


Fig 2.2. Records of bleaching on the GBR from 1994 and 1998. Grey circles are bleached reefs; white circles are unbleached reefs. Approximate overall severity of bleaching on affected reefs is indicated on a three-point scale: 'Moderate', 'High' and 'Very high'. Records for 1994 are visitor reports; records for 1998 are based on aerial surveys. Names and locations of reefs are as per Appendix A.

In 1998, mild bleaching of some coral colonies was first observed at Magnetic Island near Townsville on the 23rd of January; no bleaching was evident one week earlier. By the 30th of January, coral bleaching had become widespread around Magnetic Island, although most corals were pale, rather than white. By mid-February, bleaching had intensified at Magnetic Island with most bleached colonies appearing bone white. At this time, extensive bleaching was also reported from other inshore areas in the central and southern GBR. By late February and early March 1998, extensive bleaching occurred on virtually all inshore sites south of 15°S as well as a number of mid-shelf reefs in the central GBR (Fig 2.2, Appendix A). Both qualitative observations and aerial survey data indicate that the severity of this event was very high.

2.4.2. Aerial bleaching survey – 1998

Aerial surveys in March/April 1998 revealed a striking pattern in the distribution of bleached reefs (Fig 2.3). Overall on the GBR, 87% of inshore reefs had at least moderate (>1% of corals affected) levels of bleaching, though many had high (10 – 30%) or very high (30 – 60%) levels of bleaching. In contrast, only 28% of offshore reefs showed bleaching above the moderate category (Fig 2.4). Two thirds of all inshore reefs on the GBR had levels of bleaching classed as high or above (>10% of coral bleached) and a quarter of all inshore reefs showed extreme levels of bleaching (>60% of coral bleached). In contrast, only 14% of offshore reefs had high (or greater) levels of bleaching, while none were in the extreme range.

Aerial surveys also revealed latitudinal variation in the severity of bleaching with bleaching most intense in the lower two-thirds of the GBR, south of 15°S. In the northern GBR (north of 15°S), 72% of inshore reefs (n = 50) showed moderate bleaching (1 – 10% of corals). Only 22% of reefs were classified as having high or very high levels of bleaching (Fig 2.5c). In contrast, 63 – 68% of inshore reefs had very high or extreme levels of bleaching in the central (15 – 21°S) and southern (21 – 24°S) GBR respectively. Reefs with high coral cover and extreme levels of bleaching appeared stark white from the air and seemed to ‘glow’.

Offshore reefs in the central GBR were more affected than those either to the north or to the south. Twenty-four percent of offshore reefs in the central GBR showed moderate levels of bleaching compared to 2% to the south and 7% further north. In addition, more than three times as many offshore reefs in the central GBR had high levels of bleaching compared to the northern or southern regions (Fig 2.5a,b,c).

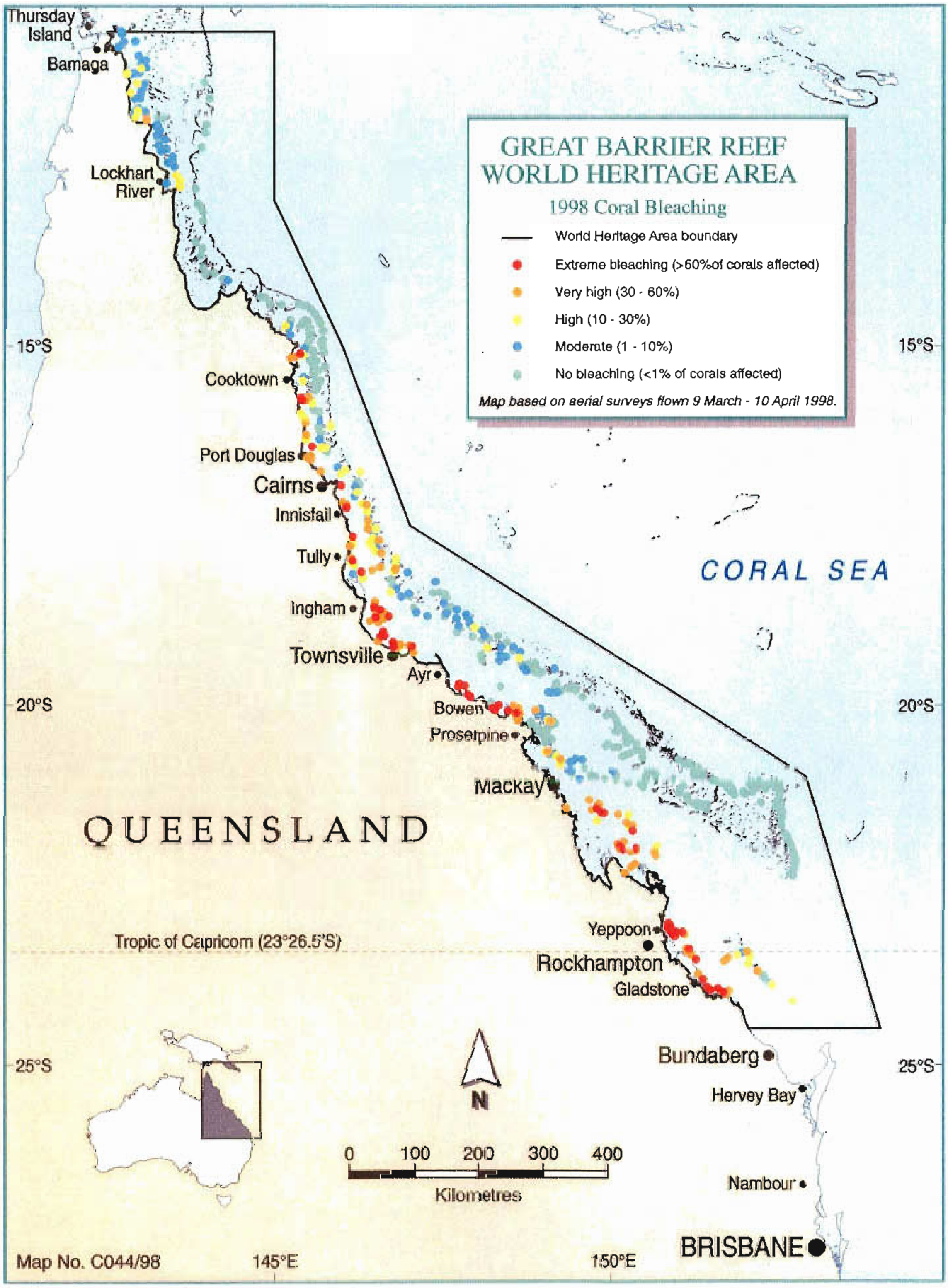


Fig. 2.3. Assessment of coral bleaching on the Great Barrier Reef based on visual aerial surveys conducted at an altitude of ~150m at or near low tide.

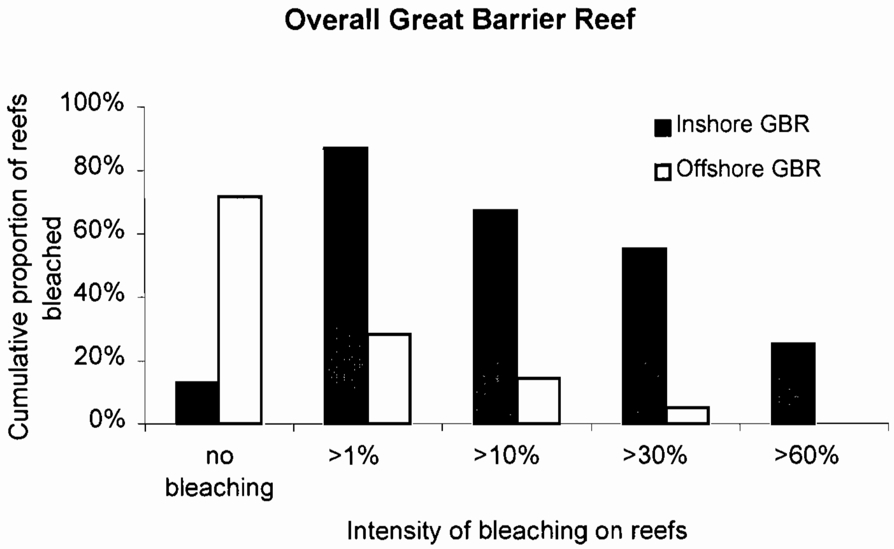


Fig 2.4. Cumulative proportion of reefs showing coral bleaching of varying intensities on the Great Barrier Reef (n = 654 reefs). Note that each bleaching intensity is cumulative and inclusive of higher levels of bleaching.

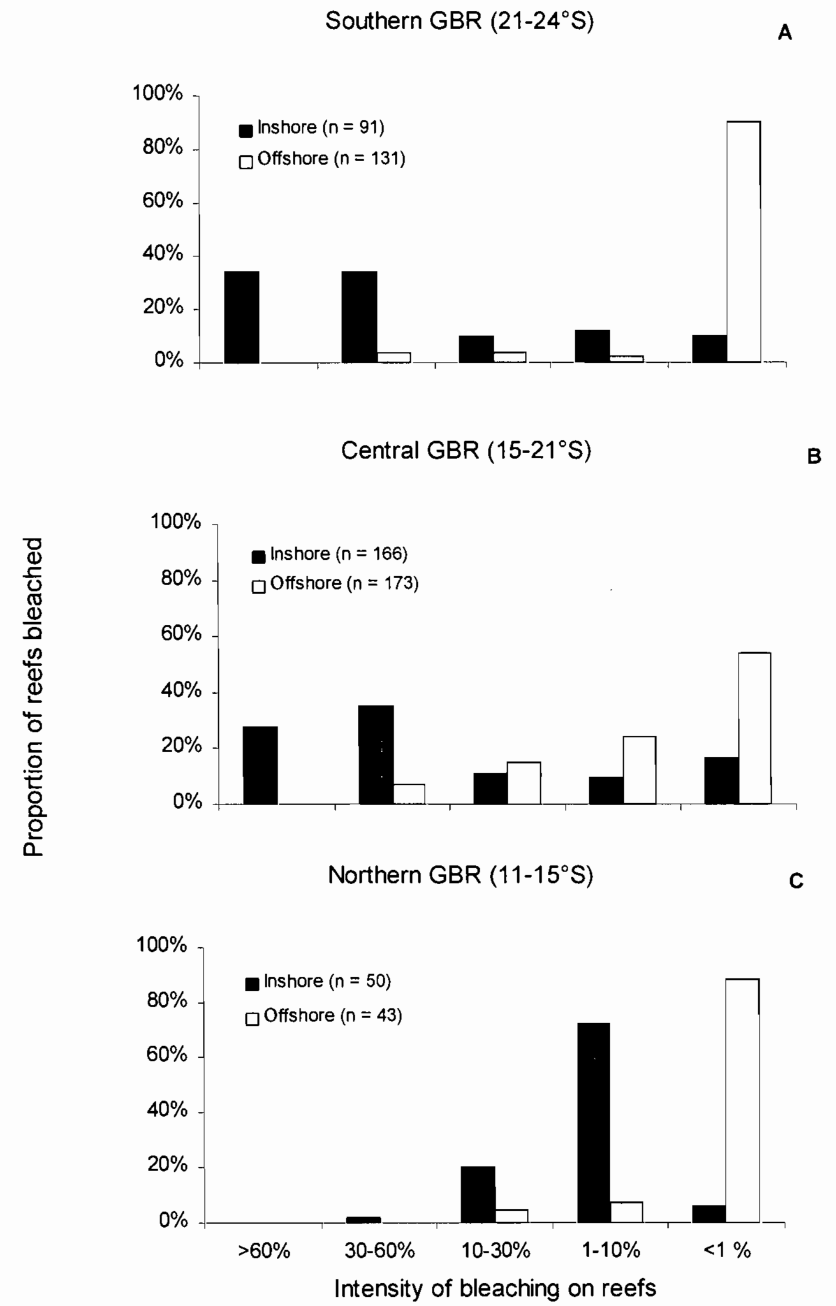


Fig 2.5. Extent and intensity of coral bleaching by region on the Great Barrier Reef (a) southern, (b) central, and (c) northern. The number of inshore and offshore reefs included in this regional classification are shown in the respective graph legends.

2.4.3. Bleaching and environmental conditions

The cause of the 1998 coral bleaching event is likely to have been a combination of elevated sea temperature and high solar radiation, possibly exacerbated in some areas (inshore central GBR) by lowered seawater salinity. At Magnetic Island, widespread bleaching occurred when average day temperatures reached 31.5°C. Daily average temperatures remained above 31°C for 25 days, reaching a maximum of 32.2°C on the 4th February (Fig 2.6).

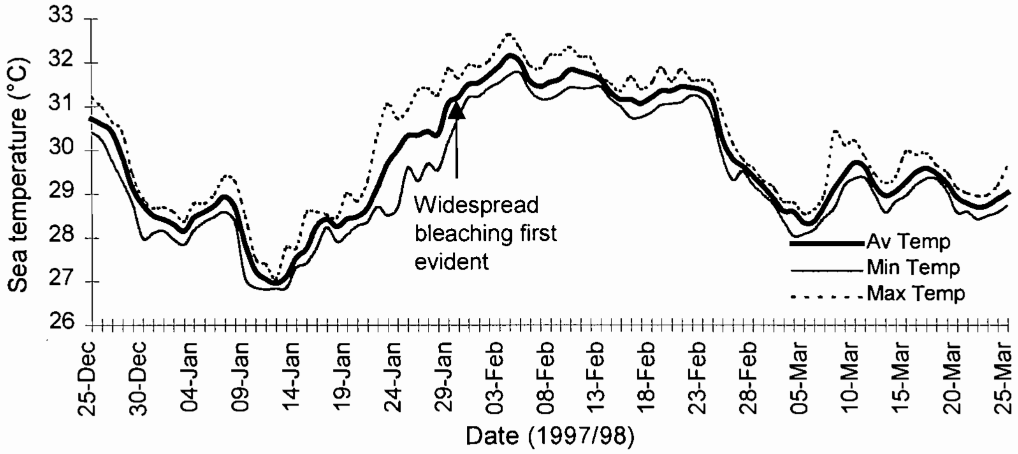


Fig 2.6 Average daily, minimum and maximum water temperatures at Magnetic Island during the 1998 bleaching event. Arrows indicate when bleaching was first noticed by the author.

Satellite sea surface temperature (SST) data indicate that temperatures were highest in near-shore waters between Innisfail and Ayr during the period 4-6 February 1998. An overlay of bleached reefs and SST data shows a good spatial correlation between temperature and bleaching intensity (Fig 2.7). Highest intensities of bleaching coincided with highest water temperature at inshore reefs from Gladstone to Cooktown. Offshore reefs in the southern GBR experienced temperatures less than 29°C and were unbleached.

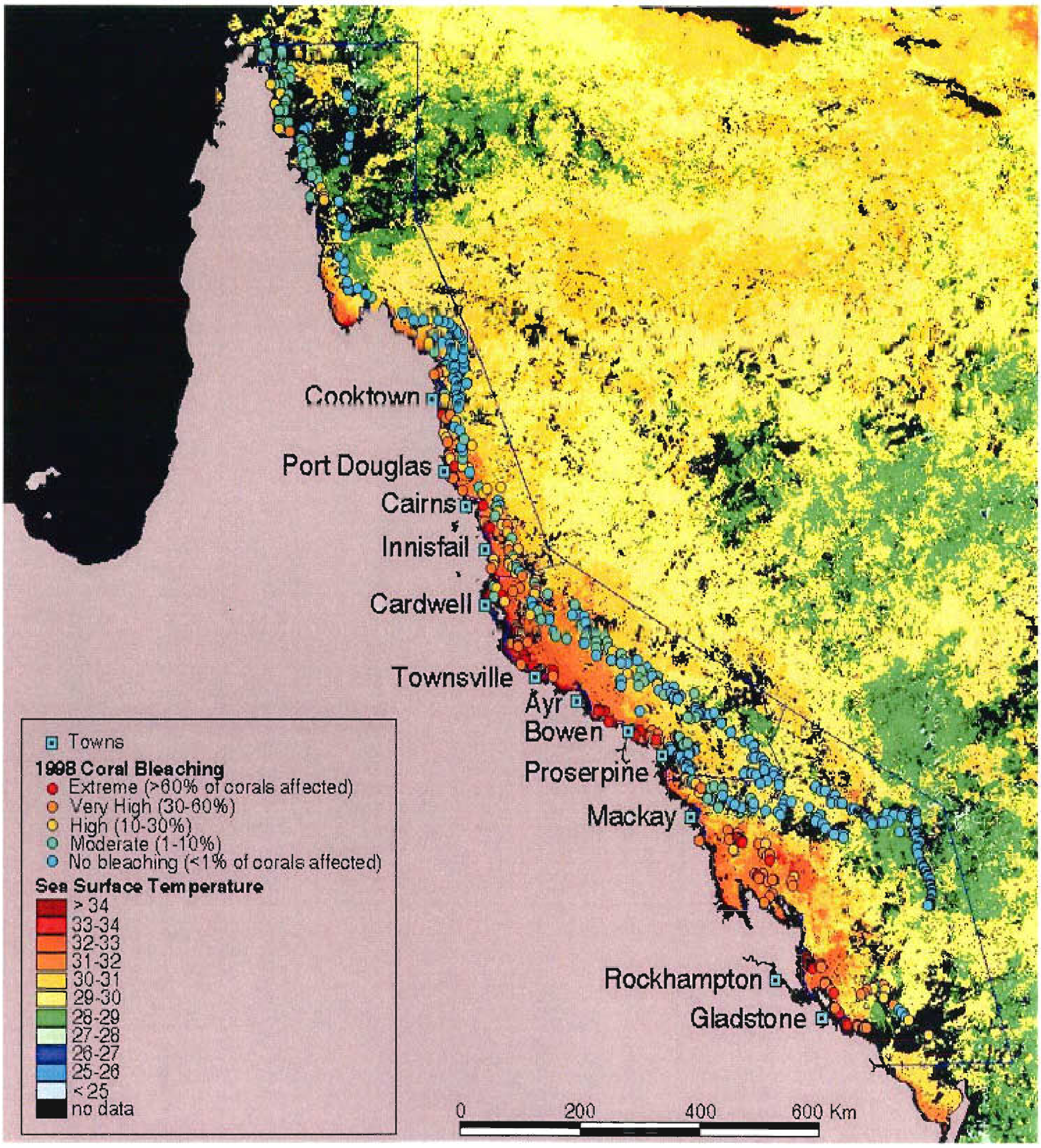


Fig 2.7. Spatial correlation between 3-day average satellite SST (4-6 February 1998) and the intensity of coral bleaching as recorded by aerial surveys. Satellite temperature data courtesy Dr. W. Skirving, Australian Institute of Marine Science.

The far northern GBR also experienced relatively cool SST's which coincided with low levels of bleaching. Offshore areas between Townsville and Cairns had relatively warm SST's and also had many reefs with high levels of bleaching.

Bleaching intensities on inshore reefs between Ayr and Cooktown (20°S - 15°S) may have been exacerbated by lowered seawater salinity. Areas near Townsville received over 500mm of rain three weeks prior to the bleaching period on 10 January 1998 and caused flooding of major river systems between Ayr and Cooktown. Seawater salinity on the reef flat at Nelly Bay at Magnetic Island was lowered for up to 7 weeks (4 weeks between 28-32 ppt and a further 3 weeks between 32 and 34 ppt). Prevailing SE trade winds kept most of the river flood plumes near shore. No significant rainfall occurred south of Ayr, however most inshore reefs in this area still exhibited very heavy or extreme levels of bleaching.

2.4.4. Aerial vs ground surveys

Ground-truth surveys conducted at 20 reefs indicate that the aerial survey data are likely to be underestimates of the true extent and intensity of the 1998 bleaching event on the GBR. Results from in-situ video estimates of bleaching on the reef crest show that the aerial survey underestimated the bleaching by one bleaching category on eight out of 20 reefs (Fig 2.8). At five reefs the aerial survey underestimated the bleaching by two bleaching categories and by three bleaching categories at another 2 reefs. The aerial survey correctly estimated the bleaching intensity at three reefs and overestimated the severity of bleaching on only two occasions compared to video estimates.

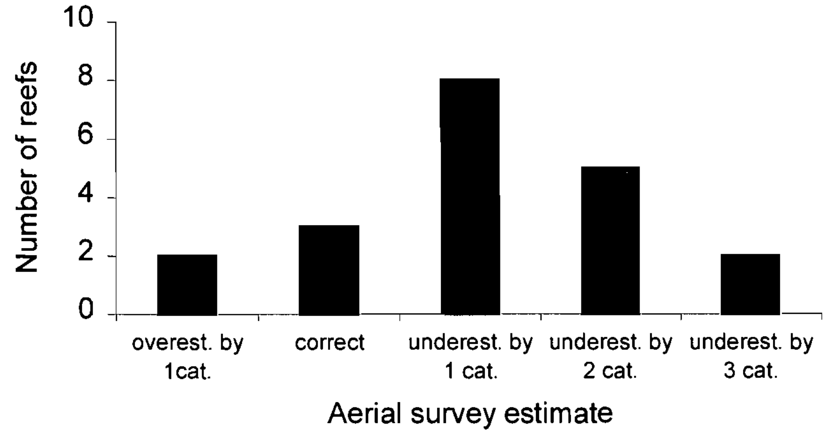


Fig 2.8. Accuracy of the aerial survey methodology in estimating bleaching intensity (5 categories of severity) compared to in-situ video estimates (averaged over 3 sites on the reef crest at each reef), binned into the same bleaching categories.

2.4.5. Comparisons of bleaching patterns between years and reefs

Transects during the 1992 bleaching event indicated that 6.5% of overall reef substratum bleached at Magnetic Island, representing 16.1% of living coral cover. However, the amount of bleaching was highly dependent on reef and reef zone (Fig 2.9). Analysis of variance indicated that bleaching was more severe on the reef slopes than on the reef crests ($p = 0.005$, Table 2.3) and the incidence of bleaching was greater at Geoffrey Bay than Nelly Bay ($p = 0.018$, Table 2.3). A different pattern was evident in 1998. There was no significant difference in bleaching between zones ($p = 0.846$) or reefs ($p = 0.403$, Table 2.4, Fig 2.10). However, overall bleaching levels were much higher in 1998 with a grand mean of 36.7% of reef surface area bleached, representing 54.7% of living coral cover (Fig 2.10). Approximately two thirds of bleached coral at Magnetic Island was partially bleached and one third white bleached.

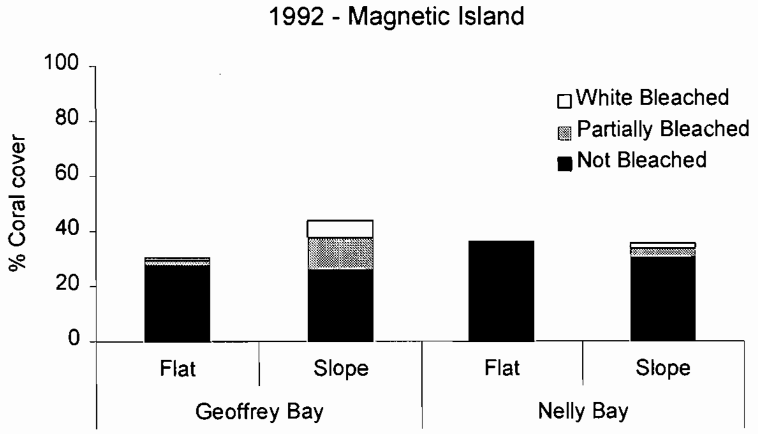


Fig 2.9. Estimates of coral bleaching at Magnetic Island during 1992, based on 20m line-intercept transcects (Geoffrey Bay: 3 sites x 2 zones x 5 transects; Nelly Bay: 2 sites x 2 zones x 5 transects). Data are means in three categories of bleaching: White bleached, Partially bleached, and Not bleached.

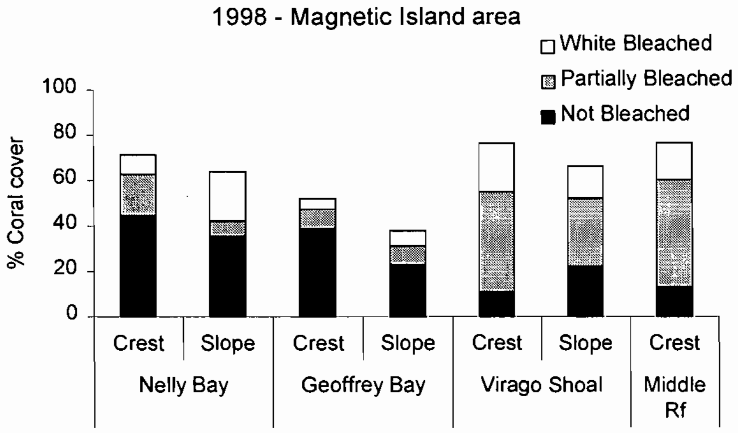


Fig 2.10. Estimates of coral bleaching in the Magnetic Island area during 1998, based on 50m video transects. Number of sites and transects as per Table 2.2. Data are means in three categories of bleaching: White bleached, Partially bleached, and Not bleached.

Highest levels of bleaching occurred in the Palm Island region with a grand mean of 42.7% of reef surface area bleached, representing 74.8% of living coral cover (Fig 2.11a). No differences in the level of bleaching were detected between the reef crest and slope (p = 0.311), nor was there an interaction between Zone x Reef (p = 0.854; Table 2.5). However, there were significant differences in bleaching among reefs in the Palm Island region with Falcon and Rattlesnake Island exhibiting higher bleaching than Curacao Island (p = 0.033, Table 2.5).

Bleaching levels were variable, but generally lower, among reefs in the Whitsunday Island region. Overall, 14.0% of reef area was bleached, representing 26.8% of living coral cover. However, analysis of variance showed that there was a significant zone x reef interaction with higher bleaching levels on the reef crest at Border and Deloraine Islands compared to the slope at these reefs and higher bleaching levels on the reef slope at Daydream Island compared to the crest (p = 0.00; Table 2.6).

Offshore reefs also had variable, but generally low levels of bleaching. A grand mean of 14.3% of reef area was bleached, of which only 3.8% was white bleached (Fig 2.11). Partially and white bleached corals made up 36.0% of the living coral cover. Averaged over all reefs, there was no significant difference between the reef slope and crest (p = 0.292), however at different reefs the reef crest and slope zones responded differently (p = 0.000; Table 2.7). The reef crest was significantly more bleached than the reef slope at Trunk, Duncan Reef, Keeper Reef and 18-017 Reef and vice versa at Otter Reef, Britomart Reef and 18-022 Reef (Fig 2.11).

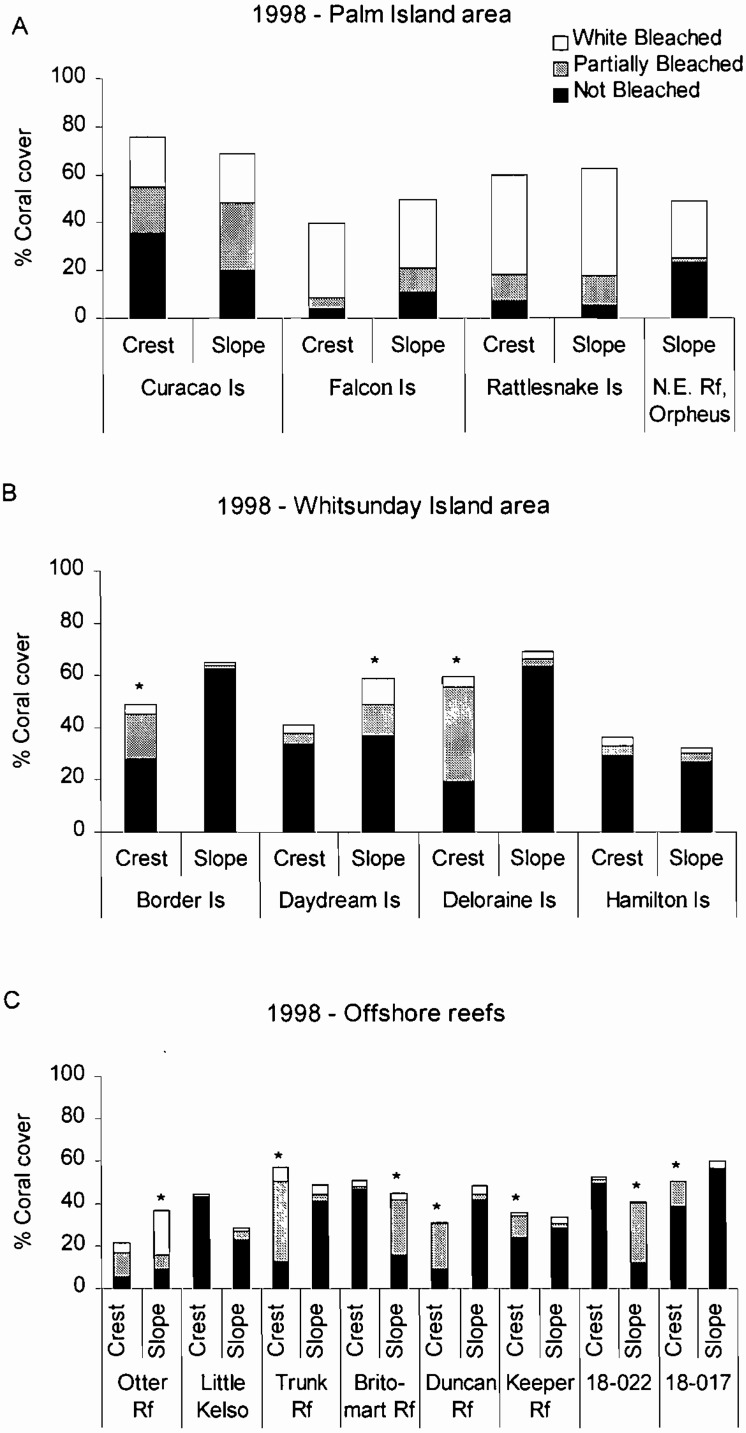


Fig 2.11. Estimates of coral bleaching during 1998 based on 50m video transects for three regions: (a) Palm Islands, (b) Whitsunday Islands, and (c) Offshore reefs in the central GBR. Number of sites and transects as per Table 2.2. Data are means in three categories of bleaching: White bleached, Partially bleached, and Not bleached.

* denotes significant difference between reef crest and slope within a reef at $\alpha = 0.05$.

Table 2.3. ANOVA table comparing bleaching among reefs (Geoffrey and Nelly Bay) and zones (reef flat and slope) at Magnetic Island in 1992. * denotes significant at $\alpha = 0.05$; ** denotes significant at $\alpha = 0.01$

Source	Type I Sum of Squares	df	Mean Square	F	Sig.	
ZONE	140.728	1	140.728	32.37	.005	**
REEF	65.399	1	65.399	15.04	.018	*
ZONE * REEF	33.593	1	33.593	7.73	.050	
Error	17.388	4	4.347			
Total	507.018	8				
Corrected Total	257.108	7				

Table 2.4. ANOVA table comparing bleaching among reefs (Geoffrey Bay, Nelly Bay and Virago Shoal) and zones (reef flat and slope) at Magnetic Island in 1998.

Source	Type I Sum of Squares	df	Mean Square	F	Sig.
ZONE	5.037	1	5.037	.040	.846
REEF	250.221	2	125.111	.982	.403
ZONE * REEF	425.863	2	212.932	1.671	.229
Error	1529.402	12	127.450		
Total	21719.254	18			
Corrected Total	2210.523	17			

Table 2.5. ANOVA table comparing bleaching among reefs (Curacao Island, Falcon Island and Rattlesnake Island) and zones (reef flat and slope) in the Palm Island region in 1998. Data were arcsine-square root transformed prior to analysis to correct for heterogeneity of variance. * denotes significant at $\alpha = 0.05$

Source	Type I Sum of Squares	df	Mean Square	F	Sig.	
ZONE	1.238E-02	1	1.238E-02	1.121	.311	
REEF	.102	2	5.080E-02	4.599	.033	*
ZONE * REEF	3.530E-03	2	1.765E-03	.160	.854	
Error	.133	12	1.105E-02			
Total	10.070	18				
Corrected Total	.250	17				

Table 2.6. ANOVA table comparing bleaching among reefs (Border, Daydream, Deloraine and Hamilton Islands) and zones (reef flat and slope) in the Whitsunday Island region in 1998. Data were arcsine-square root transformed prior to analysis to correct for heterogeneity of variance. ** denotes significant at $\alpha = 0.01$

Source	Type I Sum of Squares	df	Mean Square	F	Sig.	
ZONE	.134	1	.134	15.451	.001	**
REEF	.150	3	5.006E-02	5.759	.007	**
ZONE * REEF	.389	3	.130	14.903	.000	**
Error	.139	16	8.693E-03			
Total		24				
Corrected Total	.812	23				

Table 2.7. ANOVA table comparing bleaching among offshore reefs (Otter, Little Kelso, Trunk, Britomart, Duncan, Keeper, 19-022 and 18-017 Reefs) and zones (reef flat and slope) in 1998. Data were arcsine-square root transformed prior to analysis to correct for heterogeneity of variance. ** denotes significant at $\alpha = 0.01$.

Source	Type I Sum of Squares	df	Mean Square	F	Sig.	
ZONE	4.482E-03	1	4.482E-03	1.147	.292	
REEF	.454	7	6.485E-02	16.592	.000	**
ZONE * REEF	.968	7	.138	35.366	.000	**
Error	.125	32	3.908E-03			
Total	7.517	48				
Corrected Total	1.551	47				

2.4.6. Bleaching recovery and mortality

Surveys six to eight months after the 1998 bleaching event indicated that reefs in the Magnetic Island region had recovered well. Mean % coral cover at Virago Shoal and Middle Reef, which had the highest bleaching levels, was approximately the same during and after the event (Fig 2.12). Although there was a trend for mean coral cover to decrease slightly on the reef slope and crest at Nelly Bay and on the reef crest at Geoffrey Bay, none of these changes were statistically significant (p = 0.646; Table 2.8).

Mortality following the 1998 bleaching event was highest in the Palm Island region, where all reefs had experienced high to extreme levels of bleaching. At Falcon Island, mean coral cover on the reef crest decreased by 41.6% relative to March 1998, and by 73.4% at Rattlesnake Island (Fig 2.13a). However, coral cover did not change significantly on the reef slope at Rattlesnake Island or Falcon Island, nor in either reef zone at Curacao Island. The patchy mortality in the Palm Island area showed up as a significant Time by Zone by Reef interaction (p = 0.020; Table 2.9).

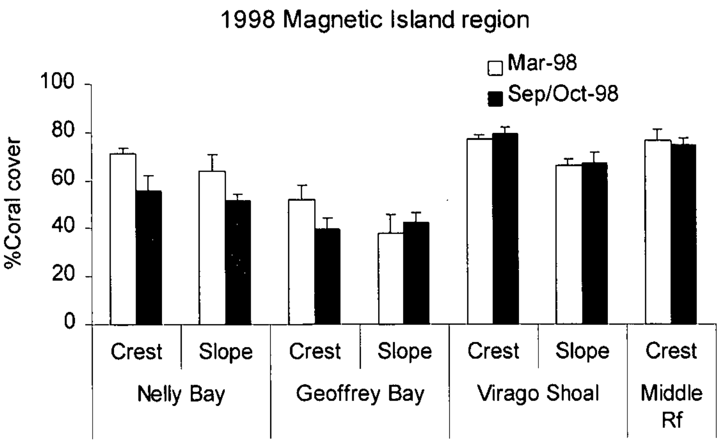


Fig 2.12. Total coral cover (hard and soft coral) in the Magnetic Island region during, and 6-7 months after the 1998 bleaching event. Data are means ± standard error. Number of sites and transects as per Table 2.2.

Mortality in the Whitsunday Island region (excluding Hamilton Island) was generally low with reef crest sites declining on average by 12.0% and reef slope sites remaining unchanged. The higher mortality on the reef crests compared to the reef slopes resulted in a significant zone by time interaction ($p = 0.007$; Table 2.10). However, there was no significant difference in mortality among reefs over time ($p = 0.307$; Table 2.10). Hamilton Island was not included in the analysis but experienced relatively high mortality on both the reef crest and slope (Fig 2.13b).

Among the offshore reefs, coral mortality between April and November 1998 was variable between reefs and zones. Coral cover changed little at most reefs, however at Otter Reef, coral cover on the reef slope declined by 54.8% relative to the first survey and at Little Kelso Reef (slope) by 49.6% (Fig 2.13c). Coral cover at on the reef crest at Britomart Reef declined by 39.2%. The variable mortality resulted in a significant Time by Reef by Zone interaction ($p = 0.021$; Table 2.11). Although mortality at Otter reef was clearly related to bleaching (recent widespread mortality was already evident at the time of the first survey), the mortality at Little Kelso Reef and Britomart Reef was likely to be a result of crown-of-thorns starfish, because large numbers of starfish and feeding scars were seen during both surveys.

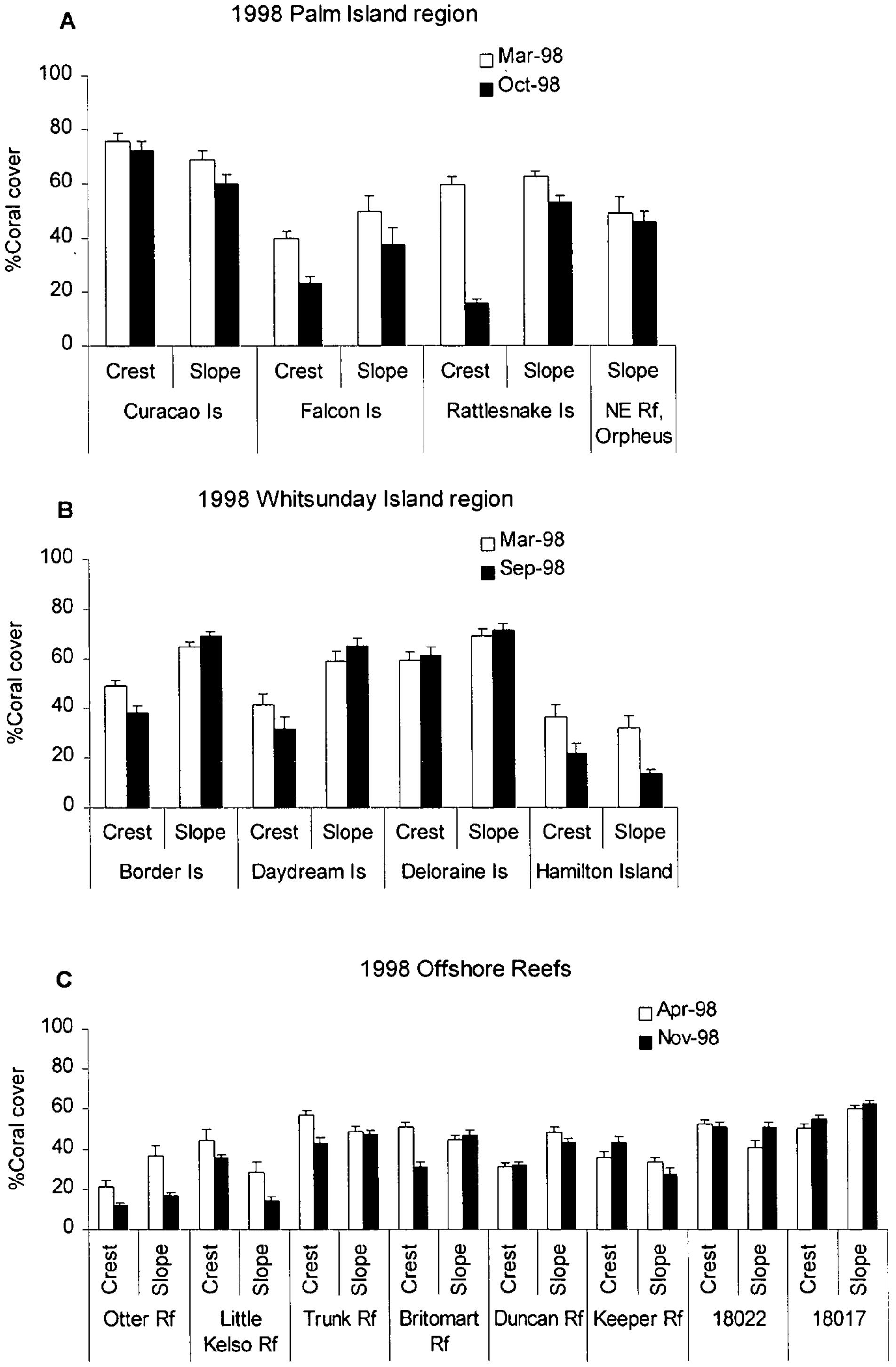


Fig 2.13. Total coral cover (hard and soft coral) on (a) Palm Island, (b) Whitsunday Island and (c) offshore reefs during, and 6-8 months after the 1998 bleaching event. Data are means ± standard error. Number of sites and transects as per Table 2.2. * denotes significant difference between t1 and t2 within zone and reef at $\alpha = 0.05$.

Table 2.8. Split-plot ANOVA table of coral cover in the Magnetic Island region with time as a repeated measure. Reefs included in the analysis are Geoffrey Bay, Nelly Bay and Virago Shoal. * denotes significant at $\alpha = 0.05$; ** denotes significant at $\alpha = 0.01$

Source		Type I Sum of Squares	df	Mean Square	F	Sig.	
REEF	Hypothesis	5285.134	2	2642.567	5.206	.049	*
	Error	3045.357	6	507.560			
SITE(REEF)	Hypothesis	3045.357	6	507.560	5.584	.066	
	Error	339.051	3.730	90.898			
ZONE	Hypothesis	525.213	1	525.213	7.796	.031	
	Error	404.218	6	67.370			
ZONE * REEF	Hypothesis	63.378	2	31.689	.470	.646	
	Error	404.218	6	67.370			
ZONE * SITE(REEF)	Hypothesis	404.218	6	67.370	1.263	.392	
	Error	320.001	6	53.333			
TIME	Hypothesis	263.569	1	263.569	3.429	.114	
	Error	461.174	6	76.862			
TIME * REEF	Hypothesis	386.699	2	193.349	2.516	.161	
	Error	461.174	6	76.862			
TIME * ZONE	Hypothesis	89.010	1	89.010	1.669	.244	
	Error	320.001	6	53.333			
TIME * SITE(REEF)	Hypothesis	461.174	6	76.862	1.441	.334	
	Error	320.001	6	53.333			
TIME * REEF * ZONE	Hypothesis	135.833	2	67.916	1.273	.346	
	Error	320.001	6	53.333			

a MS(SITE(REEF))

b MS(ZONE * SITE(REEF)) + MS(TIME * SITE(REEF)) - MS(Error)

c MS(ZONE * SITE(REEF))

d MS(Error)

e MS(TIME * SITE(REEF))

Table 2.9. Split-plot ANOVA table of coral cover in the Palm Island region with time as a repeated measure. Reefs included in the analysis are Curacao Is, Falcon Is and Rattlesnake Is. * denotes significant at $\alpha = 0.05$; ** denotes significant at $\alpha = 0.01$

Source		Type I Sum of Squares	df	Mean Square	F	Sig.	
REEF	Hypothesis	6253.749	2	3126.874	8.303	.019	*
	Error	2259.560	6	376.593			
SITE(REEF)	Hypothesis	2259.560	6	376.593	1.818	.254	
	Error	1125.019	5.432	207.093			
ZONE	Hypothesis	530.758	1	530.758	2.517	.164	
	Error	1265.044	6	210.841			
ZONE * REEF	Hypothesis	1436.524	2	718.262	3.407	.103	
	Error	1265.044	6	210.841			
ZONE * SITE(REEF)	Hypothesis	1265.044	6	210.841	5.271	.031	*
	Error	240.022	6	40.004	6253.749		
TIME	Hypothesis	2198.569	1	2198.569	60.639	.000	**
	Error	217.539	6	36.256			
TIME * REEF	Hypothesis	647.314	2	323.657	8.927	.016	*
	Error	217.539	6	36.256			
TIME * ZONE	Hypothesis	282.392	1	282.392	7.059	.038	*
	Error	240.022	6	40.004			
TIME * SITE(REEF)	Hypothesis	217.539	6	36.256	.906	.546	
	Error	240.022	6	40.004			
TIME * REEF * ZONE	Hypothesis	647.295	2	323.647	8.090	.020	*
	Error	240.022	6	40.004			

a MS(SITE(REEF))
b MS(ZONE * SITE(REEF)) + MS(TIME * SITE(REEF)) - MS(Error)
c MS(ZONE * SITE(REEF))
d MS(Error)
e MS(TIME * SITE(REEF))

Table 2.10. Split-plot ANOVA table of coral cover in the Whitsunday Island region with time as a repeated measure. Reefs included in the analysis are Border Is, Daydream Is and Deloraine Is. * denotes significant at $\alpha = 0.05$; ** denotes significant at $\alpha = 0.01$

Source		Type I Sum of Squares	df	Mean Square	F	Sig.	
REEF	Hypothesis	1621.967	2	810.983	2.824	.137	
	Error	1722.953	6	287.159[a]			
SITE(REEF)	Hypothesis	1722.953	6	287.159	1.812	.243	
	Error	955.326	6.029	158.452[b]			
ZONE	Hypothesis	3461.364	1	3461.364	22.134	.003	**
	Error	938.281	6	156.380[c]			
ZONE * REEF	Hypothesis	426.482	2	213.241	1.364	.325	
	Error	.099	6	156.380[c]			
ZONE * SITE(REEF)	Hypothesis	938.281	6	156.380	10.272	.006	**
	Error	91.345	6	15.224[d]			
TIME	Hypothesis	7.339	1	7.339	.424	.539	
	Error	103.775	6	17.296[e]			
TIME * REEF	Hypothesis	50.123	2	25.061	1.449	.307	
	Error	103.775	6	17.296[e]			
TIME * ZONE	Hypothesis	248.139	1	248.139	16.299	.007	**
	Error	91.345	6	15.224[d]			
TIME * SITE(REEF)	Hypothesis	103.775	6	17.296	1.136	.440	
	Error	91.345	6	15.224[d]			
TIME * REEF * ZONE	Hypothesis	106.147	2	53.073	3.486	.099	
	Error	91.345	6	15.224[d]			

a MS(SITE(REEF))
b MS(ZONE * SITE(REEF)) + MS(TIME * SITE(REEF)) - MS(Error)
c MS(ZONE * SITE(REEF))
d MS(Error)
e MS(TIME * SITE(REEF))

Table 2.11. Split-plot ANOVA table of coral cover in the offshore reefs region with time as a repeated measure. Reefs included in the analysis are Otter, Little Kelso, Trunk, Britomart, Duncan, Keeper, 18-022 and 18-017 Reefs. * denotes significant at $\alpha = 0.05$; ** denotes significant at $\alpha = 0.01$

Source		Type 1 Sum of Squares	df	Mean Square	F	Sig.	
REEF	Hypothesis	10894.164	7	1556.309	14.550	.000	**
	Error	1711.455	16	106.966			
SITE(REEF)	Hypothesis	1711.455	16	106.966	.889	.593	
	Error	1669.000	13.876	120.276			
ZONE	Hypothesis	1.392	1	1.392	.034	.856	
	Error	652.037	16	40.752			
ZONE * REEF	Hypothesis	2595.748	7	370.821	9.099	.000	**
	Error	652.037	16	40.752			
ZONE * SITE(REEF)	Hypothesis	652.037	16	40.752	1.094	.430	
	Error	595.777	16	37.236			
TIME	Hypothesis	510.663	1	510.663	4.374	.053	
	Error	1868.151	16	116.759			
TIME * REEF	Hypothesis	1098.986	7	156.998	1.345	.293	
	Error	1868.151	16	116.759			
TIME * ZONE	Hypothesis	9.075	1	9.075	.244	.628	
	Error	595.777	16	37.236			
TIME * SITE(REEF)	Hypothesis	1868.151	16	116.759	3.136	.014	*
	Error	595.777	16	37.236			
TIME * REEF * ZONE	Hypothesis	875.886	7	125.127	3.360	.021	*
	Error	91.345	6	15.224[d]			

a MS(SITE(REEF))
b MS(ZONE * SITE(REEF)) + MS(TIME * SITE(REEF)) - MS(Error)
c MS(ZONE * SITE(REEF))
d MS(Error)
e MS(TIME * SITE(REEF))

2.5. DISCUSSION

The Great Barrier Reef (GBR) has experienced six coral bleaching events since 1980. These events have varied in spatial extent and severity, however in general, inshore reefs were found to be more prone to bleaching than offshore reefs. This pattern cannot be explained by inshore reefs having higher proportions of thermally sensitive species, such as acroporids and pocilloporids, which are dominant both inshore and offshore on the GBR (Sweatman et al. 2000). A number of plausible explanations exist for this pattern. The most likely explanation is bathymetry. Shallow inshore waters heat up faster than deeper water because they have a much smaller thermal inertia and as a result heat up quicker (and are warmer in summer) compared to deeper offshore waters. High inshore sea surface temperatures (SST's) were a prominent feature during the 1998 bleaching event and correlated well with the severity of bleaching (Fig 2.6). A contributing factor to the inshore-offshore bleaching pattern may be turbidity. Inshore reefs on the GBR are generally subjected to higher turbidity than offshore reefs, which, during calm wind conditions often associated with bleaching, settles out of the water column exposing corals to proportionately more light stress than on offshore reefs. Additional stress from reduced salinity and/or pollution associated with river runoff is another possible explanation. However, river flooding tends to be local or regional in scale and seldom impacts on the whole inshore GBR at the same time. In 1998, the southern GBR experienced no flooding, yet the inshore-offshore bleaching pattern was very prominent. Regardless of the mechanism, the inshore-offshore bleaching pattern suggests that inshore reefs may be at greater risk during climate change-mediated warming than offshore reefs. Interestingly, repeated bleaching events at reefs such as Magnetic Island (five out of the six events) appear not to have reduced the vulnerability of reefs in this area to temperature anomalies.

Of the six coral bleaching events on the GBR since 1980, the 1998 event was clearly the worst. It affected more reefs, occurred over a wider latitudinal and longitudinal range and, despite limited data on the severity of previous events, was probably more severe on affected reefs than previous events (Oliver pers obs, Willis pers comm). Of the reefs that bleached in previous years, almost all bleached again in 1998. The 1998 event coincided with climatologically unusual weather conditions, both for the GBR and globally (Lough 1999, 2000). Monthly mean SST maxima from 'ships-of-opportunity' covering the period 1904 to 1994, show that 1987 was ranked first in 14 out of 20 latitude bands on the Queensland coast. The anomalous temperatures of 1987 also coincided with bleaching on the GBR. However, IGOSS/NMC blended ship and satellite data covering the period 1982 to 1998 show that 1998 was warmer than 1987 (Lough 1999, 2000).

The most severe bleaching event prior to the 1998 event on the GBR occurred in the summer of 1981/82 (Oliver 1985). Only a few estimates of mortality are available for this earlier event. At Myrmidon Reef, hard coral cover decreased over a 12-month period by 54% and 84% at 2 sites on the reef flat, and by 0-25% at 8m depth (Fisk and Done 1985). At Magnetic Island, a single 30m line transect conducted towards the end of the bleaching event showed 72% recent coral mortality of hard corals (Oliver 1985). Mortality rates of tagged *Pocillopora damicornis* at Lizard Island increased by 26% and *Porites sp.*, *Lobophyllia corymbosa* and *Favia favus* by 10-12% four months after the bleaching event compared to pre-bleaching rates (Harriott 1985). Interestingly, 1982 does not show up in a ranking of the 10 warmest years between 1904 and 1994, except in the southern GBR (Lough 1999). This may be because bleaching conditions during 1982 may have been restricted to heating of shallow reef waters and inshore coastal areas which are outside the areas traversed by ships. The year 1980 ranks in the top 10 warmest years in 7 latitude bands, but the mild bleaching years of 1992 and 1994 did not coincide with above average temperatures anywhere on the GBR (Lough 1999). These results highlight the difficulty in correlating long-term, ship-based SST records with coral bleaching in anything except the most extreme years.

In contrast, high-resolution (1km) satellite SST's correlated very well with bleaching patterns in 1998 (Fig 2.10). Animations of SST's (presented on CD in Skirving and Guinotte (2001)) for the month of February show that, with the exception of the outer Whitsunday Island area, inshore reefs between Gladstone and Cooktown experienced temperatures in excess of 30°C for several weeks. Inshore areas between Townsville and

Innisfail averaged between 31 and 32 °C during February 1998. Unbleached offshore reefs in the southern and far northern GBR, and in the outer Whitsunday Island area correlated with cooler water in February. These patterns suggest that temperature is the dominant cause of the 1998 bleaching event. They also indicate that, in addition to anomaly-based bleaching predictions (e.g. Strong et al., 1997), absolute temperatures from satellites may also be useful in providing early warning and spatial patterns in conditions conducive to bleaching.

The 1998 bleaching event coincided with a severe El Niño Southern Oscillation which affected coral reefs in most reef provinces. However, not all bleaching events on the GBR correlate with ENSO events. The 1982 event occurred approximately 6 months before the severe ENSO of 1982/83. The 1987 and 1992 events did occur during mild ENSO conditions, when the Southern Oscillation Index (SOI) is negative, but during the 1980 and 1994 events, the SOI was positive (Hoegh-Guldberg et al. 1997). Unlike reefs the eastern Pacific and the Atlantic Ocean, there is no clear relationship between bleaching and ENSO events on the GBR.

Coral mortality on the GBR as a result of the 1998 bleaching event contrasts sharply with mortality reported in many reef areas in the Indian Ocean and Gulf of Arabia. Reefs off India, Maldives, Kenya, Seychelles, Chagos, Western Australia and Qatar experienced mortality levels ranging from 50 to >90% (Goreau et al. 2000, Wilkinson et al. 1999). The worst affected reef on the GBR during the 1998 bleaching event was Rattlesnake Island, where coral cover decreased by 73%. However, coral mortality was much lower elsewhere, even on heavily bleached reefs in the Whitsunday and Magnetic Island area. Thus, in a world-wide context, the 1998 bleaching event on the GBR represented only a mild ecological disturbance.

Coral mortality as a result of bleaching in 1992 and 1994 was low to minimal on the GBR, although few quantitative data exist. Between 1990 and 1993, Ayling and Ayling (1998) recorded a decrease in coral cover of 30% at fixed transects on the reef slope at Geoffrey Bay (Magnetic Island), a result attributed to the 1992 bleaching event.

However, at adjacent Nelly Bay, coral cover increased marginally over this time period. These results are consistent with the relative bleaching levels found at these two sites in 1992. Mortality as a result of the 1994 event at Magnetic Island was not quantified but qualitative observations suggest that mortality was low to negligible (pers. observ). Tagged *Acropora formosa, Pocillopora damicornis* and *Stylophora pistillata* at Nelly Bay all made a full recovery in a study of zooxanthellae densities during and after the 1994 bleaching event (Jones, 1995).

There is considerable debate in the scientific literature on whether the increase in reports of bleaching since 1979 is due to increased temperature anomalies as a result of climate change, or simply a result of increased awareness (e.g. Glynn 1993, Hoegh-Guldberg 1999). Prior to the 1980's, there is only one report of bleaching on the GBR. It took place in 1929 and was observed at Low Isles (Yonge and Nicholls 1931a). It s unknown if this bleaching event was local or widespread. However, despite some meteorological evidence suggesting increased anomalies at Townsville since the 1980's (Jones et al. 1997) and a decrease in the return times of anomalies over the whole GBR since 1903 (Lough 1999), it is difficult to interpret the six observed GBR bleaching events since 1980 as a trend. No inference can be drawn from the lack of reports prior to 1980. Even from the reports since then, it is difficult to get an adequate picture of the true extent and severity of bleaching. The size of the GBR and the remoteness of a large number of reefs makes a visitation-based reporting system highly skewed towards heavily used areas. In addition, the experience of the author is that the number of reports is proportional to the effort put into soliciting them. Also, despite best efforts, unbleached reefs invariably remain unreported. The aerial survey method reported here overcomes these limitations. Approximately 23% of all reefs on the GBR were sampled using this method in a relatively short frame (10 days). Sampling covered most areas of the GBR and was undertaken in a cost-effective manner. Inshore reefs were surveyed using chartered aircraft at a cost of <A$10,000, while offshore surveys were undertaken as part of routine aerial surveillance patrols. Apart from data on the spatial extent of bleaching, data were also obtained on the approximate intensity of bleaching at each reef. Ground-truth surveys however, show that bleaching intensities were generally underestimated in aerial

survey. Underestimation may have been due to poor visibility, an inability to distinguish partially bleached corals from background colour, incorrect assumption of coral cover and/or poor estimation by the observer. Overestimation of bleaching in aerial surveys was less of a problem, occurring on only two out of 20 reefs (compared to in-situ video estimates). The aerial survey methodology must therefore be viewed as providing a conservative estimate of bleaching, but one that may be broadly comparable between events if done in a consistent manner.

In conclusion, temporal patterns of bleaching in six bleaching events on the GBR from 1980 – 1998, and spatial patterns of bleaching in 1998, suggest that inshore reefs are more likely to be affected by bleaching than offshore reefs. The 1998 bleaching event was the most severe event recorded on the GBR since 1980, however mortality was patchy and generally low on the reefs surveyed. The excellent correlation between bleaching incidence and high SST's in 1998 suggest that high temperatures were the primary cause of bleaching. The aerial survey methodology used in this study to quantify the spatial extent and severity of bleaching is superior to visitor-based reports and provides better coverage than in-situ surveys, although the intensity of bleaching is generally underestimated.

Chapter 3

Magnitude and patterns of variation in sea temperatures on the Great Barrier Reef

Approximately 100 data loggers are currently used in a long-term monitoring program of sea temperatures at 45 sites on the Great Barrier Reef. Photo courtesy GBRMPA.

3.1. ABSTRACT

Sea temperature anomalies that cause widespread environmental perturbations, such as the global coral bleaching event of 1998, highlight our limited understanding of the thermal environment normally experienced by coral populations. In order to characterize and quantify the thermal regimes experienced by corals in different environments, it is necessary to understand the pattern and magnitude of variation in sea temperatures in coral reef environments over a variety of spatial and temporal scales. In this Chapter, I examine sea temperature variation on the Great Barrier Reef from the smallest (metres) to the largest (>1000 km) spatial scales and assess this variation in terms of the physiological tolerance of corals. I found that while most coral communities exist in relatively stable thermal conditions most of the time, temperatures can vary in excess of 9°C within a tidal cycle on the reef flat at locations such as Magnetic Island and Heron Island. Coral communities experience these rapid and extreme changes in temperature without ill effects, suggesting that temperature excursions beyond local maximum ranges may be more important in causing thermal stress than temperature variability per se. While diurnal ranges on the reef flat are significantly higher than the reef slope, there are no consistent or significant differences between inshore and offshore diurnal ranges for either the reef flat or slope. Despite the higher diurnal temperature ranges on the reef flat, mean daily temperatures on the flat are nearly identical to those on the slope at most times. Inter-station differences in daily means increase in an exponential manner with increasing spatial separation, generally along latitudinal and cross-shelf gradients. However, cross-shelf differences in temperature vary in sign between seasons with warmer summers and cooler winter temperatures inshore compared to offshore. The warmer inshore temperatures in summer coincide with apparent differences in the thermal tolerance of coral populations inshore compared to offshore. The summer inshore – offshore temperature differences are further accentuated during thermal anomalies and thus do not necessarily imply reduced risk of coral bleaching at inshore reefs as a result of climate change.

3.2. INTRODUCTION

Temperature is one of the most important environmental parameters governing the distribution, abundance and physiological function of organisms. Rising background temperatures as a result of global warming (e.g. Parker et al. 1995, Brown et al. 1996, Lough 2000), and the thermal sensitivity of reef-building corals (e.g. Jokiel and Coles 1990, Glynn 1993, Goreau and Hayes 1994) have highlighted our limited understanding of the thermal conditions (magnitude and spatial/temporal scales of variation) routinely experienced and tolerated by coral populations. The correlation between coral diversity and latitude, which indicates that highest diversity occurs in warm, relatively unvarying tropical waters (Stehli and Wells 1971), has sustained a commonly held belief that corals favour relatively small temperature ranges and variation. However, there is also a considerable body of evidence to show that corals can thrive in highly variable temperature regimes (e.g. Potts and Swart 1984, Veron and Minchin 1992, Coles 1997). These examples provide insights into thermal conditions that still permit reef growth at selected locations. However, our knowledge of normal or extreme variations in temperature experienced by corals, especially at the scale of a whole reef province such as the Great Barrier Reef (GBR), is poor.

Sustained high temperatures and/or short excursions of temperature into extreme ranges are known to cause coral bleaching and mortality (reviewed by Jokiel and Coles 1990, Glynn 1993, Brown 1997b, Hoegh-Guldberg 1999). Experimental evidence (e.g. Coles et al. 1976) suggests that temperature thresholds of corals are not the same for populations in different reef provinces, but are dependent on local or regional ambient temperature regimes. Therefore defining the patterns, scales and magnitude of variation in sea temperature, together with the thermal conditions known to have been associated with bleaching of corals, provides insights into local thermal adaptation of coral populations and the range of extremes coral populations are capable of withstanding. Although spatial and temporal temperature data have been published before for coral reef environments such as the Great Barrier Reef (e.g. Moorhouse 1933, Orr 1933, Brandon 1970, Kenny 1974, Walker 1981, Potts and Swart 1984, Lough 1992), none of these studies provide data at high enough resolution (temporal and/or spatial) to adequately compare thermal regimes across reefs or identify environmental changes that may stress coral communities (Quinn and Kojis, 1999).

Detailed studies of the magnitude and variation in sea temperature are also important in evaluating how well temperatures from one site, depth or location represent those from another. Such data are of interest to reef workers wishing to assess the validity of using temperature data collected from sites away from their immediate study area for interpreting their results. Such data are also important for cross calibrating real and proxy temperature data sets (e.g. Alibert and McCulloch 1997, Kuhnert et al. 1999, Lough 1999).

In this Chapter I provide the first comprehensive description of the thermal environment of a large reef ecosystem. I quantify the magnitude and patterns of variation in temperature on reef slope and flat environments and at increasing spatial scales, and relate these to a range of physiological tolerances and thermal adaptation exhibited by corals.

3.3. METHODS

3.3.1. Spatial variation in temperature

Spatial variation in temperature, spanning 13.5° of latitude from Wongara in the south to Wallace Islet in the northern Great Barrier Reef (GBR), was investigated using a network of in-situ temperature loggers (Fig 3.1). Data loggers were placed on the reef slope at 4 – 9m depth on both inshore and offshore reefs. At each site, mean daily temperatures were calculated. Sites were paired based on distance from each other, and for each pair, the difference in mean daily temperature was calculated. Site pairs were grouped into six categories for inshore and offshore reefs (Inshore categories: <1km, 3 – 7km, 15 – 25km, 75 – 100km, 350 – 500km and 850 – 1100km; Offshore categories: <1km, 20 – 35km, 50 – 65km, 190 – 210km, 400 – 600km and 900 – 1000km). Each category contained 2 - 6 pairs of sites. A summary of site pairs, dates of observations, number of records and data summary period used, is shown in Appendices 3.1 and 3.2. The observation periods ranged from 190 to >1300 days and for many sites included a period of anomalously high temperatures during the Austral summer of 1997/98 that coincided with a major coral bleaching event on the GBR (Baird and Marshall 1998, Berkelmans and Oliver 1999, Fabricius 1999, Marshall and Baird 2000).

3.3.2. Diurnal and habitat variation in temperature

The range of thermal environments on a reef is generally encompassed by the reef flat and slope habitats, the former representing the most variable thermal environment. To characterize this variation, I documented the diurnal temperature ranges on the reef flat and slope at five inshore (Wallace Island, Black Rocks, Orpheus Island, Magnetic Island, Halfway Island) and five offshore locations (Raine Island, Norman Reef, Myrmidon Reef, Kelso Reef and Heron Island; Fig 3.1, Appendix 3.3). These locations span most of the length of the GBR from 11.5° to 23.3°S (~1600km). Apart from temporal variation within a habitat, reef flat and slope temperatures can also vary greatly relative to each other at any one time. To characterize this variation, I compared instantaneous differences between reef flat and slope habitats at three locations spanning the width of the continental shelf in the central GBR at Magnetic Island (approximately 11 km from the mainland), Kelso Reef (approximately 90 km from the mainland) and Myrmidon Reef (approximately 125 km from the mainland; Fig 3.1, Appendix 3.4). Reef flat data loggers were deployed at approximately Lowest Astronomical Tide level (0 m at chart datum) and reef slope loggers at 4 – 9m depth relative to mean tide level. These depths were chosen to coincide with the maximum temperature which may be experienced by corals without exposure to air (reef flat) and the reef zone with generally highest coral cover (reef slope).

3.3.3 Temperature measurement

Temperatures were measured using in situ data loggers (Dataflow Systems, Queensland, Australia). Loggers contained semiconductor temperature sensors with a measurement resolution of 0.02°C. Sensors were calibrated before deployment using a constant-temperature water bath and a two-point calibration protocol. A slope and offset was calculated for each sensor using 20° and 35°C as reference temperatures. Sensors were tested and confirmed to be strongly linear over this range. Reference temperatures were standardized against a digital thermometer (accurate to ± 0.04°C), certified by the National Association of Testing Authorities (Australia). Sensor calibrations were repeatable to 0.04°C however, due to the accuracy range of the calibrating thermometer, the final accuracy of the data is assumed to be around 0.1°C. Temperature loggers were programmed to record instantaneous temperatures at 30-minute intervals for the duration of the deployments. Deployments were for 6 - 12 months depending on the site. Logger calibrations were checked, and where necessary recalibrated, prior to redeployment. Logger start times were synchronized so that direct comparisons of temperature readings could be made across sites and habitats.

3.3.4. Data analysis

Although concurrent data were obtained for comparisons among sites and habitats, concurrent data were not available for all sites for the same period, thus preventing the comparison of temperature variation in one overall analysis. Instead, summary statistics were calculated separately for each comparison based on differences between sites and habitats. Cumulative frequencies were calculated to indicate how often diurnal ranges of various magnitudes occur. Student t-tests were used to test the statistical significance of reefs or habitats as appropriate.

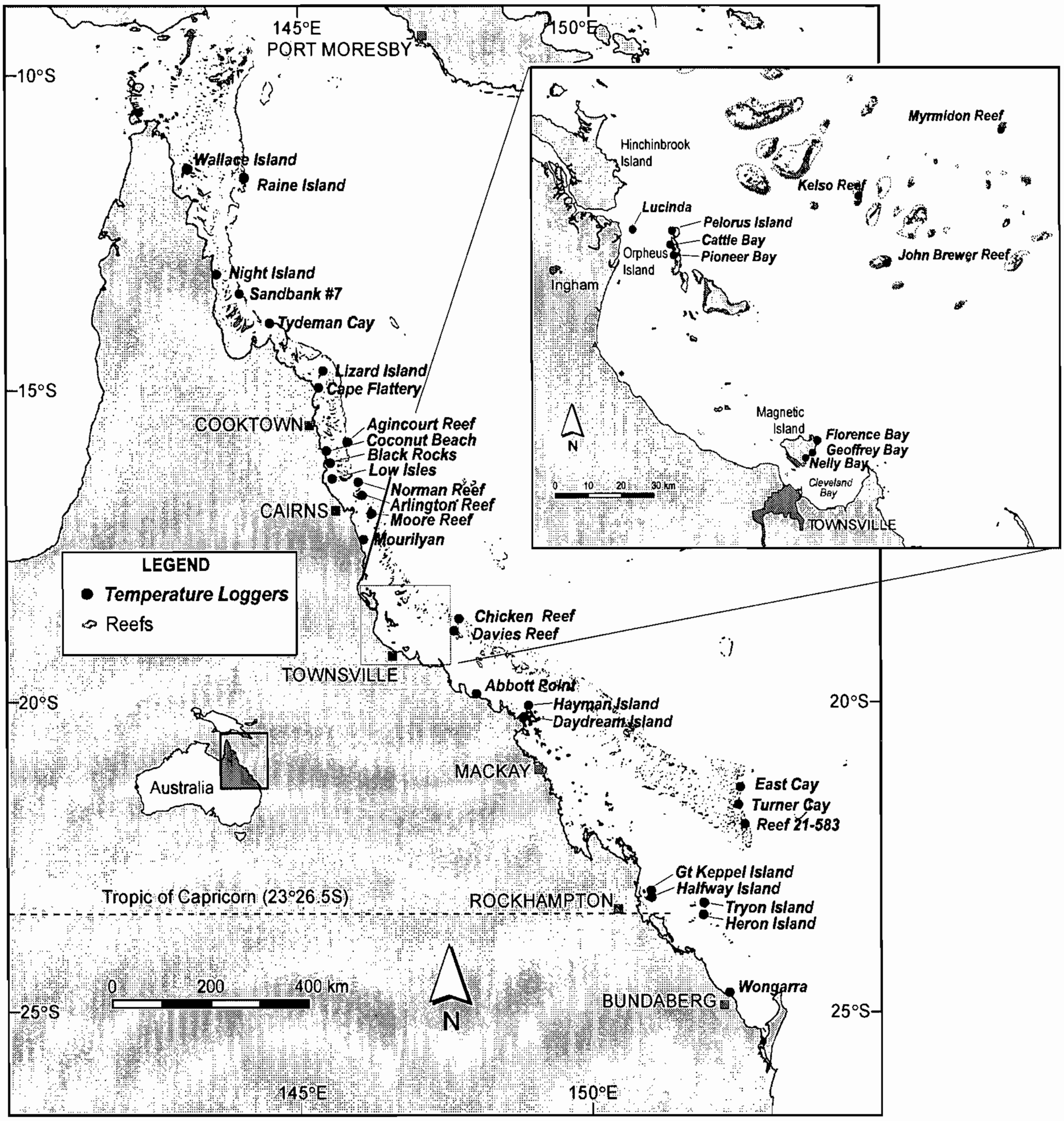


Fig 3.1. Location of temperature loggers and sites.

3.4. RESULTS

3.4.1. Variation in diurnal range

Reef flat temperatures show a large diurnal range with generally higher daytime temperatures and lower night-time temperatures compared to reef slope sites. Mean reef slope diurnal ranges were typically <1°C, whereas those for the reef flat were typically between 1 and 2°C (Table 3.1). The reef flat daily variation was particularly pronounced at Magnetic Island (inshore) and Heron Island (offshore), where the diurnal ranges were on average 2.8 and 4.1 °C respectively, but varied by up to 10.8° and 9.3 °C (respectively) in a tidal cycle (Table 3.1). At the 10 locations used in this study, both the mean and maximum diurnal ranges on the reef flat were significantly higher than on the reef slope (mean range: $t_{(2),\ 18df} = 3.12$, $p = 0.002$; maximum range: $t_{(2),\ 18df} = 2.10$, $p = 0.05$;Table 3.1).

The difference in reef flat and slope diurnal ranges is also evident in the cumulative frequency distribution of diurnal temperature ranges. These show that for most reef slope sites, diurnal ranges are between 0 – 0.6°C more than 50% of the time and between 0.7 – 1.4°C less than 10% of the time (Fig 3.2). In contrast, for most reef flat sites, 50% of diurnal ranges are between 0 – 1.2°C and 10% are between 1.4 – 2.1°C. Magnetic Island and Heron Island reef flats again show high frequencies of large diurnal ranges with 50% of observations incorporated by daily temperature ranges up to 2.5° and 4°C (respectively) and 10% of observations greater than 5.0° and 6.9°C (respectively).

At Magnetic Island, average rates of temperature change of more than 1 °C. hr^{-1} over a 6-hour period were experienced on a number of occasions without apparent ill effects to corals. The maximum temperature increase over 1 hour at Magnetic Island between 1992 and 1999 was 2.5 °C on 6 October 1995 (Fig 3.3). Reef flat temperatures increased from 28.7°C to 31.2°C shortly before a daytime low tide, followed shortly after by a 4.1 °C decrease within 1 hour of the flooding tide. Reef corals remained in good apparent health despite this temperature extreme and temperature fluctuation.

Mean and maximum diurnal ranges were not significantly different between inshore and offshore locations for either the reef flat (mean: $t_{(2),\,8df} = 0.41$, $p = 0.70$; maximum: $t_{(2),\,8df} = 0.21$, $p = 0.84$) or slope habitats (mean: $t_{(2),\,8df} = 1.31$, $p = 0.23$; maximum: $t_{(2),\,8df} = 0.50$, $p = 0.63$). Cumulative frequency distributions of diurnal ranges also show no consistent trend between inshore and offshore locations (Fig 3.2).

Diurnal temperature fluctuations on the reef flat varied substantially over time and were highly correlated with tidal range (Fig 3.3). Large daily temperature fluctuations occurred during spring tides, especially during Austral spring (September – November) and autumn (March – May) when large daytime low tides coincided with high air temperatures.

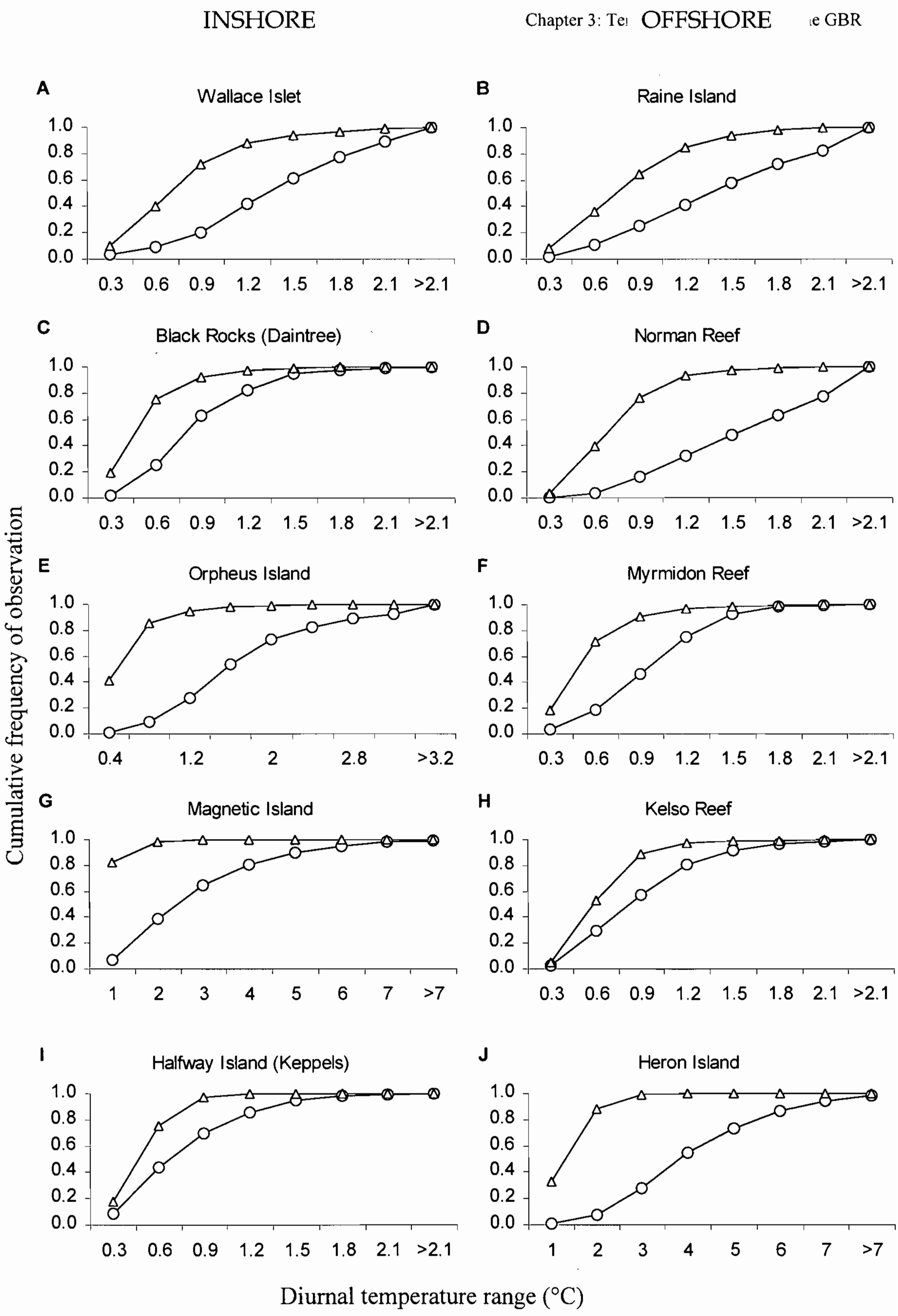


Figure 3.2. Diurnal range in temperatures at five inshore and offshore locations spanning the length and width of the GBR. At each location the cumulative frequency of observation of diurnal ranges are shown for the reef flat (o) and slope (△). Note the different scales on the x-axes of the graphs for Orpheus Island, Magnetic Island and Heron Island.

Table 3.1. Summary results of temperatures at five inshore and five offshore locations along the length of the GBR. For each site the average, minimum and maximum of all daily mean temperatures, daily maxima, minima and range are calculated for the reef flat (approx 0m at chart datum) and reef slope (4-9m at chart datum). The sampling period and number of sampling days for each location are shown in Appendix 3.1.

Location	**Statistic**	**Daily mean °C)**		**SD (°C) of daily means**		**Daily Min. (°C)**		**Daily Max. (°C)**		**Daily Range (°C)**	
INSHORE		*Flat*	*Slope*	*Flat*	*Slope*	*Flat*	*Slope*	*Flat*	*Slope*	*Flat*	*lope*
Wallace Is 11.5°S	Average	27.7	27.4	1.66	1.89	27.0	26.9	28.4	27.7	1.4	0.7
	Minimum	24.6	23.4			22.8	22.3	25.3	24.0	0.1	0.1
	Maximum	30.7	30.6			30.4	30.4	31.4	31.4	3.5	2.9
Black Rocks 16.3°S	Average	27.1	27.0	2.21	2.11	26.7	26.8	27.6	27.3	0.9	0.5
	Minimum	22.7	22.9			22.4	22.5	22.8	22.9	0.1	0.1
	Maximum	31.6	31.4			31.2	31.1	32.3	31.9	2.2	2.4
Orpheus Is 18.3°S	Average	26.0	26.1	2.64	2.43	25.3	25.8	27.1	26.4	1.7	0.8
	Minimum	20.3	20.5			18.8	18.7	20.7	20.8	0	0.1
	Maximum	31.5	31.1			30.9	30.5	33.2	31.8	7.3	2.9
Magnetic Is 19.1°S	Average	26.2	26.4	2.91	2.98	25.1	25.9	27.9	26.8	2.8	0.9
	Minimum	19.5	19.5			17.3	19.0	20.3	20.0	0.2	0.2
	Maximum	32.3	32.2			31.7	31.8	34.7	32.7	10.8	4.6
Halfway Is 23.2°S	Average	23.9	24.0	2.93	3.02	23.6	23.8	24.3	24.2	0.8	0.5
	Minimum	18.6	18.6			18.2	17.2	18.8	18.7	0.1	0.1
	Maximum	29.1	29.9			28.7	29.6	29.6	30.5	2.3	2.3
FFSHORE											
Raine Is 11.6°S	Average	26.7	27.0	1.36	1.16	26.1	26.5	27.6	27.3	1.4	0.8
	Minimum	23.9	24.8			22.6	23.6	24.5	25.2	0.1	0.1
	Maximum	29.7	29.6			29.4	29.2	31.2	30.6	4.6	2.3
Norman Rf 16.5°S	Average	26.8	26.7	1.48	1.78	26.1	26.2	27.8	27.0	1.6	0.8
	Minimum	23.9	22.6			22.7	22.3	24.6	22.9	0	0.1
	Maximum	30.1	30.4			29.6	30.1	31.7	30.5	4.5	2.7
Myrmidon Rf	Average	26.5	26.8	1.81	1.67	26.1	26.4	27.0	27.1	1.0	0.7
18.2°S	Minimum	22.6	23.2			21.3	22.2	23.1	23.5	0	0.1
	Maximum	29.9	29.7			29.4	29.4	30.7	30.2	2.7	3.1
Kelso Rf 18.5°S	Average	26.5	26.3	1.90	1.90	26.1	25.9	26.9	26.6	0.9	0.7
	Minimum	22.2	22.2			22.0	21.8	22.3	22.4	0	0.1
	Maximum	30.1	29.9			29.8	29.7	31.1	30.3	2.8	2.5
Heron Is 23.3°S	Average	23.9	24.0	2.5	2.24	22.1	23.2	26.2	24.5	4.1	1.3
	Minimum	18.0	19.8			14.3	18.4	19.7	20.2	0.2	0.2
	Maximum	29.8	28.8			27.4	28.4	35.4	29.3	9.3	3.4

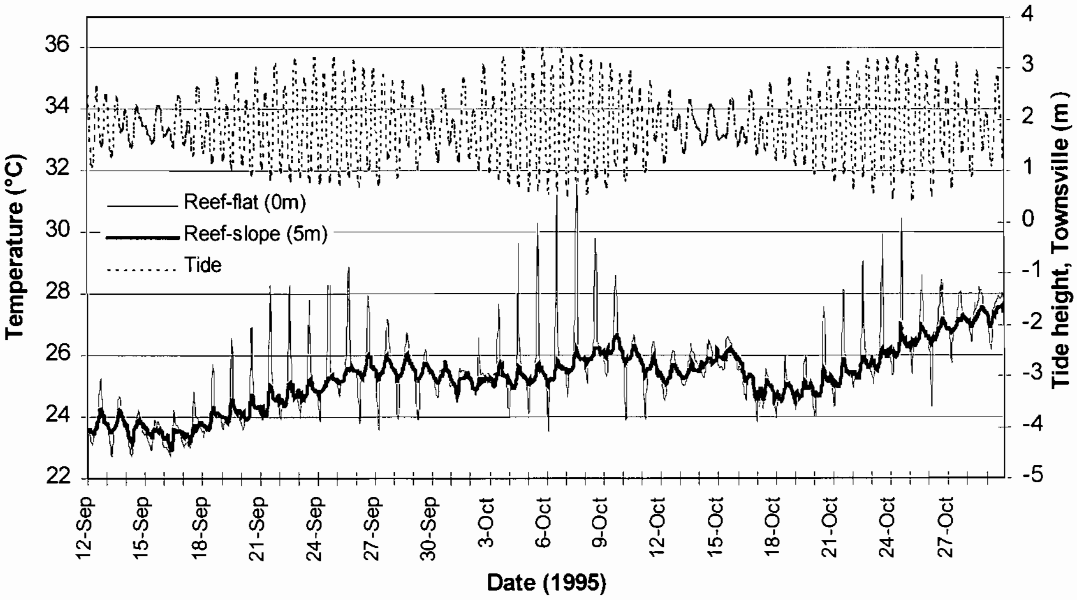


Fig 3.3. Example of the correlation between reef flat temperatures at Magnetic Island and tide height at Townsville, 7km away over a 7 week period in 1995. A regression of the difference between the highest daily reef flat and reef slope temperatures on the tidal range for each day explains 69% of the variation in the data (n = 51 days). Large hourly temperature fluctuations occur on the reef flat during spring tides, with a maximum increase of 2.5° and decrease of 4.5 °C/hr recorded on 6 October 1995.

3.4.2. Variation in temperature between reef habitats (reef flat vs slope)

When averaged over an entire day, differences between reef flat and slope temperatures were generally small at each of the locations studied. Reef flat temperatures at Magnetic Island were on average 0.1 °C warmer than the reef slope (range -0.4 to 0.5°C, Table 3.2). However, half-hourly instantaneous differences show a much larger range with the reef flat up to 5.7 °C warmer, or up to 3 °C cooler, than the reef slope at any one time. Reef habitat differences were smaller (means <0.1°C) at offshore locations in the central GBR (Table 3.2). Differences in temperature between reef habitats may be an important structuring force for coral assemblages and may become critical when corals are thermally stressed. During a period of unusual warming in January and February 1998, which coincided with widespread coral bleaching (Berkelmans and Oliver 1999, Chapter 2), average daily reef flat temperatures at Nelly Bay on Magnetic Island were >0.3 °C warmer than the reef slope on 16 days (Fig 3.4a). Daily maxima on the reef flat during this period exceeded those on the reef slope by 0.5 °C on 31 days. Offshore at Kelso

Reef, differences in average daily reef flat and slope temperatures during this period did not exceed 0.3 °C, however differences in daily maxima exceeded 0.5 °C on 23 days (Fig 3.4b).

Table 3.2. Comparison of temperatures between reef habitats (reef flat and slope) at 3 locations in the central GBR. Comparisons are differences between habitats based on average daily and half-hour instantaneous temperatures. The sampling period and number of sampling days for each location are shown in Appendix 3.1.

		Average daily temperature (°C ± SD)		**Half-hourly temperature (°C ± SD)**	
Reef	*Reef zone*	*ξ Difference*	*Range*	*ξ Difference*	*Range*
Magnetic Island	Flat – slope	0.11 ± 0.19	-0.4 to 0.5	0.11 ± 0.39	-3.0 to 5.7
Kelso Reef	Flat slope	0.05 ± 0.06	-0.1 to 0.3	0.01 ± 0.14	-0.5 to 1.5
Myrmidon Reef	Flat – upper slope	0.004 ± 0.14	-0.7 to 0.4	0.01 ± 0.30	-2.0 to 2.4
Myrmidon Reef	Upper – deep slope	-0.08 ± 0.11	-0.4 to 0.8	-0.08 ± 0.22	-2.1 to 3.8
Myrmidon Reef	Flat – deep slope	-0.08 ± 0.22	-0.9 to 1.0	-0.08 ± 0.40	-2.3 to 3.7

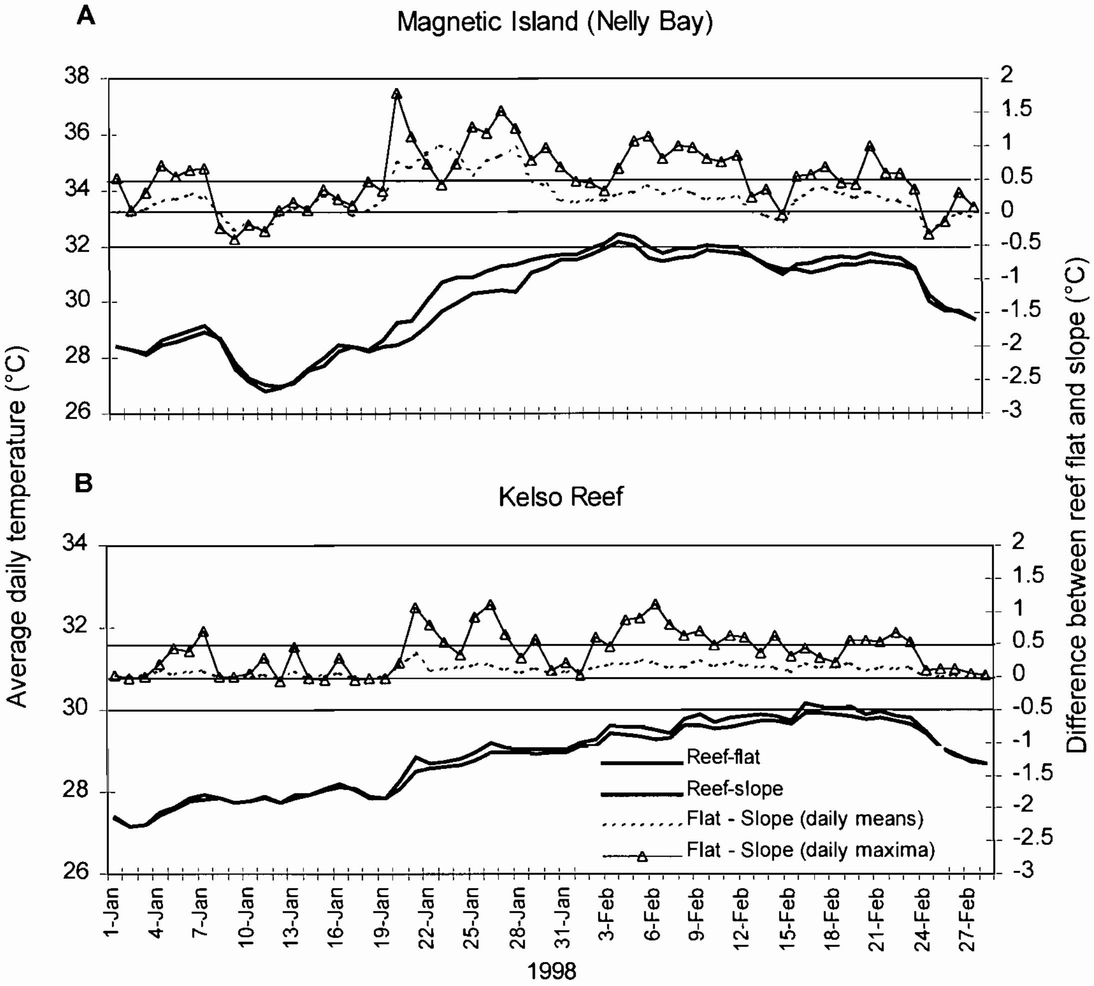


Fig 3.4. Variation in temperatures in the central GBR during an unusually warm period in the summer of 1998, coinciding with coral bleaching at (a) Magnetic Island, 7km from the mainland and (b) Kelso Reef, 85km from the mainland. The lower half of each graph shows the average daily reef flat (0m at chart datum) and slope (4-5m at chart datum) temperature and the upper half of each graph shows the difference between reef flat and slope daily average and daily maximum temperatures. Note the different scales for average daily temperature on the two graphs.

3.4.3. Spatial Variation

Differences in average daily temperatures between sites increase roughly exponentially with distance, although the standard deviations around means are high. Over spatial scales of 200 – 500m, differences in average daily temperatures between 5 pairs of inshore reef slope sites were mostly small (0.07°C ± 0.2°C SD), but reached a maximum of 0.9°C during warm periods and low tides (Fig 3.5a). Offshore, differences in average daily temperatures over similar spatial scales were smaller at 0.03 ± 0.1°C (SD) with maximum pair-wise differences of up to 1.1 °C (Fig 3.5b). Pair-wise differences between sites a few hundred metres apart are accentuated over short time scales with half-hour instantaneous temperatures varying by up to 1.8 °C on the inshore and 2.1°C offshore. Large temperature differences on the outer shelf of the GBR occurred mainly at times of cold water upwelling which are patchy in space and time on the upper reef slope.

At increasing spatial scales, the variation in sea temperature between sites increases in magnitude, as does the standard deviation. Over distances of a few kilometres, variation in average daily temperatures on the inshore reef slope increased to a mean of 0.17 °C (Fig 3.5a), with maximum deviations of up to 1.4 °C occurring at Orpheus Island during a minor coral bleaching event in February 1994. These deviations increase to 0.25°C over distances of 75 - 100km and up to a mean of 2.3 °C at 900-1100km on the inshore GBR. Over similar spatial scales on offshore reefs, equivalent differences in mean and variation around the mean are evident, although at distances of more than 400km, the magnitude of the variation is slightly less than inshore reefs (Fig 3.5a,b).

Inshore temperatures are generally cooler in winter and warmer in summer compared to offshore temperatures. However, in a cross-shelf transect, mean annual temperatures are similar as inshore seasonal deviations in temperature cancel each other out over a year (Table 3.3a,b). Seasonal inshore-offshore differences are most pronounced in the central GBR with the coolest winter month (July) inshore at Magnetic Island on average 2.7°C cooler than Kelso Reef offshore, and the warmest summer month (February) 1 °C warmer (Table 3.3a,b). Differences in daily means and maxima between inshore and offshore sites are amplified during unusually warm periods. Average daily temperatures were up to 2.9°C warmer, and daily maxima up to 4.9°C warmer, at Magnetic Island than Myrmidon Reef during the bleaching period in February 1998 (Fig 3.6). Similarly, Kelso Reef average daily temperatures were up to 0.6 °C warmer than Myrmidon Reef and daily maxima up to 1.0 °C warmer during this period.

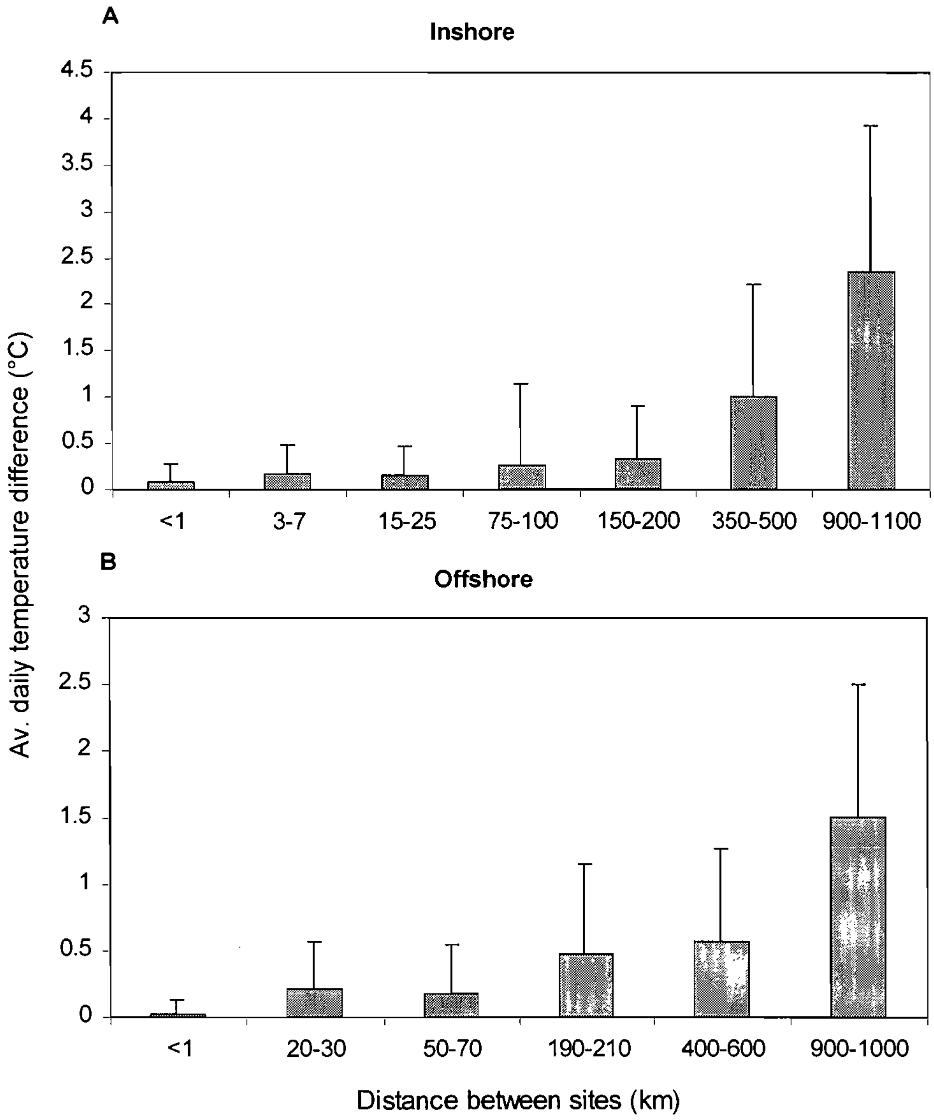


Fig 3.5. Increase in average daily temperature variation between (a) inshore sites and (b) offshore sites as a function of distance. Means for each spatial interval are the grand mean of mean differences from 2 - 6 sites. Error bars are standard deviations of all pair-wise differences among replicates (n = 2 – 6) for each spatial interval. Details of pair-wise comparisons are shown in Appendix 3.1. Note the different scales on the two graphs.

Table 3.3. Seasonal trends in average monthly temperatures at five inshore and five offshore locations along the length of the GBR. Data are from reef slope (4-9m at chart datum). The sampling period and number of months for each period and location are shown in Appendix 3.1.

(a)

NSHORE	**Wallace Island**			**Black Rocks**			**Orpheus Island**			**Magnetic Island**			**Halfway Island**		
	mean	*SD*	*n*	*mean*	*SD*	*n*	*mean*	*SD*	*n*	*mean*	*SD*	*n*	*mean*	*SD*	*n*
Jan	29.77	0.19	2	28.82	0.08	3	28.74	0.56	5	29.41	0.45	7	27.18	0.65	4
Feb	29.89	0.31	2	29.70	0.75	3	29.17	0.72	6	29.77	0.88	7	28.15	0.91	4
Mar	28.70	0.57	2	28.46	0.26	3	28.49	0.42	5	28.61	0.71	7	26.71	0.90	4
Apr	27.84	0.85	2	27.61	1.02	3	27.60	0.67	5	27.21	1.01	6	25.35	0.74	4
May	26.96	1.09	2	26.22	0.91	3	25.52	1.04	5	25.13	0.65	7	23.02	0.67	4
Jun	25.72	0.48	2	24.35	0.37	3	23.82	0.53	4	23.08	0.39	7	21.16	0.53	4
Jul	24.89	0.74	2	23.79	0.01	2	22.56	0.69	5	21.85	0.51	7	19.57	0.38	4
Aug	24.73	0.86	2	24.44	0.25	2	22.48	1.06	5	22.31	0.94	7	19.89	0.53	4
Sep	25.81	1.05	2	25.14		1	23.71	0.88	5	25.20	2.04	8	21.57	0.11	3
Oct	26.96	1.20	2	26.62		1	25.59	0.65	5	26.90	1.52	8	23.58	0.48	3
Nov	27.36		1	27.51		1	27.10	0.52	6	28.47	0.34	8	24.95	0.59	3
Dec	29.50	0.37	2	28.76	0.36	3	27.92	0.22	5	29.17	0.99	8	26.87	0.39	4
Yearly mean	**27.34**	**1.92**		**26.78**	**2.06**		**26.06**	**2.44**		**26.43**	**2.89**		**24.00**	**3.00**	
Summer mean (Dec-Feb)	**29.72**	**0.29**		**29.09**	**0.62**		**28.61**	**0.75**		**29.45**	**0.82**		**27.40**	**0.84**	
Autumn mean (Mar-May)	**27.83**	**1.02**		**27.43**	**1.20**		**27.20**	**1.39**		**26.99**	**1.68**		**25.03**	**1.74**	
Winter mean (Jun-Aug)	**25.11**	**0.73**		**24.19**	**0.38**		**22.95**	**0.96**		**22.41**	**0.81**		**20.21**	**0.84**	
Spring mean (Sep-Nov)	**26.71**	**1.08**		**26.42**	**1.20**		**25.47**	**1.58**		**26.86**	**1.97**		**23.37**	**1.52**	

(b)

OFFSHORE	**Raine Island**			**Norman Reef**			**Myrmidon Reef**			***Kelso Reef***			**Heron Reef**		
	mean	*SD*	*n*	*mean*	*SD*	*n*	*mean*	*SD*	*n*	*mean*	*SD*	*n*	*mean*	*SD*	*n*
Jan	28.33	0.23	3	28.42	0.05	2	28.44	0.28	4	28.31	0.32	4	26.32	0.62	3
Feb	28.45	0.29	3	29.02	0.67	2	28.85	0.40	4	28.77	0.65	4	27.36	0.67	3
Mar	27.71	0.53	3	28.12	0.39	2	27.89	0.53	4	27.15	2.32	4	26.33	0.85	3
Apr	27.21	0.61	3	27.28	1.59	3	27.13	1.04	5	26.79	1.76	4	25.39	0.69	3
May	26.68	1.00	3	26.42	1.34	3	26.38	0.94	5	25.95	0.75	4	23.88	0.61	3
Jun	25.64	0.47	3	25.05	0.86	3	24.96	0.74	5	25.17	0.65	4	22.48	0.70	3
Jul	25.27	0.41	3	24.33	0.91	3	24.15	0.70	5	24.52	1.90	5	21.03	0.47	3
Aug	25.02	0.57	3	24.43	0.88	3	24.17	0.79	5	24.62	2.38	5	20.72	0.31	3
Sep	25.40	0.71	3	25.36	0.97	2	24.87	0.80	5	25.46.	2.72	5	21.65	0.90	3
Oct	26.09	0.97	3	26.18	0.95	3	25.83	0.80	5	26.18	1.60	5	22.83	0.74	3
Nov	27.39	0.92	2	27.02	0.87	3	27.06	0.62	5	27.02	0.63	5	24.01	0.15	3
Dec	28.07	0.35	3	28.22	0.14	3	28.30	0.14	5	27.53	0.87	5	25.59	0.48	4
Yearly mean	**26.77**	**1.32**		**26.65**	**1.71**		**26.50**	**1.74**		**26.45**	**1.94**		**23.96**	**2.23**	
Summer mean (Dec-Feb)	**28.29**	**0.31**		**28.55**	**0.46**		**28.53**	**0.36**		**28.20**	**0.55**		**26.42**	**0.93**	
Autumn mean (Mar-May)	**27.20**	**0.78**		**27.27**	**1.30**		**27.13**	**1.02**		**26.63**	**1.02**		**25.20**	**1.24**	
Winter mean (Jun-Aug)	**25.31**	**0.56**		**24.61**	**0.84**		**24.43**	**0.78**		**24.77**	**0.67**		**21.41**	**0.93**	
Spring mean (Sep-Nov)	**26.29**	**1.10**		**26.19**	**1.04**		**25.92**	**1.15**		**26.22**	**1.13**		**22.83**	**1.18**	

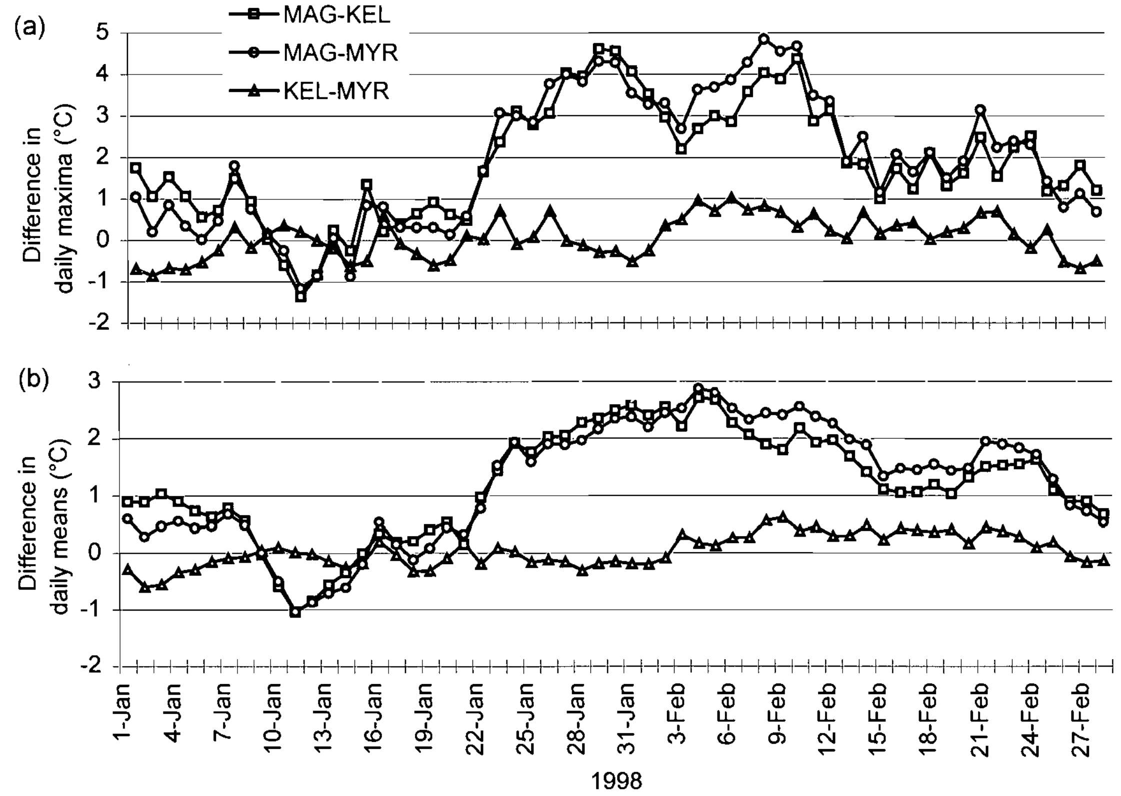


Fig 3.6. Cross-shelf variation in sea temperature between three sites in the central GBR during an unusually warm period in the summer of 1998 that coincided with coral bleaching. Data are shown as pair-wise differences in (a) daily maxima and (b) average daily temperatures between Magnetic Island and Kelso Reef (squares), Magnetic Island and Myrmidon Reef (circles) and Kelso and Myrmidon Reef (triangles). Note the different scales on the two graphs.

3.5. DISCUSSION

Most coral populations on the Great Barrier Reef (GBR) live in thermal environments that are relatively stable over short time scales (hours – days). Diurnal ranges at most reef slope locations were <1°C for more than 80% of the time. Although thermal stability characterizes most reef environments on short time scales, it is the unusually large and rapid fluctuations in temperature that provide the greatest insights into the physiological tolerances of corals and these are considered further.

Among the largest source of variation in sea temperature on the GBR at any scale is diurnal variation. Reef flat environments at locations such as Magnetic Island and Heron Island exemplify this with temperature changes of more than 9°C within a tidal cycle. Although these extreme temperature changes result in equally large diurnal ranges, such large diurnal ranges are usually only endured for short periods (mostly less than one week) when low tides combine with unusually warm air temperatures and low winds. Nevertheless, these data illustrate the extreme levels of temperature variation that some coral assemblages are exposed to. Temperature increases of 0.5 - 1 $°C.hr^{-1}$ over a 6-hour period with short-term (1-2 hours) increases of 2.5 $°C.hr^{-1}$ to temperatures approaching the upper thermal limits of Magnetic Island corals (Jones et al. 1997) occur without apparent ill health to coral communities. Coles (1997) recorded even greater temperature fluctuations at Fahal Island in Oman in summer, where maximum diurnal ranges were between 6.0° and 8.2°C, and temperatures regularly fluctuated 5 – 6°C within a 3-hr period. Coral cover and species diversity in this area were high and remained stable over a 13-year period (Coles 1997). There is also no correlation between thermal stability and either coral cover or species diversity on the GBR. Despite highly fluctuating temperatures experienced at inshore locations in the central GBR, coral diversity approaches that of outer-shelf reefs where thermal environments are comparatively stable. Of the 174 outer-shelf and 151 inshore species in the central GBR, at least 101 are shared in common (Done 1982), including thermally sensitive species in the genera *Acropora* and *Pocillopora* (Marshall and Baird 2000). Mean coral cover on three inshore reefs near Townsville ranged from 45 – 65% in 1997 (prior to the 1998 bleaching), whereas coral cover on outer-shelf reefs ranged from 25 – 35% (Sweatman et al. 2000). Similarly, Potts and Swart (1984) found that thermal stability was a poor predictor of coral growth and survivorship at Heron Island, where they recorded diurnal ranges similar to those in this study. Temperatures varying 3 – 4°C within minutes also had no discernable impact on coral mortality near a thermal discharge of a power station in Hawaii, compared to a control site (Coles 1975). There is therefore no evidence to suggest that large temperature fluctuation, below the upper thermal limits of corals, adversely impacts on coral health at the population or community level. In addition, the available evidence suggests that temperature excursions beyond local maximum ranges may be more important in causing thermal stress than variability in temperature per se.

Highly variable thermal environments such as Magnetic Island, Heron Island and the Gulf of Oman (see also a review by Brown 1997a) suggest that there are at least some coral populations that are resilient and/or adapted to large temperature extremes. However, there is little experimental evidence to support the notion that highly fluctuating temperatures enhance the thermal resistance of coral populations. The upper thermal limits of *Pocillopora damicornis* and *Acropora elseyi* at Orpheus Island from the reef flat were not measurably different from their reef slope counterparts (Chapter 4, Berkelmans and Willis 1999). This is despite a significantly greater mean, maximum and frequency distribution of diurnal temperature ranges found between the reef flat and slope (respectively) at Orpheus Island (Table 3.1, Fig 3.2). However, in some organisms the rate of temperature change has been found to be important in increasing the upper thermal limits. Ketzner and Bradley (1982), for example, found that copepods grown over 20 generations in fast cycling thermal regime were more temperature tolerant (through genetic adaptation) than those grown in a slow cycling regime. Therefore, if variable thermal environments do affect the temperature tolerance of corals, any increased tolerance may be smaller than the temperature resolution (1°C) used to investigate differences between reef flat and slope corals at Orpheus Island.

Spatial variation in mean summer temperatures of up to 1 °C across the GBR shelf and >2°C along the length of the GBR (Table 3.3, Fig 3.5), highlight differences in temperature regimes that coral populations within a species experience. Inshore-offshore and north-south differences in temperature regimes are accentuated seasonally with warmer summer temperatures at inshore and northern reefs compared to offshore and southern reefs. These cross-shelf and latitudinal temperature differences coincide with apparent differences in the thermal bleaching thresholds of coral populations over similar spatial scales. For example, at Magnetic Island average daily temperatures of <31.5°C are not high enough to cause corals to bleach (Jones et al. 1997), however widespread bleaching occurred at Kelso Reef when average daily temperatures remained below 30 °C (Fig 3.4b, Berkelmans in press, Chapter 6). These data suggest that local thermal adaptation has taken place over relatively small spatial scales (10's of kilometers). Despite the existence of comparatively thermally tolerant coral populations at locations such as Magnetic Island, these populations may not cope better than offshore populations in warmer thermal regimes as a result of climate change. Magnetic Island experiences regular bleaching events (Chapter 2, Jones et al. 1997) and inshore temperatures are likely to increase more than offshore temperatures during these bleaching events (Fig 3.6). Thus Magnetic Island populations may be at greater, not less risk of climate change compared to those from offshore areas with lower levels of thermal tolerance (see Chapters 2 and 6).

The magnitude and patterns of spatial and temporal variation found in this study have implications for the establishment of in-situ sea temperature monitoring programs. To capture sea temperature parameters (maximum, minimum, mean, variation) of interest to climate modellers, reef ecologists or managers (e.g. Pittock 1999), it is necessary to measure temperature at sites and depths that adequately represent local conditions. The data collected and presented here gives an indication of the variation in temperature that could be expected between habitats, between sites and locations at increasing spatial scales, and over a range of data aggregation levels. These data can be used as a guide to determine the number and location of data loggers that need to be deployed to answer biological or physical questions of interest. For example, if temperatures associated with coral bleaching is the primary purpose of monitoring, temperature data need to be collected at high spatial and temporal resolution because differences in temperatures of less than 0.5°C between sites (or habitats) can result in a highly variable bleaching response (Chapter 6, Berkelmans in press). On the other hand, much coarser temporal and spatial resolution may be sufficient to monitor temperature for coral growth or reproduction studies.

The spatial and temporal variation in sea temperature presented here also has implications for reef workers wishing to interpret their results using temperature data collected some distance away from the immediate study area. These results indicate that depending on the biological question being addressed, temperatures at one reef or bay may not adequately reflect those at another reef or bay. For example, spring temperatures at Magnetic Island rise more rapidly compared to Orpheus Island, approximately 75km north due to the shallow embayment enclosing Magnetic Island reefs (Table 3.3). The warmer spring temperatures are associated with variation in the timing of coral spawning between these two locations with spawning taking place 1 month earlier at Magnetic Island (Babcock et al. 1986).

The patterns of sea temperature variation presented here, which cover a broad range of spatial and temporal scales, highlight the range in thermal regimes that characterize and influence coral populations on the GBR. These patterns of thermal variation emphasize the importance of using spatially and temporally relevant data in interpreting ecological and physiological changes in coral reef environments.

Appendix 3.1. Summary of inshore spatial comparisons undertaken, showing the data recording period, data interval used and the number of samples. D = average daily temperature (48 samples per day).

Location	istance	Period	Data interval	No. Samples
Geoffrey Bay Site 1 & 2	300 m	9/3/93 – 4/9/95	D	386
Geoffrey Bay Site 2 & 3	200 m	9/3/93 – 4/9/95	D	386
Geoffrey Bay Site 1 & 3	500 m	9/3/93 – 4/9/95	D	386
Cattle Bay Site 1 & 2	200 m	5/6/98 – 16/9/95	D	588
Cattle Bay Site 2 & 3	300 m	5/6/98 – 16/9/95	D	588
Cattle Bay Site 1 & 3	500 m	5/6/98 – 16/9/95	D	588
Cattle & Pioneer Bay	4 km	17/7/94 – 26/5/99	D	1312
Pelorus Is & Cattle Bay	3 km	17/7/94 – 26/5/99	D	1312
Pelorus Is and Pioneer Bay	7 km	17/7/94 – 26/5/99	D	1312
Geoffrey & Florence Bay	7 km	26/1/96 – 5/2/99	D	590
Halfway Is & Keppel Is	18 km	7/12/95 – 21/5/97	D	532
Lucinda & Pioneer Bay	17 km	6/5/98 – 22/12/98	D	231
Daydream & Hayman Is	25 km	26/6/96 – 23/7/98	D	180
Black Rks & Coconut Bch	17 km	20/7/96 – 6/9/98	D	587
Cattle Bay & Mourilyan	100 km	7/5/98 – 20/11/98	D	198
Cattle Bay & Geoffrey Bay	75 km	30/3/93 – 20/11/98	D	1356
Cape Flattery & Mourilyan	430 km	13/5/98 – 2/2/99	D	266
Wallace Is & Cape Flattery	440 km	13/5/98 – 19/11/98	D	191
Abbot Pt & Halfway Is	490 km	6/5/98 – 23/12/98	D	232
Black Rks & Nelly Bay	360 km	25/1/96 – 6/9/98	D	764
Wallace Is & Nelly Bay	890 km	21/11/96 – 19/11/98	D	729
Night Is & Daydream Is	940 km	2/12/96 – 15/12/98	D	720
Cape Flattery & Halfway Is	1130 km	13/5/96 – 10/2/99	D	274
Low Isles & Wongarra	1075 km	7/6/98 – 24/12/99	D	263

Appendix 3.2. Summary of offshore comparisons undertaken, showing the data recording period, data interval used and the number of samples. D = average daily temperature.

Location	Distance	Period	Data interval	No. Samples
Kelso Rf Site 1 & 2	200 m	4/7/95 – 10/6/96	D	343
Myrmidon Rf Site 1 & 2	350 m	13/4/95 – 24/4/96	D	378
Myrmidon Rf Site 2 & 3	350 m	13/4/95 – 24/4/96	D	378
Myrmidon Rf Site 1 & 3	700 m	13/4/95 – 24/4/96	D	378
Kelso Rf & John Brewer Rf	23 km	23/4/96 – 28/4/99	D	673
Tryon & Heron Is	25 km	20/10/96 – 7/12/98	D	379
Arlington Rf & Norman Rf	31 km	27/3/96 – 28/4/98	D	504
East Cay & Turner Cay	26 km	30/11/97 – 7/12/98	D	373
Chicken Rf & Myrmidon Rf	54 km	1/5/98 – 24/4/99	D	359
Davies Rf & John Brewer Rf	65 km	2/5/98 – 16/4/99	D	680
Reef 21-583 & East Cay	52 km	21/11/95 – 6/11/96	D	345
Norman Rf & Agincourt3 Rf	50 km	30/11/97 – 8/12/98	D	374
Kelso Rf & Moore Rf	190 km	22/10/97 – 9/1/99	D	445
Sandbank#7 & Lizard Is	210 km	7/12/96 – 15/1/99	D	192
Lizard Is & Norman Rf	200 km	19/7/96 – 28/4/98	D	375
Raine Is & Agincourt3 Rf	520 km	30/3/96 – 30/11/98	D	608
Sandbank#7 & Norman Rf	410 km	7/12/96 – 6/11/99	D	677
Lizard Is & Myrmidon Rf	460 km	1/5/96 – 15/1/99	D	260
Davies Rf & East Cay	600 km	2/5/96 – 16/4/99	D	696
Raine Is & Davies Rf	900 km	2/5/96 – 30/1198	D	575
Agincourt3 Rf & East Cay	980 km	30/3/96 – 20/2/99	D	674
Heron Is & Moore Rf	930 km	22/10/97 – 17/12/98	D	422

Appendix 3.3. Summary of diurnal and GBR-wide comparisons undertaken, showing the data recording period, data interval used and the number of samples. D = average daily and M = average monthly temperature.

	Period	Data interval	No. Samples
Wallace Island (inshore)	6/12/97 - 19/11/98 [a], 22/11/96 - 18/11/98 [b], 12/96 - 10/98 [b]	D & M	349 [a], 727 [b] & 23 [b]
Black Rocks (inshore)	2/12/95 - 15/8/98 [a], 2/12/95 - 5/9/98 [b], 12/95 - 8/98 [b]	D & M	647 [a], 817 [b] & 28 [b]
Orpheus Island (inshore)	11/2/93 - 15/9/99 [a], 12/2/93 - 26/5/99 [b], 3/93 - 5/99 [b]	D & M	2060 [a], 1821 [b] & 61 [b]
Magnetic Island (inshore)	18/12/92 - 29/1/99 [a], 20/9/91 - 4/2/99 [b], 10/91 - 1/99 [b]	D & M	2106 [a], 2527 [b] & 87 [b]
Halfway Island (inshore)	7/12/95 - 14/9/99 [a], 8/12/95 - 15/9/99 [b], 1/96 - 8/99 [b]	D & M	1184, 983 [b] & 48 [b]
Raine Island (offshore)	27/6/96 - 29/11/98 [a], 11/12/95 - 30/11/98 [b], 1/96 - 11/98 [b]	D & M	833 [a], 718 [b] & 35 [b]
Norman Rf (offshore)	26/3/96 - 24/12/98 [a], 26/3/96 - 24/12/98 [b], 4/96 - 12/98 [b]	D & M	695 [a], 690 [b] & 32 [b]
Myrmidon Rf (offshore)	14/4/95 - 26/4/99 [a], 13/4/95 - 26/4/99 [b], 4/95 - 4/99 [b]	D & M	1474 [a], 739 [b] & 57 [b]
Kelso Rf (offshore)	5/7/95 - 26/7/99 [a], 5/7/95 - 26/7/99 [b], 7/95 - 7/99 [b]	D & M	1063 [a], 1297 [b] & 54 [b]
Heron Is (offshore)	24/11/95 - 5/2/99 [a], 24/11/95 - 16/12/98 [b], 12/95 - 12/98 [b]	D & M	1172 [a], 1121 [b] & 37 [b]

[a] Reef Flat

[b] Reef Slope

Appendix 3.4. Summary of reef flat vs slope comparisons indicating the approximate depth, data recording period, data interval used and the number of samples. D = average daily, ½H = half-hourly temperature.

Location	**Depth**	**Period**	**Data interval**	**No. Samples**
Magnetic Is (Inshore)	0 & 5m	1/7/95 - 31/3/96 [c] 1/1/98 - 28/2/98 [d]	D & ½H D	275 [c] & 13,000 [c] 58 [d]
Kelso Reef (Mid-shelf)	0 & 4m	4/7/95 – 31/3/96 [c] 1/1/98 - 28/2/98 [d]	D & ½H D	272 [c] & 13,007 [c] 58 [d]
Myrmidon Reef (Outer-shelf)	0 & 8m	1/7/95 - 31/3/96 1/1/98 - 28/2/98 [d]	D & ½H D	275 [c] & 13,094 [c] 58 [d]

[c] General analysis
[d] Bleaching analysis

Chapter 4

Seasonal and spatial variation in the upper thermal limits of corals

Partial bleaching of plate and staghorn *Acropora* at Magnetic Island (19.12°E, 146.88°W), February 1994. Photo courtesy GBRMPA.

4.1. ABSTRACT

An apparent increase in coral bleaching events worldwide in the last 2 decades has focussed attention on the sensitivity of reef corals to temperature perturbations and the need to quantify spatial and temporal variation in their upper thermal limits. Experimental studies involving temperature manipulations show that *Acropora formosa* from Orpheus Island has a 5-day 50%-bleaching threshold of 31° to 32°C in summer, only 2 to 3°C higher than mean summer temperatures (29°C). *Pocillopora damicornis* and *A. elseyi* have 5-day 50%-bleaching thresholds of between 32° and 33°C. The winter upper thermal limit of *P. damicornis* is 1°C lower, indicating that seasonal acclimatisation takes place and raising the possibility that corals are capable of short-term thermal acclimatisation. These bleaching thresholds are best considered the maximum tolerable temperatures for local populations of these species. Bleaching thresholds determined in these experiments are considered a fair indication of upper thermal limits, because >50% of colonies died when allowed to recover in situ. Neither *P.damicornis* nor *A. elseyi* showed habitat-specific (reef flat vs reef slope) differences in bleaching thresholds. Further, no discernable difference was found in the bleaching threshold of *P.damicornis* from sites 3km apart. I found a delay in the bleaching response of corals following thermal stress, a result that has implications for identifying the timing of stressful conditions in natural bleaching events.

4.2 INTRODUCTION

Although coral bleaching events have been observed as far back as the 1870's, there has been a dramatic increase in the number of reported incidents of mass coral bleaching in the scientific literature since the 1980's (Glynn 1993, Brown 1997a, Hoegh-Guldberg 1999). This has led to worldwide concern regarding the current health of coral reefs and economies dependent on them (Meehan and Ostrander, 1997). Elevated temperatures, of as little as 1-2°C above mean monthly summer values, are thought to be the primary cause of bleaching (Glynn et al. 1988, Jokiel and Coles 1990, Drollet et al. 1994). Until recently the most severe coral bleaching event on record is believed to have occurred in the eastern Pacific during 1982-83 when 51-97% of corals died between Panama and the Galapagos (Glynn et al. 1988). Two species were almost extirpated in the Gulf of Chiriqui, Panama during this event (Glynn and de Weerdt 1991; Glynn and Feingold 1992), while a third species, *Millepora platyphylla*, may have become locally extinct (Glynn and Feingold 1992). The global coral bleaching event of 1997-98 however was more severe than the 1982-83 event in terms of both spatial extent and intensity (Berkelmans and Oliver 1999, Wilkinson et al. 1999). Long-term (>50yrs) background sea temperatures in the eastern Pacific, the Andeman Sea and tropical oceans as a whole are on the increase (Parker et al. 1995, Brown et al. 1996, Lough 2000) as are the frequency of local thermal anomalies (e.g. Davies et al. 1997, Jones et al. 1997, Lough 1999, 2000). These observations support earlier suggestions that coral bleaching may be linked to global warming (Williams and Bunkley-Williams 1990, Glynn 1993). Clearly, bleaching events represent a major disturbance to reef communities and may have an increasing potential to structure coral assemblages.

To gain insights into the degree to which temperature anomalies are capable of structuring coral assemblages, we need to quantify upper thermal tolerances for a range of coral species. Results for the few species whose thermal tolerances have been investigated experimentally concur with data collected during natural bleaching events and confirm that corals live close to their upper thermal limits (Jokiel and Coles 1990, Glynn and D'Croz 1990). Experimental studies also indicate that there is considerable variation in thermal tolerance between species (Edmundson 1928, Coles et al. 1976) and between populations from widely separated geographic regions (Coles et al. 1976, Marcus and Thoraug 1981, Glynn et al. 1988). These studies explain, in part, variation in the intensity of bleaching between species in localised events and between geographically disparate populations of the same species in widespread bleaching events.

Less well understood is the common observation that bleaching is frequently patchy within species on localised scales. For example, a number of studies have documented a higher proportion of corals bleaching on the reef slope compared with the reef flat (Hoeksema 1991, Oliver and Berkelmans, unpub data), on outer rim reefs compared to inner lagoonal sites (Cook et al. 1990) and on the fore reef compared with the back reef (Goreau 1990). One of the suggested reasons for differential bleaching between habitats is that corals exposed to variable temperatures, such as those on the reef flat or lagoon, are better acclimatised to thermal stress than those experiencing less variable conditions, such as reef-slope or rim-reef corals (Cook et al. 1990, Hoeksema 1991). There are also reports of considerable variation in bleaching over small spatial scales within the same habitat (Oliver 1985) and in the proportion of corals bleached between sites separated by only a few kilometres. Hoegh-Guldberg and Salvat (1995) found a mean of 72% of corals bleached on the NE side of Moorea, French Polynesia, but fewer corals (mean = 40%) bleached on the NW side less than 10km away. Genetic variation between coral populations and/or variable thermal tolerance limits of different zooxanthellae strains may contribute to such variation in bleaching on local scales (see Buddemeier and Fautin, 1993, Knowlton and Jackson 1994, Rowan and Knowlton 1995), but the contribution of differential acclimatisation of corals at different sites due to variable thermal history is unknown. To better understand the role of temperature anomalies in structuring coral assemblages at a local scale, knowledge of variability in upper thermal limits over small spatial and temporal scales is needed.

Bleaching has been used to detect upper thermal limits of corals in a number of studies (e.g. Coles et al. 1976, Jokiel and Coles 1977, Coles and Jokiel 1978, Marcus and Thoraug 1981, Glynn and D'Croz 1990), however, the appropriateness of this response as an indicator of tolerance limits is not clear. Upper thermal limits of organisms are traditionally defined as the temperature at which 50% of the sample population dies after a specified period of exposure, often expressed as the T_{L50} (Schmidt-Nielson 1990). Using coral bleaching as an indicator for upper thermal limit is convenient because it avoids the necessity to monitor the recovery of corals or their decline to death, following a predetermined period of thermal stress. However, because corals may recover following bleaching (Gleason 1993, Drollet et al. 1994), it is not clear how to relate a bleaching threshold temperature to an upper thermal limit.

In this study I establish the upper thermal limits for three coral species and evaluate the usefulness of bleaching thresholds as indicators of traditional T_{L50}'s. I also investigate whether upper thermal limits vary seasonally or over small spatial scales to better understand the role of localised temperature anomalies in structuring coral assemblages. Specifically, I investigate whether temperature tolerances vary between winter and summer, between the reef slope and reef flat and between colonies from equivalent habitats at sites 3km apart.

4.3. METHODS

I investigated upper thermal tolerances of three coral species *(Acropora formosa* (Dana 1846), *Acropora elseyi* (Brook 1892) and *Pocillopora damicornis* (Linneus 1758)) from fringing reefs adjacent to Orpheus Island Research Station (Lat. 18.34°S, Long. 146.29°E), located on the Great Barrier Reef near Townsville, Australia. These species were chosen because they are often reported as being among the first to show bleaching symptoms during natural bleaching events (Oliver 1985, Marshall and Baird 2000) and because of their high abundance on Indo-Pacific reefs.

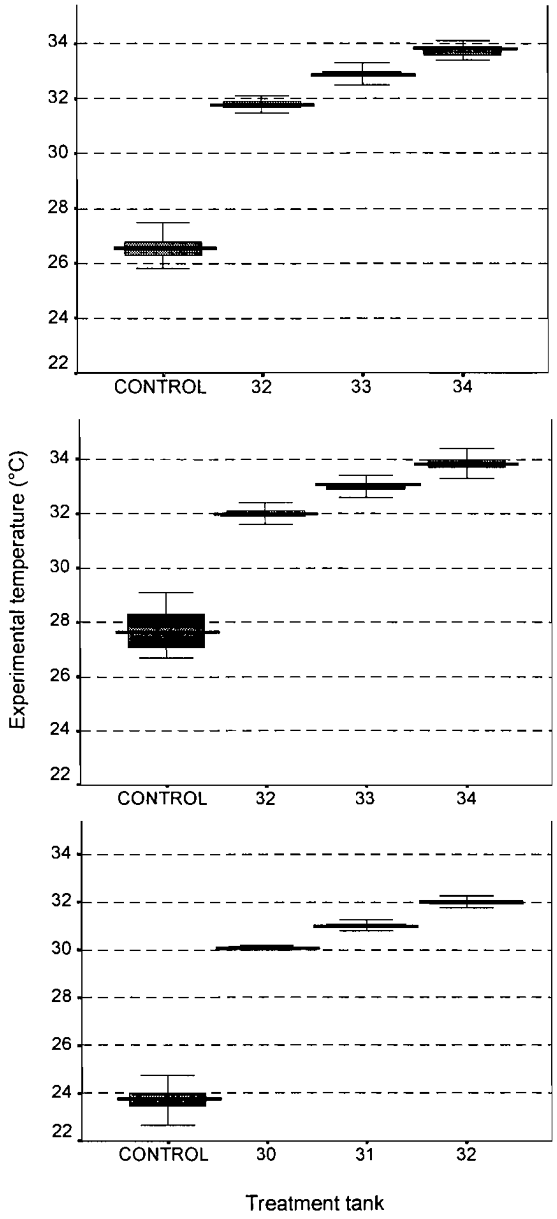
4.3.1. Experimental Protocols

Experiments were conducted at the Orpheus Island Research Station in round fibreglass tanks, each 2.4m in diameter, filled with approximately 1500 litres of seawater and fitted with a 3KW electric heating element. Filtered seawater from the upper reef slope in Pioneer Bay at Orpheus Island (~3 m depth) was pumped continuously into each tank at a rate of 4 $l\text{-}min^{-1}$, which exchanged the water on average every six hours. Submersible pumps ensured that water within each tank was well mixed. Experimental temperatures in each tank were monitored at 10-minute intervals using data loggers throughout each experimental period and on an ongoing basis in an adjacent bay (Cattle Bay) at 30-minute intervals. Data loggers were calibrated using a digital NATA certified thermometer, accurate to ± 0.2°C. Control of temperature in the heated tanks was either automatic via a computerised process control system or manual by measuring and adjusting temperatures every 15 minutes. Spot checks at different places within the tanks confirmed that spatial variation in temperature within each tank was generally less than 0.1°C. Temperature treatments and control precision during the experiments are presented in Fig 4.1. Tanks were covered with 70% shade cloth (30% transmitted light) to avoid any potentially confounding effects of high light intensity on the thermal tolerance of corals. The levels of transmitted light (ranging from approximately 400 to 550 $\mu Em^{-2}.s^{-1}$ between experiments) were equivalent to those experienced by corals at approximately 5m depth at mean tide level (Berkelmans, unpub data). Although ambient light was reduced to a level at or below what they would have experienced in the field, seasonal variation in light intensity might alter bleaching responses between summer and winter within a species. Sea surface light (photosynthetically active radiation) conditions representative of Orpheus Island were monitored at Myrmidon Reef (approximately 90 km NE of Orpheus Island). Light and temperature data at the time of the experiments are presented in Table 4.1. Light values are means of 5 second scans, recorded half-hourly and averaged between 10 am and 3 pm each day, representing the period of highest daily irradiance (data courtesy Australian Institute of Marine Science).

Table 4.1. Ambient sea temperature and surface light levels during temperature experiments. Temperatures (°C ± SD) measured by in situ data loggers recording at 30-minute intervals at Cattle Bay, Orpheus Island. Light ($\mu E.m^{-2}.s^{-2}$ ± SD) measured as photosynthetically active radiation (PAR) at Myrmidon Reef (approx. 90 km NE of Orpheus Is). Light levels are means of 5-second scans, recorded every half hour and averaged between 10 am and 3 pm each day (light data courtesy of the Australian Institute of Marine Science).

	Mean ambient conditions 14 days before experiment.		Mean ambient conditions during experiment.		Mean ambient conditions 0-34 days after experiment.	
	PAR	**Temperature**	**PAR**	**Temperature**	**PAR**	**Temperature**
1st summer experiment	1271 ± 430	Not available	1229 ± 566	28.4 ± 0.25	Not applicable	Not applicable
2nd summer experiment	2002 ± 114	28.9 ± 0.24	1864 ± 133	28.2 ± 0.14	Not applicable	Not applicable
Winter experiment	1397 ± 244	22.9 ± 0.12	1513 ± 59	23.1 ± 0.11	1569 ± 275	23.4 ± 0.44

Four tanks were used in the following experiments, three for simultaneously heating experimental corals to different target temperatures and a fourth for maintaining them at ambient temperatures as a control. Temperature treatments were allocated randomly to tanks for the first experiment and deliberately rotated for later experiments to avoid potential bias from tank effects. Corals were allowed to adjust to tank conditions for two days prior to commencement of temperature experiments. Treatment tanks were heated slowly (<0.5°C/h) to target temperatures and maintained there for five days. This rate of temperature rise is less than that experienced by local reef flat corals during spring tides when temperatures commonly vary by more than 1°C/h (Chapter 3). Temperature experiments were conducted on three occasions: two in summer/autumn (15 – 20 February 1993: Effects of species and summer bleaching threshold; and 4 – 9 April 1993: Effects of species and habitat) and one in winter (10 – 15 August 1993: Effects of location and winter bleaching threshold).



(a) 1st Summer Experiment

Treatment (°C)	Mean (°C)	SD (°C)
Control	26.6	0.56
32	31.8	0.19
33	32.8	0.24
34	33.8	0.27

(b) 2nd Summer Experiment

Treatment (°C)	Mean (°C)	SD (°C)
Control	27.7	0.68
32	32.0	0.24
33	33.0	0.21
34	33.8	0.27

(c) Winter Experiment

Treatment (°C)	Mean (°C)	SD (°C)
Control	23.7	0.53
32	30.1	0.05
33	31.0	0.09
34	32.0	0.16

Fig 4.1. Experimental conditions during: (a) First summer experiment (effects of species and summer temperatures on upper thermal limits); (b) Second summer experiment (effects of species, habitat and handling on summer upper thermal limits); and (c) Winter experiment (effects of location and season on winter upper thermal limits, bleaching as an indicator of upper thermal limits). Box plots show median, 50^{th} quartile and the total range in temperature. Adjoining tables show means and standard deviations.

4.3.2. Bleaching thresholds

I used a visual estimate of the degree of bleaching as the variable for measuring the response of corals to experimental temperature manipulations. Corals were allocated to one of three categories based on appearance: 'normal' - no visible loss of colour; 'moderate bleaching' - corals pale, but still with a significant amount of colour; and 'heavy bleaching' - corals mostly white or dead. Upper thermal limits were defined as the temperature at which 50% or more of corals were moderately or heavily bleached at the end of the 5-day exposure period. Zooxanthellae densities were measured in samples from each bleaching category for two of the study species, *Pocillopora damicornis* and *Acropora formosa*, to determine the approximate relationship between tissue colour and zooxanthellae density under the experimental conditions. Zooxanthellae densities were determined from branch tips *(P. damicornis*: 2.5 - 3.0cm in length and *A. formosa:* 4.5 - 6.0cm in length) subsampled from four experimental colonies per bleaching category. Tissues were removed using a Water-Pik into 100ml of seawater and homogenised with a blender for 1 minute. Eight replicate zooxanthellae counts per branch sample were made using a haemocytometer.

4.3.3. Summer upper thermal limits and the effect of species

To determine summer upper thermal limits for three coral species and establish whether they differ, I subjected 20 fragments (15 - 20cm in length) of *Acropora formosa, A. elseyi* and *Pocillopora damicornis* to four temperature treatments (32°, 33°, 34°C and an unheated control (26.6°C ± 0.6° (SD)). Corals were collected from the upper reef-slope between 2 and 4m depth at mean tide level. Branches were sampled from colonies that were spaced over a distance of approximately 200m along the narrow fringing reef in Cattle Bay (Orpheus Is.). Fragments collected for all experiments included a range of morphological types and were therefore likely to have represented a range of genetic variants. Only one fragment was collected from each colony. Branches were allocated haphazardly between treatments. The 32°C temperature treatment selected was close to or slightly above the range of local maxima in daily summer temperatures (Chapter 3, GBRMPA 2001). Treatment tanks were heated slowly (<0.5°C/hr) to target temperature and maintained there for five days, after which the condition of each fragment was visually assessed. Chi-squared analysis was used to compare the proportions of bleached corals between species in each temperature treatment (2 x 4 contingency tables).

4.3.4. Effect of tanks and habitat of origin on upper thermal limits

To determine if tank effects were confounding determinations of upper thermal limits, I repeated the summer temperature experiments during a similar ambient temperature regime (Table 4.1) assigning temperature treatments to different tanks. To simultaneously establish if conspecifics from different habitats have different upper thermal limits, I collected 30 fragments (10 - 15cm in length) of each of *Pocillopora damicornis* and *Acropora elseyi* from both the reef flat and reef slope in April 1993. Thirty fragments (10 – 15 in length) from each habitat for each species were randomly allocated to one of four temperature treatments (32°, 33°, 34°C and an ambient control (27.7°C ± 0.7°(SD), n = 15 fragments per temperature treatment per habitat). To maximise the chance of detecting differences in tolerance limits in corals from different habitats, corals from the reef flat were collected from the shallowest zone in which they occur (~ mean low water springs) and those from the reef slope from the deepest zone in which they occur (~ 6m). The duration of the treatments was again five days with corals being heated slowly to their respective target temperatures (<0.5°C/hr).

4.3.5. Winter upper thermal limits and the effect of site of origin

To determine whether upper thermal limits of *Pocillopora damicornis* differed among seasons or among colonies from different sites, I conducted a similar temperature experiment in August 1993 (austral winter) using corals collected from two adjacent reefs. Fragments (10 - 15cm in length) were collected from fringing reefs at Orpheus

Island and adjacent Pelorus Island at a depth of approximately 3m at mean tide level. These sites are approximately 3km apart and colonies at equivalent depths responded differently during a natural bleaching event in 1994. During this event, 80 – 100% of *P.damicornis* at Orpheus Island bleached, whereas less than 10% of colonies at Pelorus Island were affected (Berkelmans unpublished data). Thirty fragments from each site were placed in each of four treatment temperatures (30°, 31° and 32°C and an ambient control (23.7°C ± 0.5°(SD)). Treatments all represented temperatures below bleaching thresholds found during the summer experiments (see Results section). Treatment tanks were slowly heated (<0.5°C/hr) to target temperatures and maintained at that temperature for five days, after which the condition of the corals was visually assessed. Chi-squared analysis was used to compare the proportion of bleached coral between sites and between habitats in each temperature treatment (2 x 4 contingency tables).

4.3.6. Relationship between bleaching and upper thermal limit

To determine whether bleaching is a good indicator of traditional T_{L50}'s, I allowed corals from the winter experiment, including ambient 'controls', to cool to ambient temperatures (~23°C) over 36 hours (temperature change <0.5°C/hr). Corals were then returned to a recovery site at the depth and reef of their origin. Corals were transported submerged in bins of water and then secured to wire racks in situ. Their recovery was assessed at 14 days, 34 days and 84 days after experimental heating. At each census, corals were classified according to their condition into four categories: unbleached, moderately bleached, heavily bleached and dead (> 50% partial mortality).

4.4 RESULTS

4.4.1. Bleaching thresholds

Zooxanthellae counts of representative samples for each of the response categories showed that my visual assessment of colour corresponded to easily discernable bleaching categories. The pale colour of moderately bleached corals corresponded to a 57% reduction in the density of zooxanthellae in *P. damicornis* and a 59% reduction in *A. formosa* compared to unbleached tissue (Fig 4.2). Similarly, the white colour of heavily bleached corals corresponded to an 88% reduction in the density of zooxanthellae in *P. damicornis* and an 89% reduction in *A. formosa.*

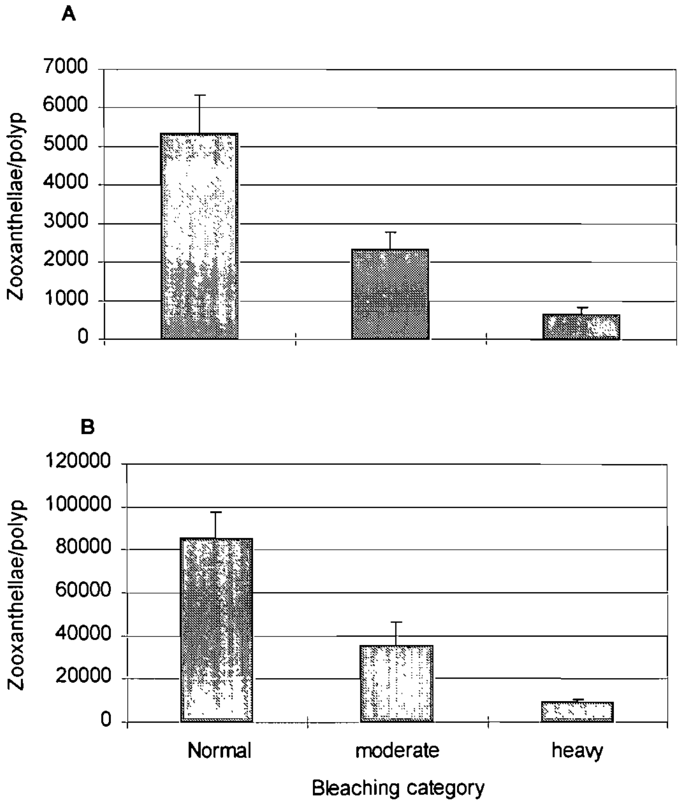


Fig 4.2. Mean zooxanthellae densities (± SE, n = 4 colonies/species) in the bleaching categories recognised visually for: (a) *Pocillopora damicornis* (mean polyp density = 60 ± 4 (SE) polyps.cm^{-2}), and (b) *Acropora formosa* (mean polyp density = 21 ± 2 (SE) polyps.cm^{-2}).

4.4.2. Summer upper thermal limits

Experimental temperature manipulations revealed a distinct bleaching threshold for the three coral species examined. No colonies of *Pocillopora damicornis* bleached at 32°C after experiencing five days of heating to this temperature in summer. At 33°C, however, 60% of colonies were either moderately or heavily bleached and at 34°C, all were either heavily bleached or dead (Fig 4.3a). Daily observations of corals throughout the experimental period showed a continuing increase in the number of colonies bleaching and in the intensity of the response for the first four days. Patterns in responses were clear and consistently different between temperature treatments. Twenty-four hours after reaching target temperatures, only three fragments of *P. damicornis* had commenced to pale slightly in the 33°C treatment, whereas all 20 colonies showed evidence of bleaching in the 34°C treatment. After 48 hours, all colonies of *P. damicornis* at 33°C were pale (moderately bleached) except for one that was white (heavily bleached), whereas all colonies at 34°C were white. After 72 hours, the loss of colour intensified in the 33°C treatment, whereas tissue began to slough off in 11 out of 20 colonies in the 34°C treatment. Therefore, the summer upper thermal limit for *P. damicornis*, defined as the temperature at which 50% of corals were moderately or heavily bleached after five days of thermal exposure, is between 32°C and 33°C.

A. elseyi's summer bleaching threshold did not differ significantly from that of *P. damicornis* ($\chi^2 = 4.95$, df = 3, $p > 0.25$), but *A. formosa*'s threshold was significantly lower ($\chi^2 = 13.63$, df = 3, $p < 0.01$). Only 25% of colonies of *A. elseyi* showed signs of bleaching after five days at 32°C, compared to 90% of *A. formosa* colonies (Fig 4.3b, 4.3c). However, for *A. elseyi* and *A. formosa,* all were heavily bleached or dead at 33°C (Fig 4.3b, 4.3c). The summer upper thermal limit is therefore between 32° and 33°C for *A. elseyi* and less than 32°C for *A. formosa*. If *A. formosa,* like *P. damicornis,* exhibits an 'all-or-nothing response' one degree either side of its bleaching threshold, the upper thermal limit for *A. formosa* is likely to be between 31 and 32°C.

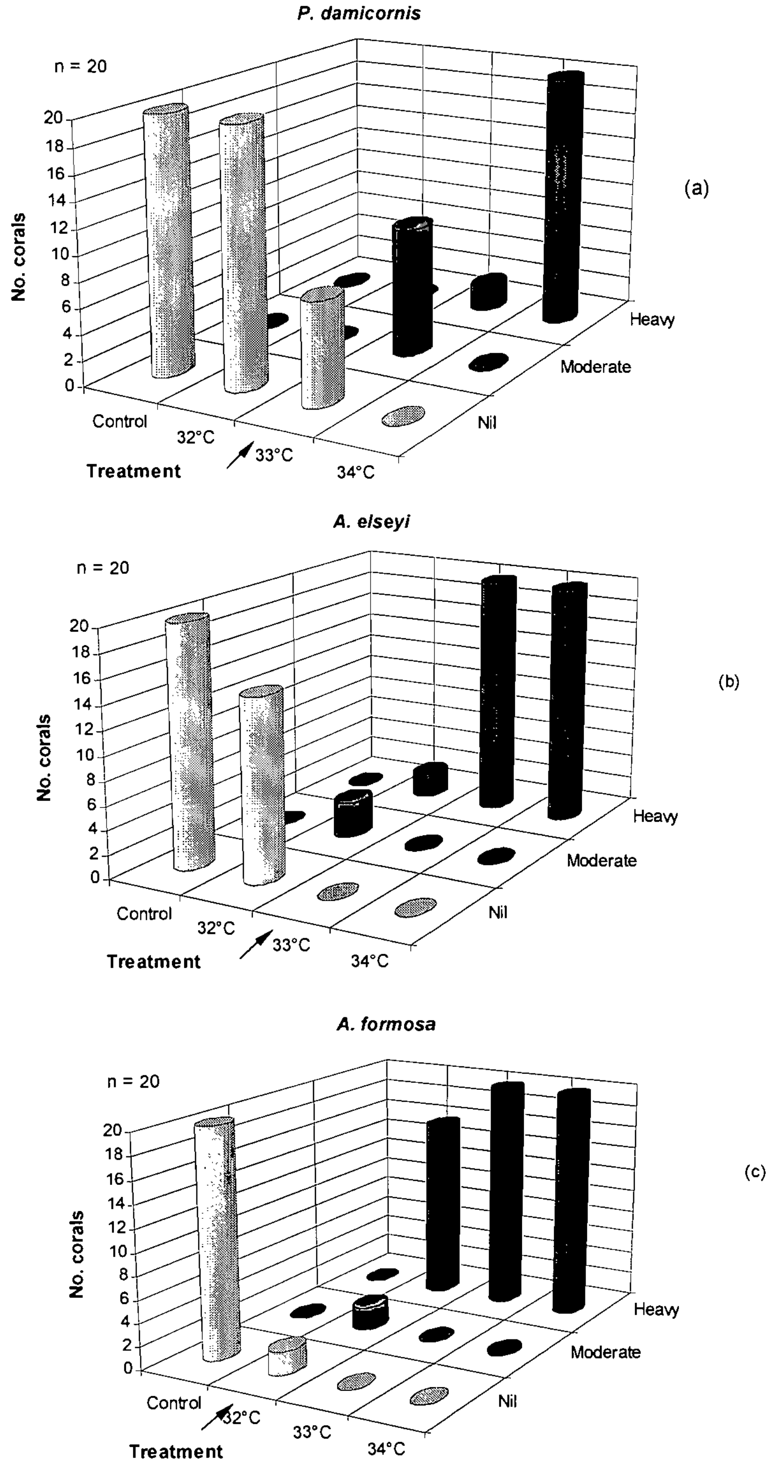


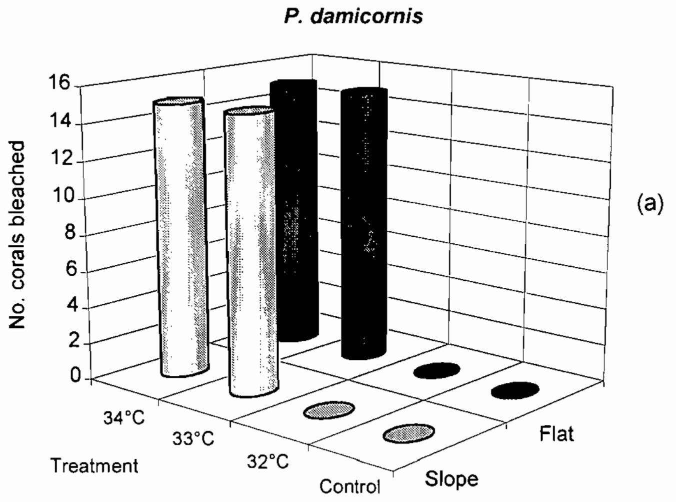
Fig 4.3. Experimental determination of summer upper thermal limits for three coral species: (a) *Pocillopora damicornis*, (b) *Acropora elseyi* and (c) *A. formosa*. Bleaching state of corals is represented on the z-axis. Arrows approximate species-specific upper thermal limits (n = 20 colonies per species for each temperature treatment).

The onset of bleaching in *A. formosa* was rapid in the highest temperature treatments with 17 out of 20 colonies becoming pale after 12 hours at 33°C and 15 out of 20 colonies being white or dead at 34°C. After 24 hours, half the 33°C colonies were white or dead, while all colonies where white or dead at 34°C. The onset of bleaching in *A. elseyi* was intermediate with 4 out of 20 colonies pale and none white after 24 hours at 33°C, and 11 out of 20 white and the rest pale at 34°C.

A repeat of temperature experiments in April, when ambient temperature regimes were similar (Table 1), produced similar bleaching responses. No colonies of *Pocillopora damicornis* bleached at 32° whereas most bleached at 33°C, although more corals were heavily bleached in the latter treatment in the second experiment (Fig 4.4a). Bleaching threshold temperatures were also identical for *A. elseyi* in the second experiment (Fig 4.4b). The consistency in results between the two summer experiments and the clear differences in the number of corals in the bleached and unbleached categories suggest that tank effects were negligible.

4.4.3. Effect of habitat of origin on upper thermal limits

Results of the habitat comparison showed little difference in the bleaching responses of corals from the reef flat and reef slope. For *Pocillopora damicornis*, neither the reef flat nor the reef slope corals bleached at 32°C after five days of exposure, but all colonies from both habitats were moderately or heavily bleached at 33°C (Fig 4.4a). Four out of 15 colonies of *A. elseyi* from the reef-slope were moderately or heavily bleached at 32°C compared to one out of 15 reef flat colonies, but this difference was not significant ($\chi^2 = 1.65$, df = 3, $p > 0.5$, Fig 4.4b).



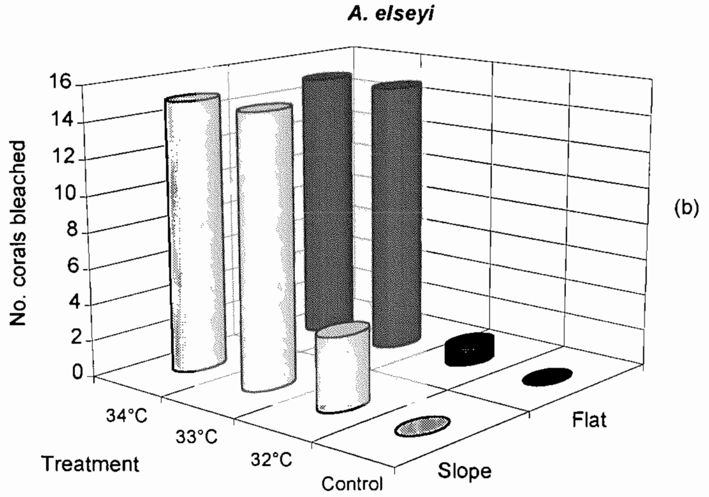


Fig 4.4. Effect of habitat on summer upper thermal limits of: (a) Pocillopora damicornis and (b) A. elseyi. Reef-flat corals were collected from 0m depth (chart datum) and reef-slope corals from approximately 6m depth at mean tide. (n = 15 colonies per species for each treatment).

4.4.4. Seasonal variation in upper thermal limits

Temperature experiments repeated for *Pocillopora damicornis* in winter indicate that upper thermal tolerances vary between seasons. Sixty-five percent of corals (combined for the Orpheus and Pelorus Island sites) were either moderately or heavily bleached after five days at 32°C in winter (Fig 4.5). In contrast, no colonies bleached at this temperature in the summer experiments following equivalent thermal exposures (Fig 4.5). The winter 5-day maximum upper thermal limit for *P. damicornis* is therefore between 31° and 32°C, approximately 1°C lower than the summer threshold.

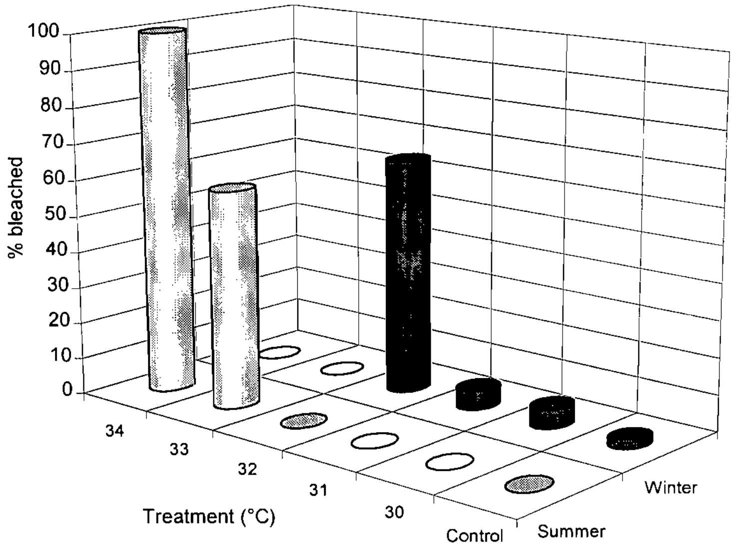


Fig 4.5. Seasonal variation in the upper thermal limits of *Pocillopora damicornis*. Histograms are totals for the moderate and heavy bleaching categories combined (n = 20 colonies in the summer and 60 in the winter treatment).

4.4.5. Effect of site of origin on upper thermal limits

A comparison of winter thermal tolerances between colonies of *Pocillopora damicornis* from Orpheus and Pelorus Islands, as measured by the 5-day no-bleaching threshold, showed little difference in bleaching response between sites. Corals from both sites showed little (<10%) or no bleaching at 30° and 31°C, but exhibited dramatic and equivalent bleaching responses at 32°C (Fig 4.6). There was no significant difference in the winter upper thermal limits of *P. damicornis* for colonies originating from the two sites ($\chi^2 = 4.51$, df = 3, $p > 0.1$).

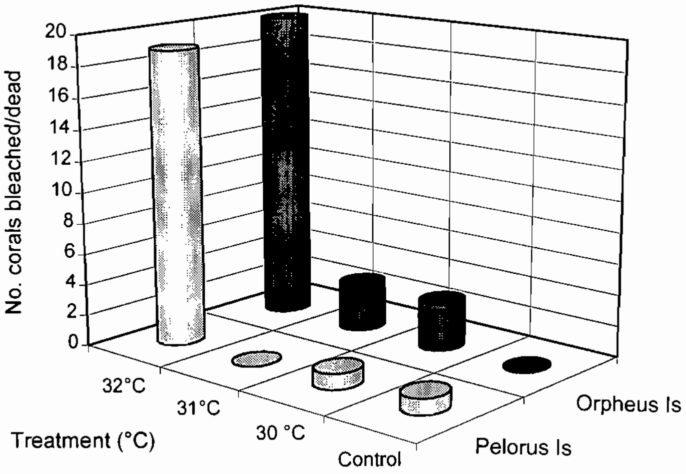
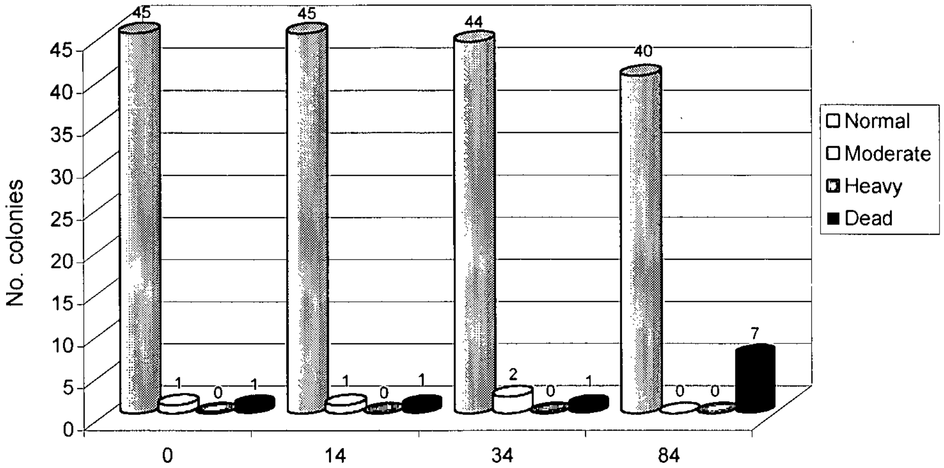


Fig 4.6. Site variation in the bleaching response of *Pocillopora damicornis* during winter from reefs approximately 3km apart at Orpheus and Pelorus Islands (n = 30 colonies per temperature treatment).

4.4.6. Relationship between bleaching and upper thermal limit

The recovery of *Pocillopora damicornis* colonies returned to their site of origin following the winter bleaching experiment correlated with the post-experiment bleaching state of colonies. I found that the initial number of heavily bleached corals approximately predicted the number that died within one month (Fig 4.7). This was despite the fact that there was a substantial delay in the bleaching response of corals from the warmest temperature treatment (32°C). In the first 14 days after experimental warming, the proportion of the total corals that were unbleached decreased by 17%, while heavily bleached corals increased by 8% (Fig 4.7b). Overall, nearly half of the corals deteriorated in condition during the first 14 days, while only two recovered. Over the next 20 days, the number of dead corals increased by 22%. Between 14 and 34 days after the experiment, more than half of the total number of colonies continued to deteriorate, while only six (11%) improved in condition. Light levels are unlikely to have been a factor in bringing on this delayed bleaching response, as average light levels during the first 34 days of recovery were very similar to those experienced during the temperature experiment (Table 1). Eighty-four days after thermal treatment, the condition of the corals appeared to have stabilised: corals had either recovered or died, except for one colony that remained pale. All of the heavily bleached corals and approximately half of the moderately bleached corals (i.e. 51% of the total sample) died. Thus the heavily bleached category (as scored immediately following the temperature treatment) was a good predictor of subsequent mortality in these species, but the ultimate fate of moderately bleached corals was more variable. Nevertheless, in combination, these two categories provide a rough indicator of the classic physiological determination of 'upper thermal limit' (i.e. more than 50% dead, Schmidt-Nielson 1990) under these experimental conditions. The comparatively low incidence of mortality and general lack of a delayed response only 1°C below the winter thermal maximum of *Pocillopora damicornis* (Fig 4.7a), suggests that a discrete threshold exists between tolerable and intolerable temperatures.

The approximate correlation between 'upper thermal limit' and bleaching intensity immediately following stress is further illustrated by the fate of unbleached colonies during the recovery period. Although ten out of 53 colonies were in good apparent health at the end of the temperature experiment, their condition deteriorated 14 – 34 days later with colonies undergoing moderately or heavily bleaching. However, all these colonies made a full recovery 84 days after their return to the field. In contrast, all 15 corals that were heavily bleached at the end of the temperature experiment died.



(b) 32°C

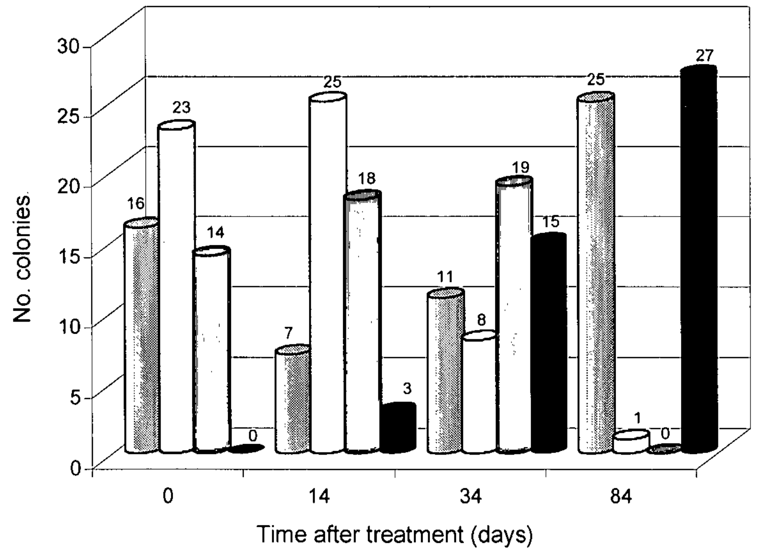


Fig 4.7. Delayed bleaching response of *Pocillopora damicornis* returned to the field after: (a) 5 days at 31°C (n = 47); and (b) 5 days at 32°C (n = 53).

4.5. DISCUSSION

These results confirm the precarious balance between tolerable and intolerable thermal conditions that exists for some tropical corals. The upper thermal limit of Orpheus Island corals in summer, based on experimental bleaching thresholds for 5-day exposure periods, is between 32° and 33°C for *Pocillopora damicornis* and *Acropora elseyi* and is likely to be between 31 and 32°C for *Acropora formosa.* As these limits were determined in the absence of high levels of visible light, a potentially synergistic stress factor (Coles and Jokiel 1978, Jokiel and Coles 1990), these figures may be close to the *maximum* upper thermal limits for these species locally and this exposure period. Mean summer temperatures at Orpheus Island averaged 28.6°C ± 0.9°SD between 1993 and 1998 and temperatures periodically rise above 31°C for short time intervals (GBRMPA 2001). Coles et al. (1976) reported a similar upper thermal limit of approximately 31°C for two species of *Acropora* (*A. formosa* and *A. hyacinthus*) at Enewetak in the Marshall Islands. Enewetak also has mean summer temperatures of approximately 29°C (Coles et al. 1976). In contrast, the upper thermal limit for *P. damicornis* in my experiments is approximately 2°C higher than the limit Coles et al. (1976) reported for this species from Hawaii (mean summer temperature, 26.5°C) for a similar exposure period, and 1°C higher than the limit Glynn and D'Croz (1990) reported for *P. damicornis* from the Gulf of Panama for 14 days of exposure (mean summer temperature, 28°C). Interestingly, the upper thermal limits for P. damicornis is these experiments was 1 – 2°C higher than hose of two other pocilloporid species (*Stylophora pistillata* and *Seriatopora histrix*) on northern GBR (Hoegh-Guldberg and Smith, 1989). These comparisons suggest local adaptations in the thermal resistance of corals that are dependent on ambient summer temperatures. Irrespective of geography, upper thermal limits of thermally sensitive corals appear to be within 2 - 2.5°C of mean summer temperatures.

I found that the threshold between tolerable and intolerable thermal conditions that governs the loss of zooxanthellae is very clearly defined, illustrating the thermal sensitivity of the coral-algal symbiotic relationship. The bleaching response was triggered as an almost 'all or nothing' effect in temperature treatments only 1°C apart. At temperatures 1°C below the 5-day upper thermal limit, very few corals of *Pocillopora damicornis* bleached either immediately following exposure or as a delayed response. These results are consistent with physiological data that show a sharp decline in growth of corals at temperatures only a few degrees above optimum levels. Jokiel and Coles (1977) showed that growth and calcification in *Montipora verrucosa*, *P. damicornis* and *Fungia scutaria* declined rapidly at only 2°C above the temperature of optimal growth. Similarly, Houck et al. (1977) showed that the linear extension of *Porites lobata* decreased to zero at 28.5°C, which was only 1.5°C above the temperature at which its growth peaked.

The vulnerability of corals to bleaching is likely to depend largely on how frequently average daily temperatures of 2 - 2.5°C above mean summer values are exceeded in nature and the duration of such critical thermal exposures. Sea temperature records at Orpheus Island show that average daily temperatures (determined from half-hourly recordings) exceeded 31°C on six days between 1993 and 1998, while daily maxima exceeded 31°C on 76 days and 32° on ten days during this period. Therefore, sensitive coral species like the acroporids and pocilloporids must live either at their thermal tolerance limits for short periods of time or at a fraction of a degree below them for significant periods of time during summer. This will almost certainly make these genera highly vulnerable to any kind of additional stress during 'normal' summer conditions.

This is the first reported experimental determination of between-season differences in upper thermal limits of corals. My results suggest that limited natural acclimatisation to temperature may take place seasonally in some coral species. The winter maximum upper thermal limit for *Pocillopora damicornis* for a 5-day exposure is between 31° and 32°C or 1°C lower than its summer limit (Fig 4.5). The reduced thermal tolerance of *P. damicornis* in winter is not explained by differences in light conditions between summer and winter. Winter light levels of 1513 ± 59 $\mu E.m^{-1}.s^{-1}$ were intermediate between those experienced during the two summer experiments, as were the light levels in the 14 days prior to each experiment, yet the winter bleaching threshold was lower. Furthermore, light intensities between the two summer experiments were quite different at 1229 ± 566 and 1864 ± 133 $\mu E.m^{-1}.s^{-1}$ (Table 1), yet the transition temperature for bleaching remained at 33°C in both summer experiments (Figs 3a, 4a).

In monitoring the recovery of experimentally heated corals, my results also show a substantial delay in the bleaching response of many colonies (Fig 4.7). Overall, this apparent delay was evident in the deterioration of nearly half the colonies in the first 34 days after thermal treatment, including colonies in good health after the 5-day thermal stress period. The delay in response has important implications for the interpretation of natural coral bleaching events. These results imply that factor(s) causing a natural bleaching event may have been at critical levels a fortnight to a month prior to the onset of large scale bleaching. Furthermore, field monitoring to determine the full extent of bleaching should be continued for a month or so after a stress event to document all colonies that may bleach or die.

The lack of difference in the thermal resistance of *P. damicornis* and *A. elseyi* between the reef flat and slope (Fig 4.4) was unexpected. Reef-flat corals, which normally experience a highly variable temperature regime at Orpheus Island (up to 7°C over 6 hours), might be expected to have a higher upper thermal limit than their reef-slope counterparts, which normally experience considerably less diurnal variation (<3°C/day, Chapter 3). The lack of habitat difference implies that daily, short-term variations in thermal history have limited potential to induce natural temperature acclimatisation in corals. In addition, the reef slope corals would have experienced comparatively higher UV light in our experimental tanks than at their site of origin, whereas reef flat corals would have experienced approximately equivalent levels. The similar bleaching responses of reef slope and reef flat corals suggest that UV radiation levels were not high enough to cause a synergistic stress (e.g. Gleason and Wellington 1993) during these experiments. The lack of difference in the thermal resistence of *P. damicornis* colonies collected from Pelorus and Orpheus Islands was also unexpected given the quite different responses of colonies from these two sites during a mild bleaching event in 1994 (RB, unpub data). Factors other than temperature may have contributed to the differential in situ bleaching at these two sites.

In summary, these results highlight that upper thermal limits in coral populations at Orpheus Island, as in other reef regions, are only slightly above ambient mean summer temperatures, although a small amount of seasonal variation in upper thermal limits can take place. Seasonal variation in upper thermal limits suggests that coral species may have some potential to acclimatise to elevated temperatures. For temperatures inducing moderate levels of stress, a substantial delay may exist before symptoms of bleaching become evident. Moreover the severity of bleaching can continue to increase for at least four weeks after removal of the thermal stress. This delayed response must be taken into account in evaluating potential sources of stress in natural bleaching events.

Chapter 5

Thermal acclimation in reef corals: a short-term experimental investigation

Fringing reef around Brisk Island (18.78°E, 146.53°W) in the Palm Island region showing extreme levels of bleaching. Hot, still conditions persisted in this area for most of February 1998. Photo courtesy GBRMPA.

5.1. ABSTRACT

Determining whether corals can increase their temperature tolerances through thermal acclimation is a key issue in predicting if corals can cope with anticipated temperature increases associated with global climate change. In this Chapter, I investigate whether short-term (10-day) acclimation at sub-lethal temperatures increases the upper thermal tolerances of two species of scleractinian coral, *Pocillopora damicornis* and *Porites cylindrica*. My results indicate that neither species is able to increase their thermal tolerance limits beyond existing summer limits and that exposures to high acclimation temperatures (1 – 2°C below upper thermal limits) have a compounding and negative effect on coral health. Thus the higher the acclimation temperature, the higher the level of bleaching and the lower the post-treatment survival of corals following exposure to experimental temperature treatments. The inability of corals to raise their upper thermal limits could be because: (i) any biochemical/physiological changes as a result of high temperature took place rapidly and equally in both acclimated and unacclimated corals as they were being raised to their respective stress temperatures, and either (ii) longer-term (weeks – months) biochemical/cellular responses did not have sufficient time to develop, or (iii) these two species have reached their thermal acclimation limit. Continued loss and breakdown of zooxanthellae for up to six weeks after removal of thermal stress suggests that either a positive-feedback mechanism may be involved in bleaching (dysfunction zooxanthellae themselves cause a chain-reaction), or the initial stress causes the long-term production of a chemical resulting in a continued slow breakdown of symbiosis and ejection of zooxanthellae.

5.2. INTRODUCTION

A recent risk assessment of the impact of global climate change on coral reefs has highlighted the thermal sensitivity and vulnerability of reefs (Hoegh-Guldberg 1999). Based on the four best global climate models, Hoegh-Guldberg (1999) argues that bleaching, of the severity of the 1998 event (Chapter 2, Berkelmans and Oliver 1999) or worse, is likely to be an annual occurrence on the Great Barrier Reef (GBR) by the year 2030 and for corals in most other reef regions by the year 2050. However, a key assumption in this assessment is that the upper thermal limits of corals are unlikely to increase at a rate sufficient to track predicted changes in the thermal environment of corals. The fact that corals of the same species have different thermal tolerances in different parts of the world (e.g. Coles et al. 1976, Marcus and Thorhaug 1981, Chapter 4) and that reefs with similar communities have different bleaching thresholds (Chapter 5) indicates that thermal adaptation can, and has, taken place over a number of spatial scales. Given that many species of coral currently live close to their upper thermal limits (e.g. Jokiel and Coles 1990, Brown 1997a, Berkelmans and Willis 1999, Chapter 4) and the projected increases in magnitude and return time of temperature extremes (Pittock 1999, 2000), it is doubtful that sufficient time is available for genetic adaptation to occur to keep pace with these changes. Increased thermal tolerance will need to come about by other means, such as dispersal of resistant populations, variation in the combination of symbionts and hosts, and/or acclimatization of corals and their symbionts.

Although corals and their zooxanthellae are known for their remarkable ability to acclimatize to changing light conditions (Chalker et al. 1988, Brown et al. 1999), there is little evidence available to assess their ability to acclimatize to increasing temperature extremes. The upper thermal limits of *Pocillopora damicornis* in the inshore central GBR were 1°C warmer in summer than in winter (Chapter 4, Berkelmans and Willis 1999), indicating that seasonal thermal acclimatization does take place. However, these results do not necessarily mean that corals can acclimatize beyond existing summer limits. Experimental evidence indicating that some corals may be capable of such resistance acclimation comes from work by Coles & Jokiel (1978) who found increased survivorship in *Montipora verrucosa* stressed at 30 and 32°C after acclimation at 28°C, compared to lower acclimation temperatures. However, these early studies have so far not been extended to investigate acclimation in other coral species, or the effects of varying acclimation times and temperatures.

The time required for temperature acclimatization is generally considered to be short (days to weeks). This is because acclimatization mechanisms generally involve biochemical changes which occur over relatively short time intervals (Hochaka and Somero 1984, Brown 1997b, Gates and Edmunds 1999, Feder and Hofmann 1999). The synthesis of heat shock proteins (to maintain protein integrity) and the regulation of enzymes (e.g. to ameliorate the buildup corrosive oxygen radicals), in particular, are thought to be important potential mechanisms in thermal acclimatization of corals (Gates and Edmunds 1999). As biochemical responses from both these mechanisms generally occur within hours of exposure to heat stress (Walsh and Somero 1981, Hayes and King 1995), it could be hypothesized that any acclimation potential may be found within similar timeframes, or at least within several days of pre-exposure to warm temperatures.

In this Chapter I describe an experimental investigation to test whether ten days of acclimation at sub-lethal temperatures is sufficient to increase the upper thermal limits of two species of scleractinian coral, *Pocillopora damicornis* and *Porites cylindrica.*

5.3. METHODS

5.3.1. Experimental Protocols

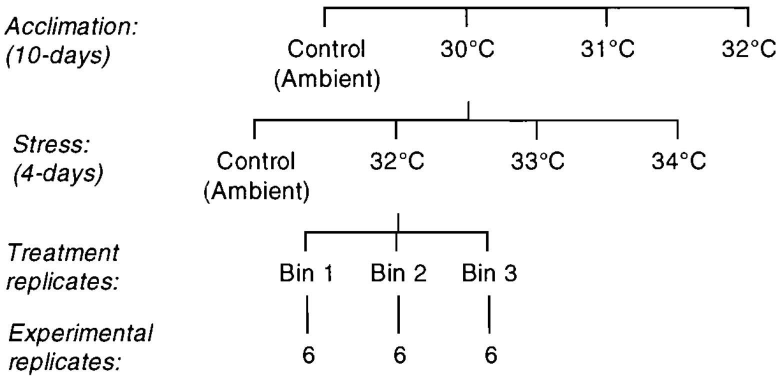
Thermal acclimation was investigated in two species of scleractinian corals that had contrasting sensitivities to bleaching in an earlier pilot experiment. Experiments were carried out at the Orpheus Island Research Station (Lat. 18.34°S, Long. 146.29°E), located on the inshore Great Barrier Reef near Townsville, Australia. Separate experiments were conducted for each species: *Porites cylindrica* (Dana, 1846) between 21

February and 7 March 1996; and *Pocillopora damicornis* (Linneus 1758) between 13 - 28 March 1996.

Experiments were conducted in 30-litre plastic bins placed on cement blocks in 2.4m-diameter round fibreglass tanks filled with seawater to just below the margin of the bins. Four fibreglass tanks were used as temperature treatments, each containing 3 plastic bins (treatment replicates). Temperature treatments were randomly allocated to tanks and bins randomly allocated within temperature treatments. Tanks were filled with approximately 1500 litres of seawater, each fitted with two 3KW electric heating elements. Filtered seawater from the upper reef slope in Pioneer Bay at Orpheus Island (~3 m depth) was supplied continuously into each large tank via calibrated nozzles at a rate of approximately 11 $l\text{-min}^{-1}$. A submersible pump in each tank distributed water to each of the three bins at a balanced flow rate of approximately 3.6 $l.\text{min}^{-1}.\text{bin}^{-1}$, from which water overflowed to waste. Water from the bins did not come into contact with water from the tanks. The pressure of the water entering the tanks and bins via directed nozzles ensured that water was well mixed and temperatures remained even throughout the tanks and bins. Spot checks confirmed that variation in temperature between bins within a tank was less than 0.1°C. Air was supplied via air stones to each bin to ensure the water remained well oxygenated. Tanks were located under a clear polycarbonate roof which prevented dilution by rainwater and blocked >99% of ultraviolet light. In addition, shade cloth was fixed under the roof to reduce photosynthetically active radiation (PAR) to approximately 30 – 40 % of ambient surface PAR (Fig 5.1). PAR was monitored just above the water surface in the middle of each tank as a measure of light available to experimental corals (10cm below the surface) and above the shade structure as a measure of ambient light. Temperatures in the heated tanks were controlled automatically via a computerized process control system. Experimental temperatures were monitored in one bin per tank at 5-minute intervals using data loggers throughout each experiment. Temperature control precision was within 0.4°C SD of target temperature in all temperature-controlled treatments (Fig 5.2).

Corals were collected from the upper reef slope in 2-3m of water over an area of approximately 2km by haphazardly snipping 7-8cm branches off parent colonies. Colonies were sampled randomly and were representative of the populations found at this location. For both *P. damicornis* and *P. cylindrica*, care was taken to ensure that each fragment contained at least 4 branches so that they could be sub-sampled during the recovery phase without removing more than 40% of the total experimental colony.

Corals were tagged, placed on wire racks and allowed to acclimatize to tank conditions for 5 days prior to experimentation. For *P. damicornis*, 288 corals were allocated as to treatments as follows:



Stress temperatures were chosen because previous experiments (Chapter 3, Berkelmans and Willis, 1999) showed that the upper thermal limit for this species is between 32° and 33°C. Acclimation treatments were chosen 1°C apart up to an anticipated maximum sub-lethal limit of 32°C. Corals were raised to acclimation temperatures and held there for 10 days. After acclimation, 6 corals from each acclimation treatment were randomly allocated to each of 3 bins in each of 4 stress treatments. Tanks were raised to their respective stress temperatures for 4 days, after which they were cooled to ambient temperature and monitored for recovery or demise over a period of 12 weeks. To avoid thermal shock, care was taken to ensure corals were not treated to temperature changes of more than 0.5°C/hr (both in heating and cooling), a rate less than that commonly encountered in their natural environment (Chapter 3).

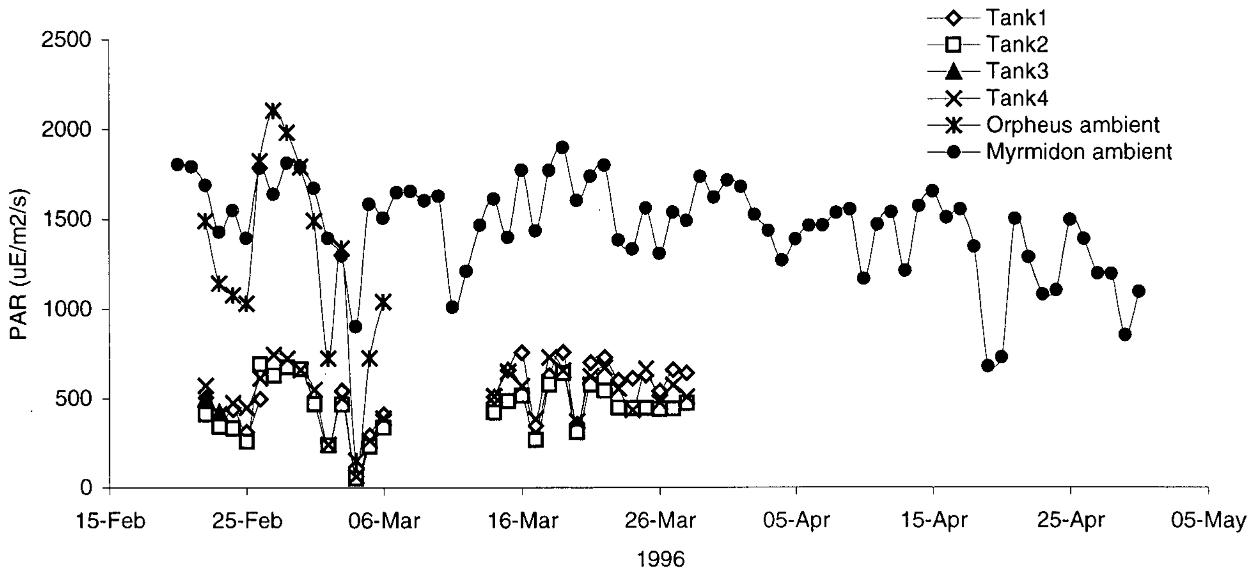


Fig 5.1 Temperature control precision in acclimation experiments. Date are means (± SD).

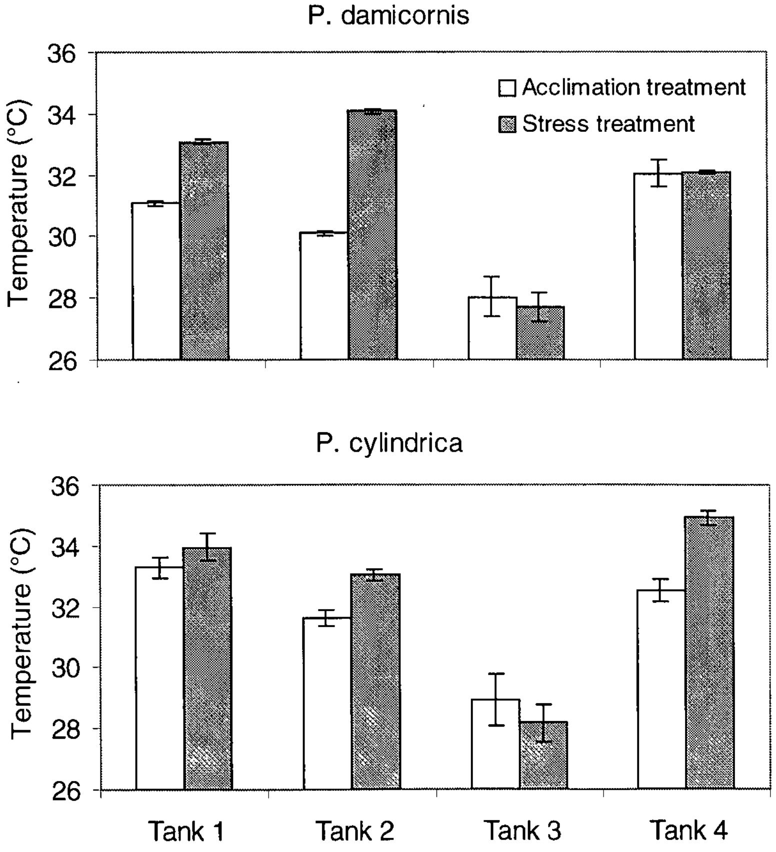
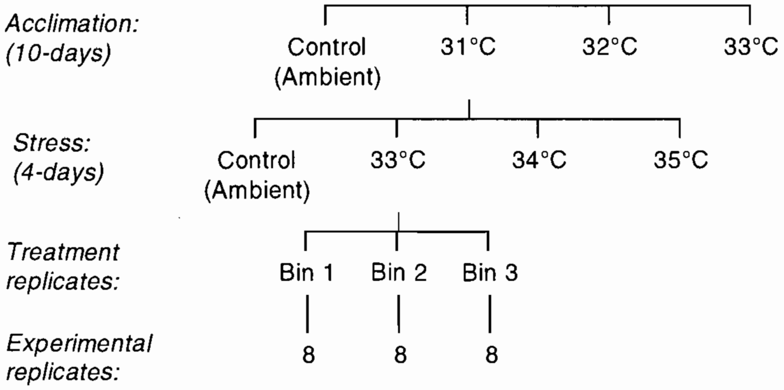


Fig 5.2 Ambient and tank surface light conditions at Orpheus Island during experiments and longer-term ambient light levels at Myrmidon Reef. Myrmidon data courtesy of the Australian Institute of Marine Science.

For *P. cylindrica*, a similar treatment regime was imposed on 384 corals, according to the experimental design:



Stress treatments between 33° and 35°C were chosen because a pilot experiment indicated that the upper thermal limit for this species is between 33° and 35°C. Acclimation treatments were chosen 1°C apart up to an anticipated maximum sub-lethal limit of 33.5°C.

5.3.2. Measurements and analysis

Two response variables were used to measure experimental outcomes: a visual estimate of the degree of bleaching and zooxanthellae density. For the visual estimates of bleaching, corals were allocated to one of three categories based on appearance: 'normal' - no visible loss of colour; 'moderate bleaching' - corals pale, but still with a significant amount of colour; 'heavy bleaching' - corals mostly white; and 'dead' - >50% tissue mortality (Chapter 4). In the case of *P. cylindrica*, stressed corals did not necessarily move progressively between categories with increasing levels of stress. This species reacted to heating stress by retracting its polyps and producing mucous sheaths, which became fouled with sediment and, after ~ one week, also with turfing algae. This condition is commonly encountered in *Porites* species which commonly produce mucus sheaths in response to sediment, temperature or salinity stress and such sheaths can last for days to months (Kato 1987, Coffroth 1988). Microscopic examination was required to determine whether corals were alive or dead. Sometimes corals went into this state after bleaching commenced, but at other times, it happened before visible signs of bleaching were evident. Because of this state, the condition 'heavily bleached' in the *P. cylindrica* experiment was replaced by 'fouled' – corals covered in mucus and fouled with sediment and/or algae.

Zooxanthellae densities were measured before acclimation, after stress treatment, and 3, 6 and 12 weeks after recovery for *P. damicornis.* For *P. cylindrica,* densities were measured before acclimation, after stress and 3 and 9 weeks after recovery. Zooxanthellae densities were determined from 4 branches (2 - 3cm) snipped from corals in each acclimation and temperature treatment. Because of the requirement to sub-sample individual corals a number of times and to prevent sampling individual colonies to <40% of their original size, samples were not replicated at the treatment replicate level (bins). Coral tissue was removed with a WaterPik (Johannes and Wiebe 1970) and samples prepared according to the methods outlined in (Chapter 4, Berkelmans and Willis 1999). Zooxanthellae were classed as 'normal' if they appeared round, 10-12μm in size and olive-green in colour, and 'degenerate' if they appeared shrivelled, <10μm in size and brown in colour (Yonge and Nicholls 1931b, Taylor 1968).

Categorical data of the physical condition of corals were analysed for differences in the counts of healthy corals among the factors 'acclimation', 'stress' and 'bin' using log-linear modelling. To test for goodness-of-fit of models, the likelihood ratio statistic (G^2) was used in preference to the Chi-square statistic because of it's additive properties (similar to sums of squares in ANOVA) and because it performs better under low cell frequency counts (Tabachnick and Fidell 1996). To obtain the simplest possible model capable of adequately explaining the observed variation, a backward step-wise model selection process was employed according to procedures available in the statistical package SPSS. The starting point in these procedures is a full hierarchical model and, through an iterative process, the least significant term is eliminated in a stepwise fashion from the highest order effects (interactions) to the lowest until no more terms can be excluded from the model without significantly weakening its predictive power (SPSS 1997). Because of the relatively small sample size, model significance through each step was tested at $\alpha = 0.1$ (Tabachnick and Fidell 1996). For both species, the final model consisted only of the main effect terms 'acclimation' and 'stress'; interaction effects were not significant (Table 5.1). The final models were examined in more detail using SPSS' General Loglinear Analysis procedures by comparing parameter estimates (log-odds ratios) and 'odds ratios' of individual terms in the models. In this context, 'odds' is defined as the ratio of the probability of an event occurring, to that of it *not* occurring. An 'odds ratio' is the ratio of two odds, while a 'log-odds ratio' is the natural logarithm of an odds ratio (SPSS 1997).

Data for zooxanthellae counts are presented as means ± SE and were analysed by a 3-factor ANOVA (Type 1, $\alpha = 0.05$) to test the null hypothesis that acclimation, stress or their interaction had no effect on the final zooxanthellae density at each sampling time. Data were log + 1 transformed to correct for heterogeneity of variance among treatments prior to analysis. As the interaction of stress and acclimation were significant in both species at all sampling times, custom hypothesis tests were constructed to examine the nature of significant differences between means of unacclimated and acclimated corals within each stress treatment and between unstressed and stressed corals within each acclimation treatment and at each sampling time (SPSS 1997).

5.4. RESULTS

5.4.1 *Pocillopora damicornis*

Ten days of acclimation at temperatures between 30 and 32°C did not increase the upper thermal limit of *Pocillopora damicornis*, nor did it improve the post-stress survival rate of stressed corals. Instead, colonies acclimated at these temperatures bleached more readily when raised to stress temperatures than colonies held at ambient temperatures during the acclimation period (acclimation control). For example, approximately half of the corals acclimated at 31°C and all corals acclimated at 32°C were moderately or heavily bleached when stressed at 32°C (Fig 5.3). However, only 4 out of 18 unacclimated colonies were moderately bleached in the same stress treatment. All corals in the 30°, 31° and 'Control' acclimation treatments made a full recovery 6 weeks after being stressed at 32°C (Fig 5.3, 5.4). In contrast, two thirds of colonies in the 32°C acclimation treatment died after the 32°C stress treatment. The ten-day acclimation treatment at 32°C was thus deleterious to the health of *P. damicornis* and is more appropriately considered a stress.

At stress temperatures of 33°C and 34°C, bleaching rates and intensities increased dramatically across all acclimation treatments and all corals eventually died. Loglinear analysis revealed that none of the interactions of the factors 'stress', 'acclimation' or 'bin' were significant and that a reduced model based on the main effects of 'stress' and 'acclimation' could adequately model the survivorship of corals after 12 weeks recovery ($p = 1$, Table 5.1).

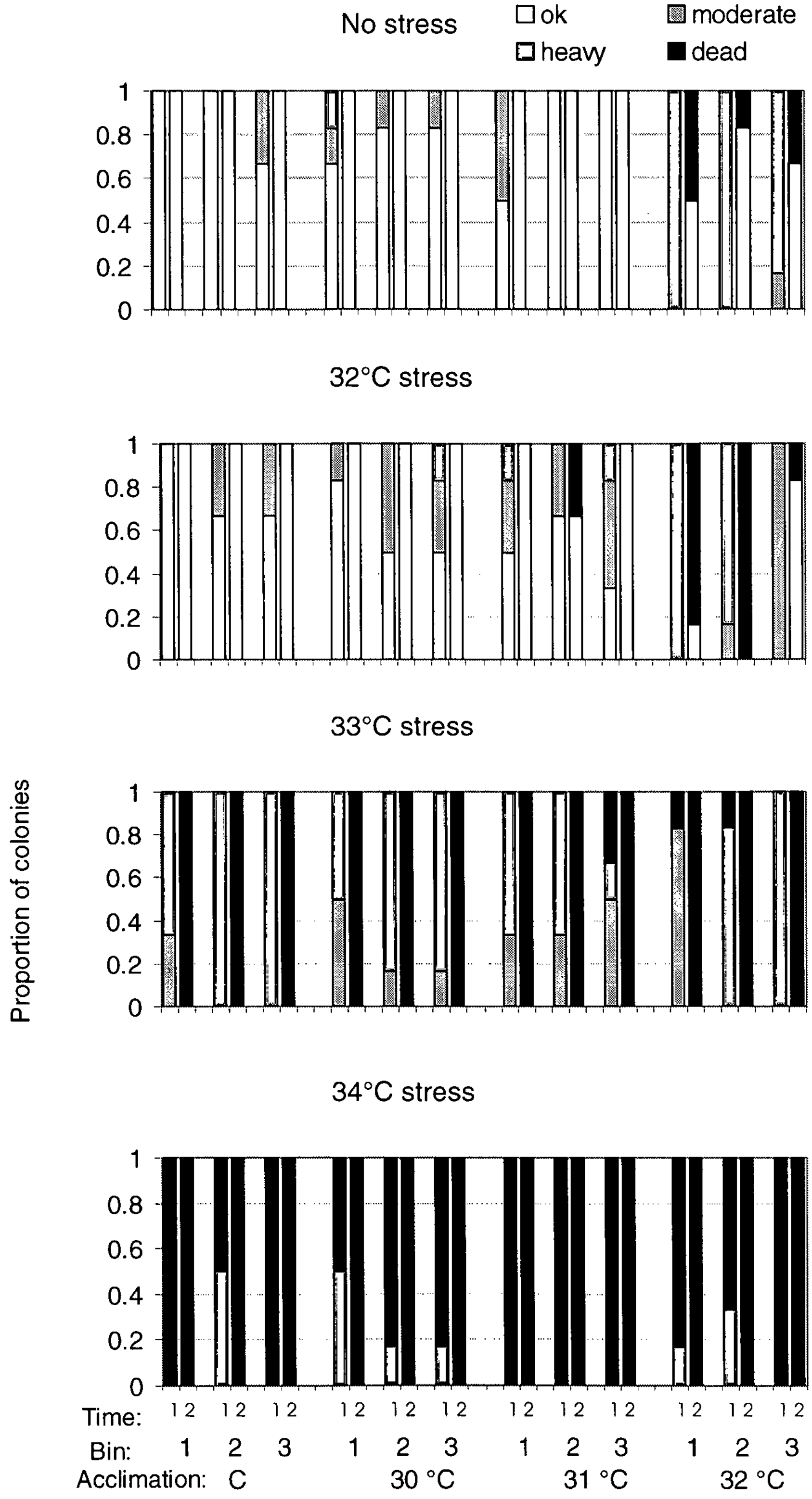


Fig 5.3. Proportion of *Pocillopora damicornis* colonies in each bleaching category (see text for definition of categories) immediately after (t1) and 12 weeks after stress treatment (t2) for each of three treatment replicates (bins), four acclimation treatments and four stress treatments (n = 6 colonies per treatment combination).

Table 5.1. Results of backward stepwise selection of a log-linear model best able to explain the observed variation in the number of normal (healthy) colonies of *Pocillopora damicornis* and *Porites cylindrica* following acclimation and stress treatment.

	P. damicornis				***P. cylindrica***			
k-way interactions	G^2	DF	Prob[1]		G^2	DF	Prob[1]	
1	181.155	8	0		134.709	8	0	
2	4.721	21	.9999		20.366	21	0.4982	
3	5.233	18	.9984		5.001	18	0.9989	
Deleted terms from final model	G^2 change	DF	Prob[2]	Step	G^2 change	DF	Prob[2]	Step
STRESS*ACCLIMAT*BIN	5.233	18	.9984	1	5.001	18	.9989	1
STRESS*ACCLIMAT	1.874	9	.9933	2	14.508	9	.1054	5
STRESS*BIN	.869	6	.9901	3	5.298	6	.5063	4
ACCLIMAT*BIN	1.978	6	.9217	4	.561	6	.9970	2
BIN	.494	2	.7812	5	.571	2	.7516	3
Final model terms	G^2	DF	Prob[3]		G^2	DF	Prob[3]	
STRESS and ACCLIMAT	10.4473	41	1.000		25.9381	41	.968	

[1] Null hypothesis: K-way interactions are not significantly different from zero

[2] Null hypothesis: A reduced model without this term will not significantly affect the overall model

[3] Null hypothesis: The final reduced model is not significantly different from the full model

Table 5.2. Log-linear model parameter estimates for *Pocillopora damicornis.*

Parameter	Log odds ratio	SE	Odds ratio	Z-value	Lower 95% CI	Upper 95% CI
Constant	2.1305					
no acclim	0.6931	0.2886	1.99	2.4	0.13	1.26
30° acclim	0.6931	0.2886	1.99	2.4	0.13	1.26
31° acclim	0.636	0.2915	1.89	2.18	0.06	1.21
32° acclim	0					
no stress	0.1292	0.18	1.14	0.72	-0.22	0.48
32° stress	0					

An examination of the parameter estimates (log-odds ratios) of the reduced model shows that the control and 31°C acclimation treatments have equal log-odds ratios, indicating that odd of corals surviving the control acclimation treatment is the same as the odds of corals surviving the 30°C acclimation treatment ($e^{0.6931-0.6931} = 1$, Table 5.2). Equally, the odds of corals surviving the 30°C acclimation treatment is almost the same as surviving the 31°C acclimation treatment. However, the odds of corals surviving the 31°C acclimation treatment is on average 1.89 ($e^{0.636}$) greater than the corresponding odds of surviving the 32°C acclimation treatment. Corals in the stress control treatment had between 0.8 and 1.6 times (refer upper and lower 95% CI for 'no stress' in Table 5) more chance of surviving compared to those in the 32°C stress treatment. Because this analysis included only corals in the control and 32°C stress treatments (there were no surviving corals at 33° or 34°C), none of the parameters in the 'stress' treatment featured in the model.

Examination of zooxanthellae densities over time confirms that ten days of acclimation at temperatures between 30 – 32°C did not reduce the loss of zooxanthellae following exposure to stress temperatures. Stress temperatures of 33°C and higher had a rapid and significant impact on zooxanthellae density, a state from which corals could not recover (Fig 5.4). When stressed at 32°C, only those corals that had also been subjected to an additional 10 days at 32°C during acclimation failed to recover from their initial zooxanthellae loss. The significant interaction between stress and acclimation due to this treatment combination thus indicates a negative, rather than a positive, effect of acclimation on zooxanthellae density. A comparison of the trajectories of zooxanthellae densities over time of all 33°C stressed corals, and also the treatment combination '32°C acclimation + 32°C stress', indicates that a continued loss of zooxanthellae took place up to 6 weeks after cessation of stress. Although corals did not recover in the '33°C stress + no acclimation' and '32°C acclimation + 32°C stress' treatments, the trajectories in several treatments ('32°C acclimation + no stress', '30°C acclimation + 32°C stress' and 31°C acclimation + 32°C stress' treatments) indicate that corals are still capable of recovering, even with very low levels of zooxanthellae (Fig 5.4).

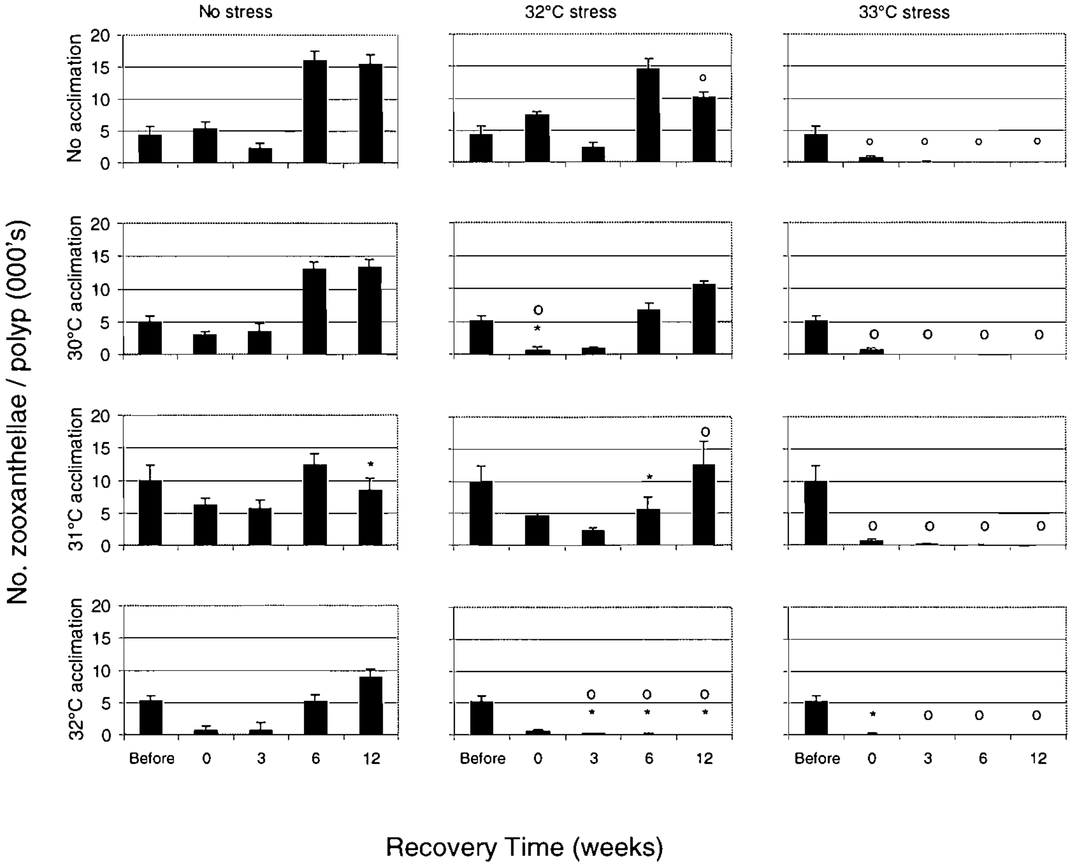


Fig 5.4. Mean zooxanthellae densities of *Pocillopora damicornis* ± SE (4 colonies) before and immediately after experimentation, and after 3, 6 and 12 weeks of recovery in each of 4 acclimation treatments (Control/No acclimation, 30°C, 31°C and 32°C) and 3 stress treatments (Control/No stress, 32°C and 33°C). Data for 34°C stress treatments are not shown as most colonies were dead immediately after experimentation. Circles (o) denote significant difference (α = 0.05) between stress and control treatments at each time interval. Stars (*) denote significant difference between acclimation and control acclimation treatments at each time interval.

The lowest zooxanthellae density found in any treatment where corals still recovered was 12% of pre-experiment levels. This occurred immediately after experimentation in the '30°C acclimation + 32°C stress' treatment. Zooxanthellae density remained low for a further 3 weeks, but showed a sharp recovery after 6 weeks. At 12 weeks, zooxanthellae densities had surpassed pre-stress levels, but were still significantly lower than control colonies at the same time. The rapid increase in zooxanthellae densities of other acclimation treatments in the 'no stress' group after 6 weeks recovery corresponds to a decrease in ambient light from a mean of 1602 $\mu E.m^{-2}.s^{-1}$ (10am – 3pm PAR) during the 10-day acclimation experiment to 1230 $\mu E.m^{-2}.s^{-1}$ (10am – 3pm PAR) during the last 10 days of the recovery period prior to the last sampling occasion (Fig 5.2). This decrease in light follows a seasonal decrease in ambient light intensity from summer to winter (February – July).

Densities of degenerate zooxanthellae remained below 10% of the total number of zooxanthellae before experimentation and in treatment controls. However, at stress temperatures of 32°C, the proportion of degenerate zooxanthellae increased in all acclimation treatments, reaching a peak of 31% of the total zooxanthellae population in the 32°C acclimation treatment (Fig 5.5). At stress temperatures of 33°C, the proportion of degenerate zooxanthellae reached a peak of 67% in the 30°C acclimated corals immediately after stress and remained high in all acclimation treatments for at least 6 weeks before all corals died some time prior to the 12 week sampling period.

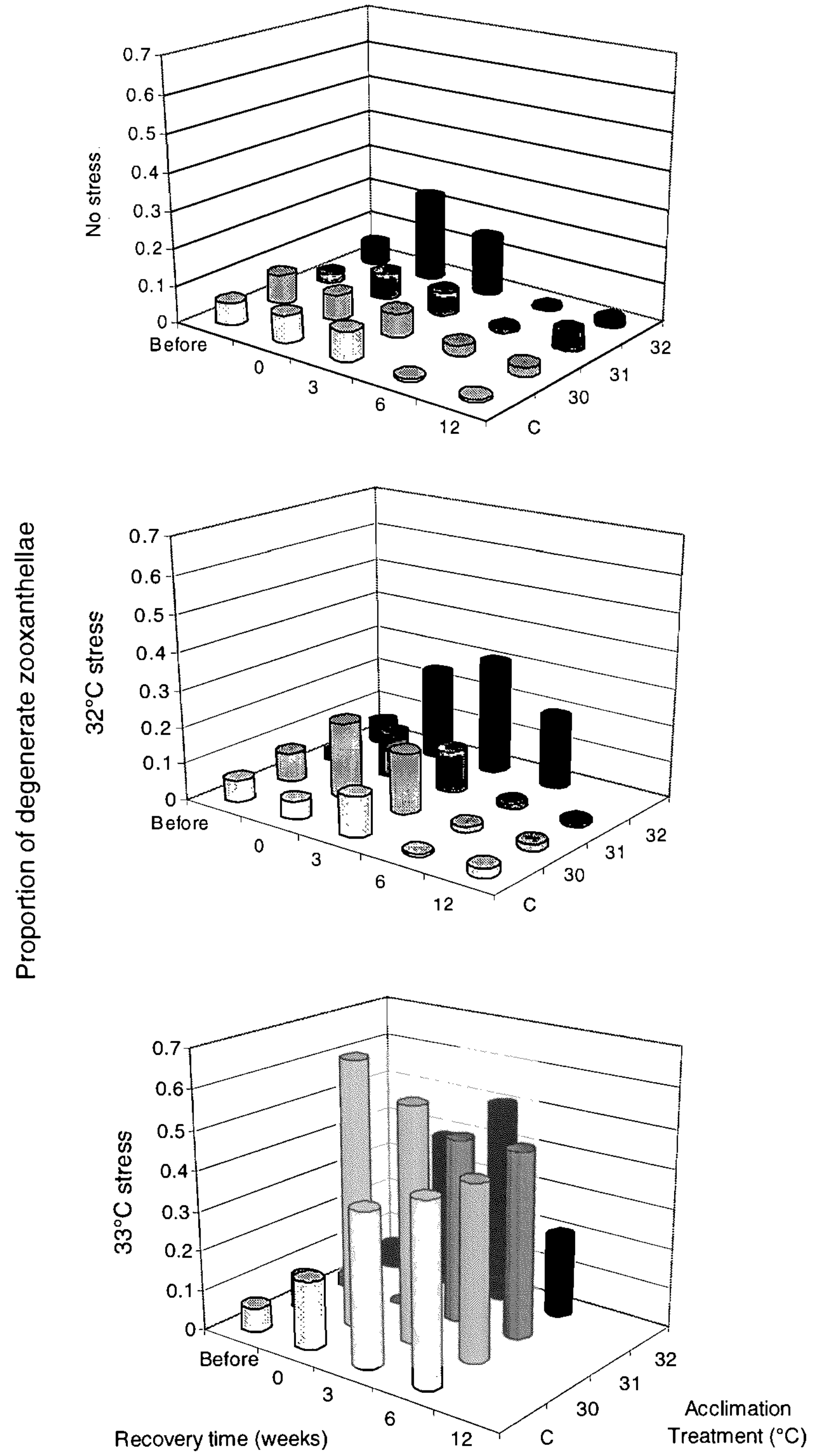


Fig 5.5. Proportion of degenerate (unhealthy) to normal zooxanthellae before and immediately after experimentation, and 3, 6 and 12 weeks after recovery in each of 4 acclimation treatments (Control/No acclimation, 30°C, 31°C and 32°C; each group a different shade in the bars) and 3 stress treatments (Control/No stress, 32°C and 33°C). Data for the 34°C stress treatments are not shown as most colonies were dead immediately after experimentation.

5.4.2. *Porites cylindrica*

Porites cylindrica colonies also suffered increased levels of bleaching, fouling and mortality with increasing stress and acclimation temperatures. In the absence of stress, corals that had been exposed to 10 days in control or 31.5°C acclimation treatments did not bleach or foul immediately after experimentation (Fig 5.6). However, at acclimation temperatures of ≥ 32.5°C, or at stress temperatures of ≥ 33°C, most corals bleached or showed symptoms of stress by retracting their polyps, becoming covered with mucus or fouled with sediment immediately after experimentation. In the 34°C and 35°C stress treatments, all corals were fouled immediately after the experiment, irrespective of acclimation treatment. Corals were able to maintain this state for the entire 9-week post-treatment observation period by which time they were completely covered with turfing algae. Microscopic examination revealed that many corals were still alive and contained apparently healthy zooxanthellae. During the course of the 9-week post-treatment observation period, some corals shed their mucus sheaths and recovery fully, while others died. In the 'control acclimation + no stress' treatments, two corals died and two became fouled during the last few weeks of the 'recovery' phase, indicating that tank conditions for this species were probably less than ideal during these last few weeks. This decline in coral health is coincident with a reduction in water flow into the recovery tank, which was first evident at the time of the last sampling on 10/5/96.

As with *P. damicornis*, loglinear analysis of the number of healthy *P. cylindrica* colonies at the end of the 9-week recovery period indicated that none of the interactions of the factors 'stress', 'acclimation' or 'bin' were significant and that a reduced model based on the main effects of 'stress' and 'acclimation' could adequately explain the variation in the data (p = 0.968, Table 5.1). Examination of the parameter estimates shows that the odds of having healthy corals following the control acclimation treatment is 6.7 times greater than the corresponding odds following 10-days at 33.5°C (Table 5.3). Similarly, corals acclimated at 31.5°C for ten days have on average 4.83 times more chance of being healthy than to those acclimated at 33.5°C, while the odds of healthy corals following 32.5°C acclimation are 1.83 times those of the 33.5°C acclimation treatment (Table 5.3). Parameter estimates for the stress treatments show that unstressed corals and coral stressed at 33°C, have on average 10.8 and 5.4 times more chance (respectively) of being healthy than those stressed at ≥ 34°C. These data therefore indicate that high acclimation and stress temperatures both contribute to stress and/or mortality and that acclimation does not help corals cope better with thermal stress.

Zooxanthella densities also indicate that acclimation has no ameliorating influence on the expulsion of zooxanthellae when *P. cylindrica* is subjected to thermal stress. In fact, unacclimated corals lost significantly fewer zooxanthellae in all stress treatments after 3 weeks than those acclimated for ten days, irrespective of the acclimation temperature (Fig 5.7). Zooxanthellae densities also indicate that in some treatments (eg 33.5°C acclimation + 33°C stress), corals continued to lose zooxanthellae for up to 9 weeks after thermal stress whereas in other treatments (eg. 31.5°C acclimation + 33°C stress) corals zooxanthellae densities declined initially, but showed substantial recovery 9 weeks after treatment (Fig 5.7).

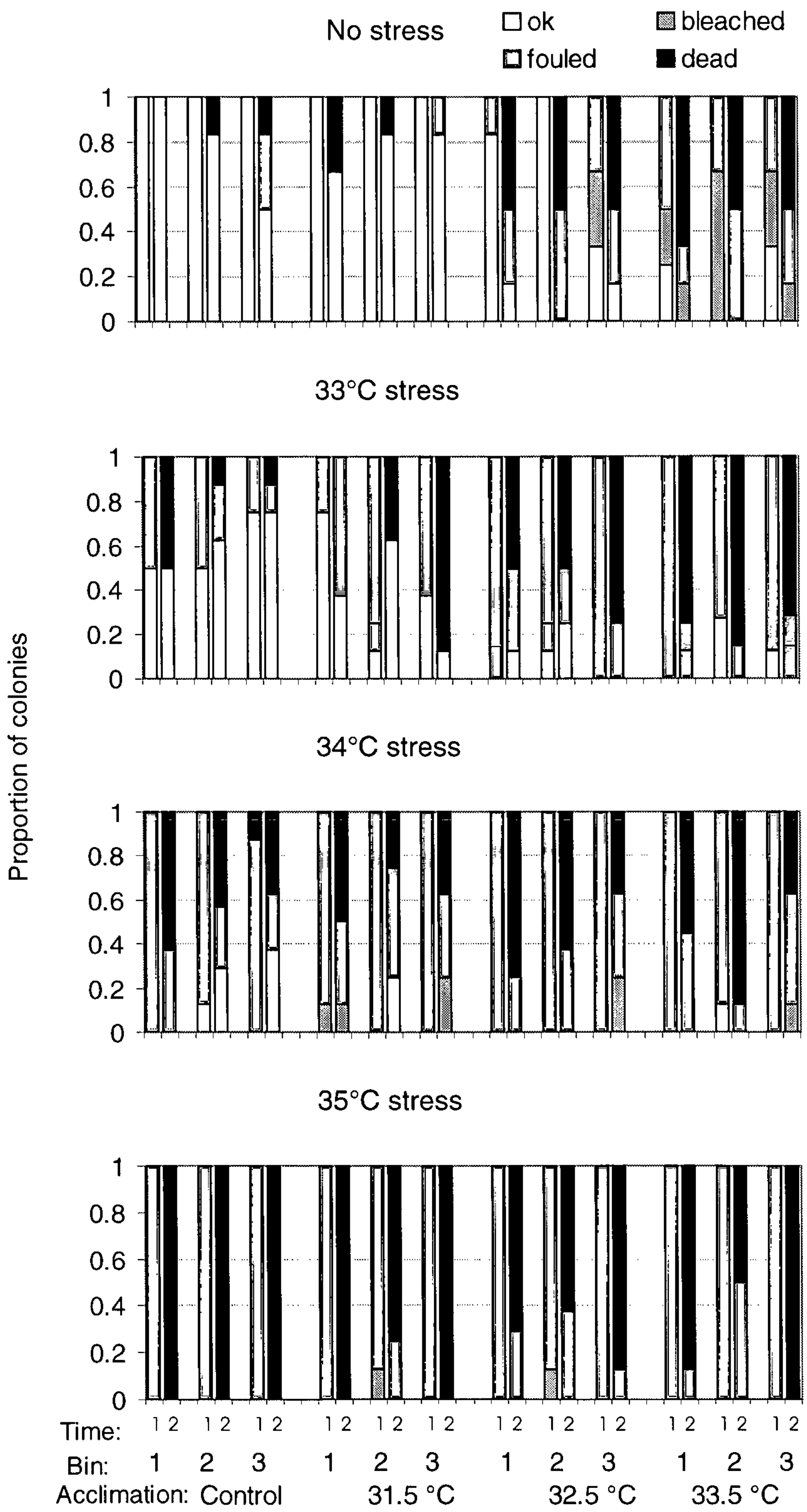


Fig 5.6. Proportion of *Porites cylindrica* colonies in each bleaching category (see text for definition of categories) immediately after (t1) and 9 weeks after stress treatment (t2) for each of three treatment replicates (bins), four acclimation treatments and four stress treatments (n=8 colonies per treatment combination).

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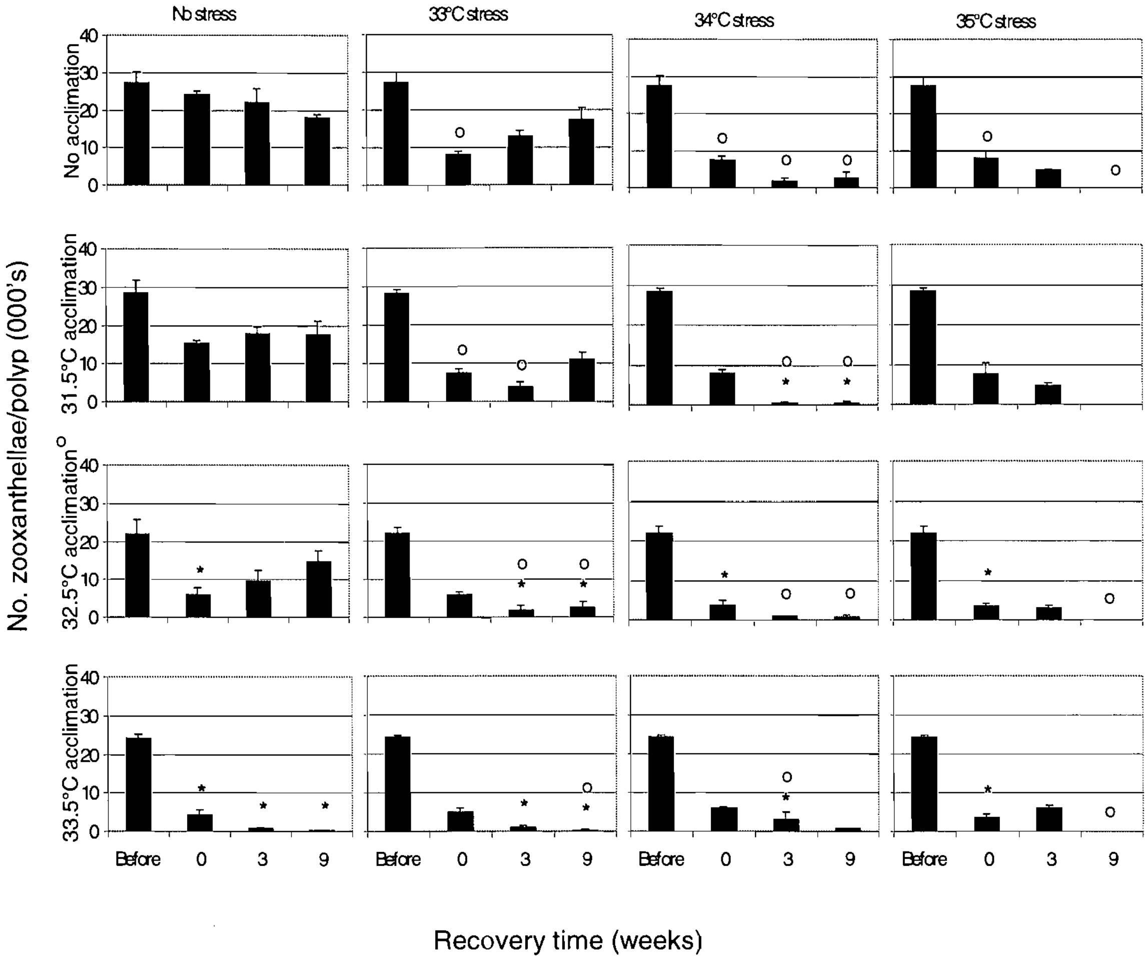


Fig 5.7. Mean zooxanthellae densities of *Porites cylindrica* (± SE, n = 4 colonies) before and immediately after experimentation, and after 3 and 9 weeks of recovery in each of four acclimation treatments (Control/No acclimation, 31.5°C, 32.5°C and 33.5°C) and four stress treatments (Control/No stress, 33°C, 34°C and 35°C). Circles (o) denote significant difference ($\alpha = 0.05$) between stress and control treatments at each time interval. Stars (*) denote significant difference between acclimation and control acclimation treatments at each time interval.

Table 5.3. Log-linear model parameter estimates for *Porites cylindrica*.

Parameter	Log odds ratio	SE	Odds ratio	Z-value	Lower 95% CI	Upper 95% CI
Constant	-1.0531					
no acclim	1.8971	.4378	6.67	4.33	1.04	2.76
31.5°C acclim	1.5755	.4485	4.83	3.51	.70	2.45
32.5°C acclim	.6061	.5075	1.83	1.19	-.39	1.60
33.5°C acclim	0					
no stress	2.3795	.4674	10.80	5.09	1.46	3.30
33°C stress	1.6864	.4868	5.40	3.46	.73	2.64
34°C stress	0					

5.5. DISCUSSION

Resistance acclimation is often used to refer to the ability of an organism to increase its thermal tolerance levels (Precht 1958). Resistance acclimation, as well as capacity acclimation (acclimation of physiological processes such as respiration, photosynthesis etc.), are common in organisms at all taxonomic levels (Precht 1958, Prosser 1973, Hochacka and Somero 1984). Therefore, the distinct lack of resistance acclimation in the two experimental coral species, *Pocillopora damicornis* and *Porites cylindrica,* is surprising and in marked contrast to its widespread occurrence elsewhere. Neither bleaching resistance nor increased survivorship was enhanced by 10-day exposures to sub-lethal temperatures.

The time required for plants and animals to acclimatize to temperature change is generally short (hours – days) because the acclimatization response is a result of rapid biochemical changes (Hayes and King 1995, Sharp et al. 1997). In corals, the two most likely thermo-protective mechanisms involve the synthesis of heat shock proteins (HSP's) and enzyme regulation (Gates and Edmunds 1999), both of which occur over time spans of minutes - hours. Therefore, one would expect ten days to be more than sufficient time for these processes to take place. However, the lack of thermal acclimation detected in this study does not imply that these processes do not occur. It may be that they take place so rapidly that their benefits are already encompassed in the responses observed following the ~12 hours it took to elevate both control and acclimated corals to desired stress temperatures. Thus, unacclimated corals receive the same benefits of rapid biochemical changes as acclimated corals and no change in upper thermal limits is detected. The implications of this are that if the thermal acclimation response of corals is limited to rapid biochemical adjustments to maintain certain levels of function (i.e. capacity acclimation), then corals like *P. damicornis* or *P. cylindrica* may not be capable of increasing their upper thermal limits beyond existing natural levels. This is because extreme temperature events leading to bleaching take days to weeks to build up (e.g. Chapter 3, Berkelmans and Oliver 1999, Lough 2001b) by which time any acclimation response will also have already been incorporated by the corals.

The results of these experiments are also contrary to those of Coles and Jokiel (1978) who found significantly improved survivorship in acclimated *Montipora verrucosa.* Their experiments involved a 56-day acclimation period at each of 4 treatment temperatures (20°, 24°, 26° and 28°C) and two consecutive stress temperatures (30° and 32°C) for three and four days respectively. 73% of corals from the 28°C incubation temperature survived compared to 61% in the 26°C treatment, 30% in the 24°C and 47% in the 20°C treatment. The present results also contrast with a previous acclimatization experiment at Orpheus Island where *P. damicornis* was found to have a higher bleaching threshold in summer than winter (Chapter 4, Berkelmans and Willis, 1999). One possible explanation for these contrasting results and the present study is that the acclimation/acclimatization times were longer, possibly eliciting slower biochemical or cellular responses. Alternatively, some species of coral may simply be incapable of resistance acclimation beyond existing summer conditions, as has been noted in some amphibians, reptiles and most insects (Bullock 1954). The lack of acclimation in the present study and the possibility that some coral species may have reached their thermal acclimation potential in summer, supports the general conclusion of Hoegh-Guldberg (1999) that reef-building corals may have a limited capacity to acclimatize. Evidence of repeated bleaching of the same coral communities at sites like Magnetic Island between 1980 and 1998 (five bleaching events; Chapter 2; Berkelmans and Oliver, 1999) indicate that upper thermal limits have not increased substantially over this time period.

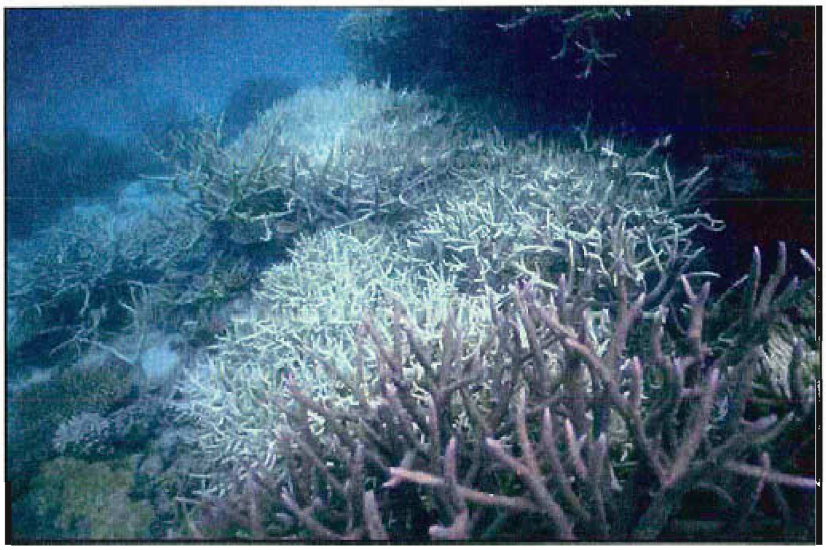
The results from this study suggest that there is no clear relationship between thermal resistance and acclimation potential. Sixty-three percent of unacclimated colonies survived and were in good health after a 33°C stress exposure for 4-days. Several more were alive but fouled after 9 weeks of recovery and may have returned to good health under suitable conditions and a longer period of recovery. None of the *P. damicornis* colonies survived this treatment, but all survived the 32°C treatment. The upper thermal limits of 32°C for *P. damicornis* agrees with the limit determined twice previously (Chapter 4, Berkelmans and Willis 1999), indicating that summer upper limits are repeatable both within a season and between years. These results also indicate that the upper thermal limit of *P. cylindrica,* under these controlled conditions, is at least 1°C higher than *P. damicornis*. This differential in thermal tolerance is consistent with tissue thickness. *P. cylindrica* has thick tissues (4-6mm) whereas those of *P. damicornis* form a very thin veneer over the surface of the skeleton (<1mm thick). Field studies of in differences in the susceptibility to bleaching and mortality among species show that thick tissued species such as poritids and faviids are often more temperature tolerant than thin tissued corals such as pocilloporids and acroporids (e.g. Marshall and Baird, 2000). High bleaching resistance in thick-tissued species has been attributed to self-shading of zooxanthellae layers (Hoegh-Guldberg, 1999), however large lipid reserves in thick-tissued species may also help them to cope better with thermal stress and post-bleaching recovery. Despite their contrasting responses and tissue morphology, neither species was able to increase it temperature tolerance beyond existing levels. Therefore, while there is some evidence linking morphological features with thermal resistance, there is no evidence linking temperature acclimatization to tissue morphology.

Zooxanthellae densities and the proportion of degenerate (unhealthy) zooxanthellae during the 12 week recovery period add important new insights into the time lag between biochemical damage and its ultimate effect on the organism, as well as into the process of bleaching itself. After 33°C stress, *P. damicornis* continued to lose zooxanthellae for up to 6 weeks, during which time the proportion of degenerate zooxanthellae increased in all but one acclimation treatment (Fig 5.5). Thus, despite the host coral expelling unhealthy symbionts, more degenerated until the colonies died sometime between 6 and 12 weeks after removal of temperature stress. The reduction in degenerate zooxanthellae in the 32°C stress treatment at 6 weeks also marked the turnaround to full recovery in all but the highest acclimation treatment. These results confirm observations of continued decline in health for up to 34 days in the same species left to recover in the field after 5 days at 32°C (Chapter 4, Berkelmans and Willis 1999). Such a 'delayed' response however was not evident in another Great Barrier Reef (GBR) study where the recovery of *Stylophora pistillata*, and *Seriatopora hystrix* was monitored after a 32°C stress treatment for 7 hours (Hoegh-Guldberg, 1999). Zooxanthellae density, photosynthesis and respiration rates of these species began to recover within four days of thermal stress and had returned to pre-stress levels within 23 days (Hoegh-Guldberg, 1999). The lack of continued post-stress decline in coral health in this experiment may be a function of the short exposure times to thermal stress. Evidence for a delayed visual effect from environmental stress is also available from field observations. During the 1998 bleaching event on the GBR, reef interpretation staff who run daily visits to a tourist pontoon at Hardy Reef (offshore central GBR) first saw signs of bleaching on 14 March, 26 days after an initial temperature peak (29.9°C) and 18 days after a second peak (also 29.9°C, J Shields pers comm). Surface light intensity, measured by a weather station on the pontoon, was consistently high between the high temperature peaks and the first visual indication of bleaching (mean daily 10am-3pm PAR range = 1100 – 2000 $\mu E.m^{-2}.s^{-1}$), except for a 3-day period in the middle (mean daily 10am-3pm PAR range = 690 – 1020 $\mu E.m^{-2}.s^{-1}$, unpublished data). These observations are also consistent with a continued decline in zooxanthellae density of *Acropora formosa* at Magnetic Island after a natural bleaching event in 1994 which took place for up to 4 weeks after maximum temperatures were reached (Jones 1997b). However, while monitoring the post-bleaching recovery of this species, the author found only one degenerate zooxanthella despite extensive searching (Jones 1995). This is in contrast to the large and increasing proportion of degenerate zooxanthellae with time (up to 6 weeks) found in *P. damicornis* in the present study. These results are consistent however with other workers who found a dramatic increase in the number and proportion of degenerate zooxanthellae of corals kept in darkness for an extended period (Yonge and Nicholls 1931b, Kevin and Hudson 1979), or in corals subjected to temperature stress (Yonge and Nicholls 1931a). The zooxanthellae being ejected from the corals in these studies consisted mostly of degenerate cells and contained relatively few normal cells. In combination with these observations, the results from the present study suggest that the continued degradation and loss of zooxanthellae for up to 6 weeks may be symptomatic of a longer-term 'domino-style' breakdown in the coral-algal symbiosis. Support for this interpretation is provided by field observations of the progressive spreading of patches of bleaching in massive and encrusting corals over several weeks, a process which could not be accounted for by light interaction or the prior distribution of zooxanthellae (Jones 1995). Jones (1995) speculates that a positive-feedback mechanism may be involved in coral bleaching. This notion implies that chemical cues are generated as a result of earlier losses of zooxanthellae, or breakdown of symbiosis, which stimulate further bleaching. Alternatively, the production of chemicals initially triggered by thermal stress may continue to be produced for a long time, or take a long time to diffuse through coral tissues, causing dysfunction and loss of zooxanthellae over many weeks.

In conclusion, the lack of resistance acclimation in *P. damicornis* and *P. cylindrica* observed following 10-day exposure periods to sub-lethal temperatures, indicates that although rapid biochemical changes take place to assist corals in coping with elevated temperatures, they occur over too short a time frame (minutes - hours) to be evident as increased summer upper thermal limits. Resistance acclimation beyond existing summer levels may take place over time periods longer than 10 days, but is yet to be demonstrated for any GBR species.

Chapter 6

Time-integrated thermal bleaching thresholds of reefs and their variation on the Great Barrier Reef



Bleached staghorn *Acropora* on the upper reef slope at Trunk Reef (18.35°E, 146.83°W), April 1998. Photo courtesy GBRMPA.

6.1. ABSTRACT

Knowledge of the critical levels for key environmental variables that are likely to cause bleaching in reef corals is of fundamental importance in conducting risk assessments of potential climate change effects on coral reefs. Such knowledge can also be used to provide early warning of mass bleaching events. A number of factors have contributed to the difficulty in determining critical levels for coral bleaching The factors include the fact that multiple stressors may be involved in bleaching, the duration of stress required to elicit a bleaching response varies with temperature, and bleaching triggers are known to be variable in space, time and by species. In this chapter I identify sea surface temperature (SST) as the most important parameter for predicting coral bleaching from four possible environmental variables collected over 10-12 years from weather stations at two locations on the Great Barrier Reef (GBR): temperature, solar radiation, wind speed and barometric pressure. Predicted bleaching-response curves are constructed from high-resolution in-situ temperature records and historical observations of coral bleaching for 13 locations. These curves approximate reef-wide stress response thresholds for bleaching of thermally sensitive (and often dominant) coral species. Distinct spatial trends exist in the thermal sensitivity of coral populations that correspond with position across the shelf and latitude, in the case of mid- and outer-shelf reefs. This suggests that considerable thermal adaptation has taken place over small (10's km) and large (100's – 1000's km) spatial scales. Bleaching curves for inshore reefs do not correspond with latitude and are more variable, reflecting greater local-scale variability in temperature regimes.

6.2. INTRODUCTION

Concern about the possible link between climate change and major impacts on the worlds' coral reefs as a result of coral bleaching (e.g. Glynn 1993) has stimulated research into modeling potential future scenarios of sea temperatures in reef regions (e.g. (Hoegh-Guldberg 1999). Such models provide a basis for undertaking sensitivity and risk analyses aimed at identifying and quantifying threats to coral reefs from climate change. Risk assessments thus provide a scientific basis for policy and management responses at local, regional and global scales. To assess risks to coral reefs, impact thresholds for a variety of climate variables must be identified which can be combined with climate model forecasts to estimate exceedence probabilities (Pittock 1999). One of the most important environmental criteria defining the existence of coral reefs is temperature (see reviews by e.g. Stoddart 1969, Achituv and Dubinsky 1990, Kleypas et al. 1999). However, defining the upper thermal limits of coral reefs in anything but general terms has proved surprisingly difficult. While considerable progress has been made in establishing the experimental upper thermal limits of corals from a variety of species and from a number of areas (e.g. Coles et al. 1976, Marcus and Thorhaug 1981, Berkelmans and Willis 1999), it is not clear how these experimentally derived upper thermal limits apply in-situ, where a number of stress factors may work in concert to alter the effective bleaching thresholds (see reviews by Jokiel and Coles 1990, Glynn 1993, Brown 1997, Hoegh-Guldberg 1999). Low winds and high irradiance, for example, are commonly associated with reef-wide bleaching events (Dennis and Wicklund 1993, Drollet et al. 1994, McField 1999). Barometric pressure may also be correlated with bleaching because of its regional influence on winds and ocean currents (Lough 2001a). Bleaching responses also vary with exposure time, species and location (eg. Coles et al. 1976, Marcus and Thoraug 1981, Glynn et al. 1988). In combination, these factors have made it difficult for temperature thresholds to be used in modeling the effects of climate change on coral reefs. Determining in-situ, time-integrated bleaching thresholds and their spatial variation, especially over local and regional scales, is thus essential to advance our knowledge in this area.

Knowledge of realized in-situ bleaching thresholds also allows for near real-time prediction of bleaching events using automatic weather stations (Hendee et al. 1998). Early warning of local conditions likely to cause coral bleaching could augment regional satellite-based 'Hotspot' alerts (Strong et al. 1997) to assist (1) science - in documenting and researching the phenomenon; (2) public relations - in keeping reef-based commercial operators, politicians and the general public informed; and (3) coral reef managers - in ameliorating local-scale human impacts which might exacerbate coral bleaching.

In this chapter I examine 10-12 years of automatic weather station data to establish the relative importance of sea surface temperature (SST), wind speed, photosynthetically active radiation (PAR) and barometric pressure as predictor variables of coral bleaching on the GBR in 1998. I establish best-estimate, time-integrated thermal bleaching thresholds based on 3 - 8 years of in-situ temperature data for 13 locations on the Great Barrier Reef (GBR) and examine their characteristics and variation with latitude and shelf position.

6.3. METHODS

Data from the Australian Institute of Marine Science automatic weather stations at Myrmidon Reef (Lat 18.2°S, Long 147.2°E) and Hardy Reef (Lat 19.8°S, Long 149.2°E) in the central Great Barrier Reef covering 12 and 10 years (respectively), were used to determine conditions associated with the major Great Barrier Reef (GBR) bleaching event of early 1998 (Baird and Marshall 1998, Berkelmans and Oliver 1999, Marshall and Baird 2000; Fig 6.1). Weather station sensors, including sea temperature (Omega Interchangable Thermister), wind speed (R.M. Young 5103), photosynthetically active radiation (PAR, Licor 192SA, 400-700nm), and barometric pressure (Vaisala PTB101B), were scanned and averaged every 30-min. I compared average monthly values of these variables for the warmest month during the 1998 bleaching event (February), with weather conditions occurring between January and March of all other years. These months are when bleaching on the GBR has previously occurred (Oliver 1985, Jones et al. 1997). PAR was averaged between 10am and 3pm each day to capture the mean maximum daily irradiance as an indicative measure of potential light stress to corals.

Data logger SST data from 13 locations on the GBR were examined for which concurrent information was also available on the intensity of bleaching during 1998 (Table 6.1, Chapter 2, Berkelmans and Oliver 1999). These locations included six inshore reefs (Wallace Island, Daintree, Orpheus Island, Magnetic Island, Daydream Island, Halfway Island), three mid-shelf reefs (Low Isles, Kelso Reef, Davies Reef) and four outer-shelf reefs (Norman Reef, Myrmidon Reef, Chicken Reef, Heron Island; Fig 6.1). Temperatures at each location were continuously monitored over periods of 3 – 9 years (Chapter 3). Loggers were calibrated against a certified reference thermometer after every download (6 - 12 months). Daily mean SST's (n = 48 records) were calculated for the reef flat (Lowest Astronomical Tide) and slope (5 – 9m) at all sites. At locations where more than one logger was deployed within 15km from each other (Magnetic Island, Daintree coast, Orpheus Island, Halfway Island), data were also spatially averaged. Temperatures used in this analysis, therefore, broadly represent the general area at each location and the depth-range of the majority of corals.

For each location, the cumulative time (in days) at each temperature was calculated for the period December – March each year, which includes the austral summer. The resultant curves, therefore, are the tail end of cumulative frequency distributions of temperatures for each year. For each location, a polynomial bleaching threshold curve was then interpolated between the curves for the warmest non-bleaching year and the coolest bleaching year. The exact position of the threshold curve was determined by the severity of bleaching as recorded on a five-point scale, with 1 being the most severe bleaching state and 5 being the least severe bleaching state (ie. 'no bleaching', Table 6.1), according to the equation:

$$b_c = T_b - s/5(T_b - T_n), \text{ for } T_b > T_t$$

where, b_c is predicted bleaching curve, s is the bleaching severity score (integer between 1 and 4, excludes the 'no bleaching' category), T_b is the temperature distribution curve for the coolest bleaching year (if the temperature data include more than one bleaching year), T_n is the temperature distribution curve for the warmest non-bleaching year, and T_t is the threshold temperature (°C). The threshold temperature is the highest temperature at which no bleaching is predicted to occur irrespective of exposure time and is taken as the point where the bleaching and no-bleaching temperature curves overlap (i.e. when $T_n > T_b$). A bleaching threshold curve, therefore, represents a profile of average daily exposure temperatures and durations at which coral bleaching in thermally sensitive species is predicted to commence. As the resultant curves are based on distribution curves, the number of days exposure do not necessarily represent consecutive days. However, because temperatures from day-to-day are highly autocorrelated, the periods of warm weather of primary interest in this study generally occurred in one or several closely following blocks of time.

Table 6.1. Location of reefs used to construct bleaching curves and bleaching status as assessed from aerial surveys undertaken using fixed wing aircraft at an altitude of ~160m between 9 March and 10 April 1998. Reefs were classified into five categories of bleaching severity: 1 (extreme, >60% bleached), 2 (very high, 30-60% bleached, 3 (high, 10-30% bleached), 4 (moderate, 1-10% bleached), and 5 (no or low bleaching, <1% bleached).

Reef	Latitude	Longitude	Bleaching category
Wallace Islet	11.4° S	143.0° E	4
Daintree coast	16.2° S	145.4° E	2
Low Isles	16.4° S	145.6° E	1
Norman Reef	16.4° S	146.0° E	4
Myrmidon Reef	18.3° S	147.4° E	4
Orpheus Island	18.6° S	146.5° E	1
Kelso Reef	18.4° S	147.0° E	4
Chicken Reef	18.7° S	147.7° E	4
Davies Reef	18.8° S	147.6° E	4
Magnetic Island	19.2° S	146.8° E	1
Daydream Island	20.3° S	148.8° E	4
Halfway Island	23.2° S	151.0° E	1
Heron Island	23.4° S	151.9° E	4

Because the bleaching threshold curves are derived from highly autocorrelated data, modeling these curves with traditional statistical routines based on least squares regression procedures is technically flawed. The end result is an underestimation of the error around the curve. This would therefore make statistical comparisons of individual curves difficult. However, as I was mainly interested in the predictive capacity of the curves at a particular location (i.e. how much temperature for how long?) and in gross regional trends in bleaching thresholds, I proceeded with modeling the curves. In doing so, I acknowledge that there is variation around each curve, but also show that this variation is likely to be relatively small (see Discussion). Regional trends in bleaching threshold curve slopes and intercepts (based on linear models) were undertaken on the basis that the slope and intercepts of curves for each location are independently estimated and thus can be used legitimately in regression models.

To test the efficacy of the concept of accumulated thermal stress as calculated for corals by e.g. Gleeson and Strong (1995), Podestá and Glynn (1997), I converted bleaching threshold curves to 'degree-days' by multiplying exposure days tolerated x temperature in excess of the threshold temperature, T_t. The nature of the relationship between accumulated heat stress, calculated in this manner, and temperature was then investigated by plotting degree-day values against temperature in excess of the threshold temperature.

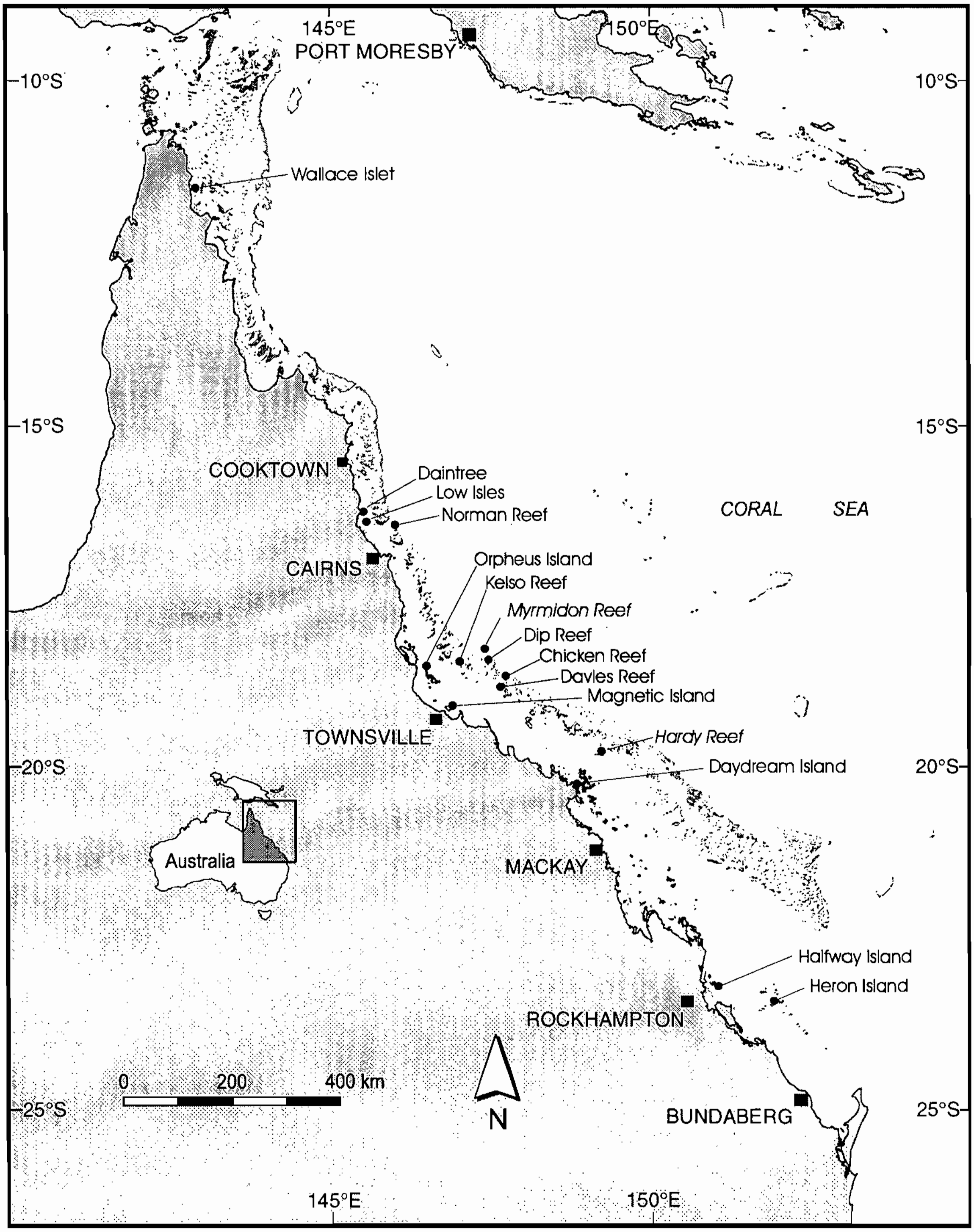


Fig 6.1. Map of the Great Barrier Reef showing the location of reefs for which bleaching curves were estimated and the location of automatic weather stations at Myrmidon and Hardy Reef (italics).

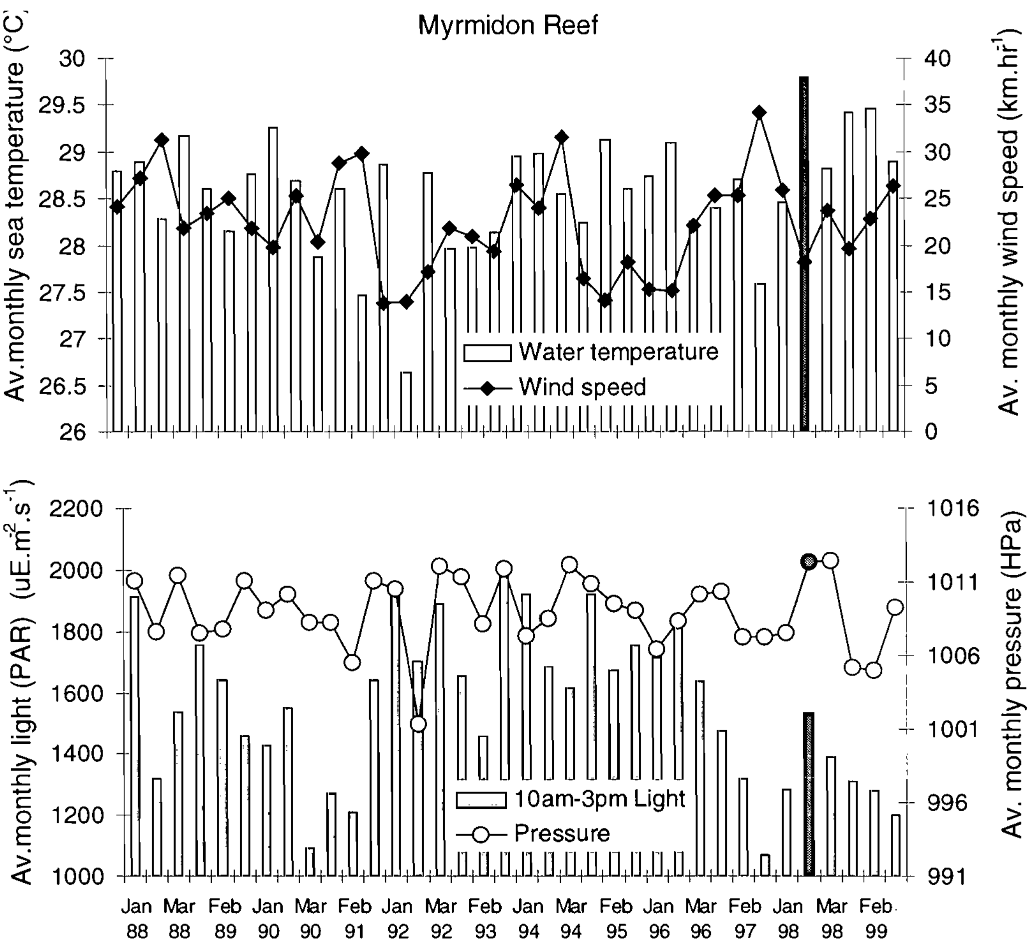


Fig 6.2. Average monthly sea temperature (°C), wind speed (km/hr), daytime (10am-3pm) solar radiation (μE.m^2.s^{-1}) and barometric pressure (HPa) for Myrmidon Reef for the months of January, February and March between 1988 and 1999. Widespread coral bleaching was evident at this reef in February 1998 (highlighted), but at no other time during this 12-year period.

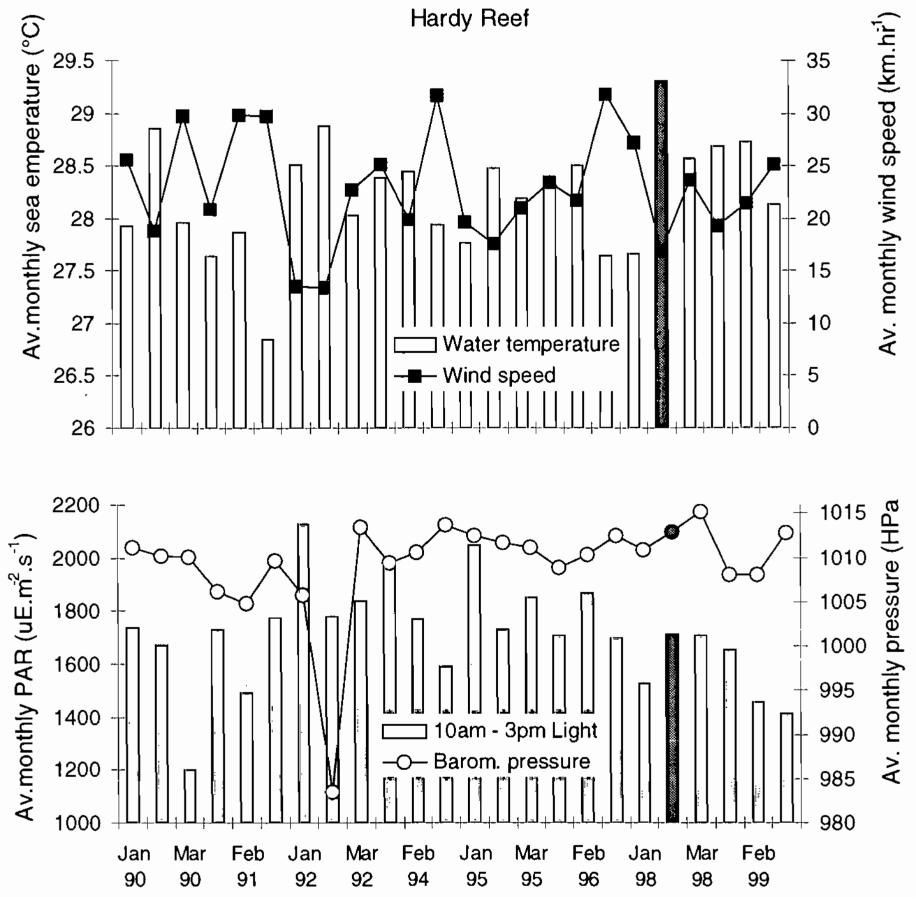


Fig 6.3. Average monthly values of sea temperature (°C), wind speed (km/hr), daytime (10am-3pm) solar radiation ($\mu E.m^2.s^{-1}$) and barometric pressure (HPa) for Hardy Reef for the warmest three months (January to March) between 1990 and 1999. Widespread coral bleaching was evident at this reef in February 1998 (highlighted), but at no other time during this 10-year period. Data for 1993 and 1997 are omitted due to large gaps in the data.

6.4. RESULTS

An analysis of 10-12 years of meteorological variables at Myrmidon and Hardy Reefs showed that SST associates more strongly with the 1998 coral bleaching event than wind speed, PAR or barometric pressure. At Myrmidon Reef, the monthly mean SST during the height of the bleaching in February 1998 was 29.8°C, 0.3°C warmer than the next warmest month (February 1999; Fig 6.2). Similarly, at Hardy Reef the average monthly temperature in February 1998 was 0.4°C warmer than the next warmest month (February 1992; Fig 6.3). No bleaching was recorded at either of these two reefs in 1992 or 1999 (Berkelmans and Oliver, unpublished data). At both reefs, average monthly wind speed was relatively low during February 1998 (17 - 18 km/hr), but not as low as 1992 when the average monthly wind speed was 13 - 14 km/hr (Figs 6.2 and 6.3). Similarly, barometric pressure was unusually high during the 1998 bleaching period compared to other summers, but no higher than in March 1992 and 1994 when no bleaching occurred. Average monthly PAR (10am – 3pm) was intermediate during the 1998 bleaching period at both reefs compared with previous years (Figs 6.2, 6.3). Temperature is thus clearly the most important determinant of coral bleaching and a good variable to use in modeling bleaching thresholds.

Bleaching threshold curves based on thermal criteria can be constructed with high resolution using relatively few years of data. For example, at Kelso Reef thermal tolerance curves were estimated using data from four years (Fig 6.4). Exposure times and temperatures in summer represent the right hand side of a normal cumulative distribution for each of three non-bleaching years (1996, 1997 and 1999) and one bleaching year (1998). During the non-bleaching years, average daily temperatures remained <29.8°C for one-day exposure, and <29.2°C for 25 days exposure (Fig 6.4). However, the time-temperature curve for 1998 deviated at 29.1°C and had a longer tail with a maximum temperature of 30.0°C experienced for 2 days. Since Kelso Reef suffered mild bleaching in 1998 (score 4 on a 5-point scale; Table 6.1), the suggested threshold line is closer to the 1998 curve than the 1999 curve (Fig 6.4). The suggested bleaching threshold curves for 12 other reefs were derived in the same way and are shown in Fig 6.5. At Magnetic (Fig 6.5i) and Orpheus Islands (Fig 6.5f), longer-term temperature records were available

(8 and 6 summers respectively), and included a number of bleaching events (three at Magnetic Island (1992, 1994, 1998) and two at Orpheus Island (1994, 1998)). For these locations threshold curves could be estimated with higher precision. For other reefs, like Halfway Island in the southern GBR, the threshold curve is less precise because the time-temperature curve for 1998 deviated greatly from, and did not cross over, the warmest non-bleaching year (Fig 6.5k).

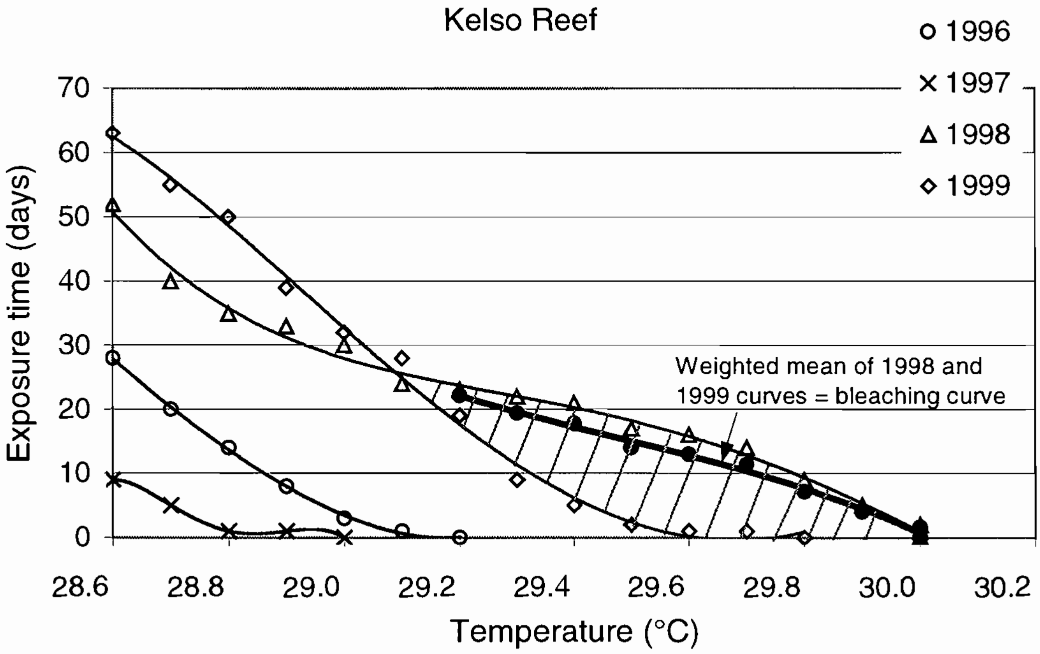
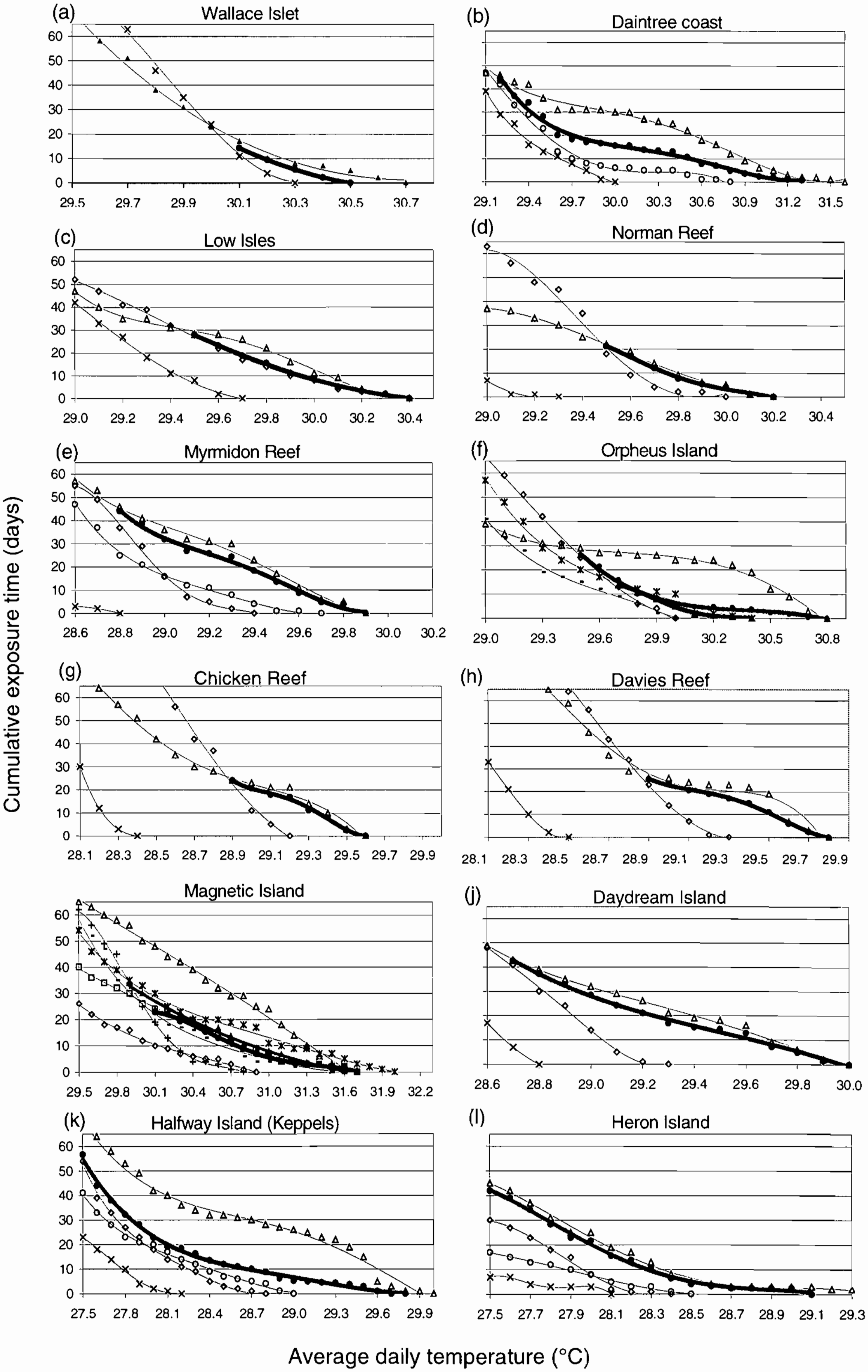


Fig 6.4. Example of how the bleaching threshold curve was estimated for Kelso Reef. Cumulative exposure times and temperatures are shown for 4 consecutive years, one of which coincided with mild bleaching (1998), for the period when the warmest average daily temperatures are recorded (December to March). The hatched area between the 1998 curve and that for the warmest non-bleaching year (1999) indicates the potential area in time-temperature space in which bleaching could occur. The predicted bleaching curve (bold solid line, closed circles) was estimated by weighting the mean on a 5-point scale according to the intensity of bleaching (see text).

Fig 6.5. (Over page). Estimation of bleaching curves for 12 reefs. Bleaching threshold curves fitted with polynomial trend lines. Legend: ♬ = 1999, ρ = 1998, X = 1997, ⫯ = 1996, - = 1995, ☂ = 1994, + = 1993, ⊠ = 1992. ● = Estimated bleaching curve. Note the different temperature scales in each graph. 1996 and 1997 were cool years for Magnetic Island and Orpheus Island and data were omitted from graphs for clarity. Double bold lines at these two sites indicate proximity of bleaching curves estimated with reference to different bleaching years (1998 and 1994 at both sites, plus 1992 at Magnetic Island).


(a) Wallace Islet
0 10 20 30 40 50 60
29.5 29.7 29.9 30.1 30.3 30.5 30.7
(b) Daintree coast
29.1 29.4 29.7 30.0 30.3 30.6 30.9 31.2 31.5
(c) Low Isles
0 10 20 30 40 50 60
29.0 29.2 29.4 29.6 29.8 30.0 30.2 30.4
(d) Norman Reef
29.0 29.2 29.4 29.6 29.8 30.0 30.2 30.4
(e) Myrmidon Reef
0 10 20 30 40 50 60
28.6 28.8 29.0 29.2 29.4 29.6 29.8 30.0 30.2
(f) Orpheus Island
29.0 29.3 29.6 29.9 30.2 30.5 30.8
(g) Chicken Reef
0 10 20 30 40 50 60
28.1 28.3 28.5 28.7 28.9 29.1 29.3 29.5 29.7 29.9
(h) Davies Reef
28.1 28.3 28.5 28.7 28.9 29.1 29.3 29.5 29.7 29.9
Magnetic Island
0 10 20 30 40 50 60
29.5 29.8 30.1 30.4 30.7 31.0 31.3 31.6 31.9 32.2
(j) Daydream Island
28.6 28.8 29.0 29.2 29.4 29.6 29.8 30.0
(k) Halfway Island (Keppels)
0 10 20 30 40 50 60
27.5 27.8 28.1 28.4 28.7 29.0 29.3 29.6 29.9
(l) Heron Island
27.5 27.7 27.9 28.1 28.3 28.5 28.7 28.9 29.1 29.3
Cumulative exposure time (days)
Average daily temperature (°C)

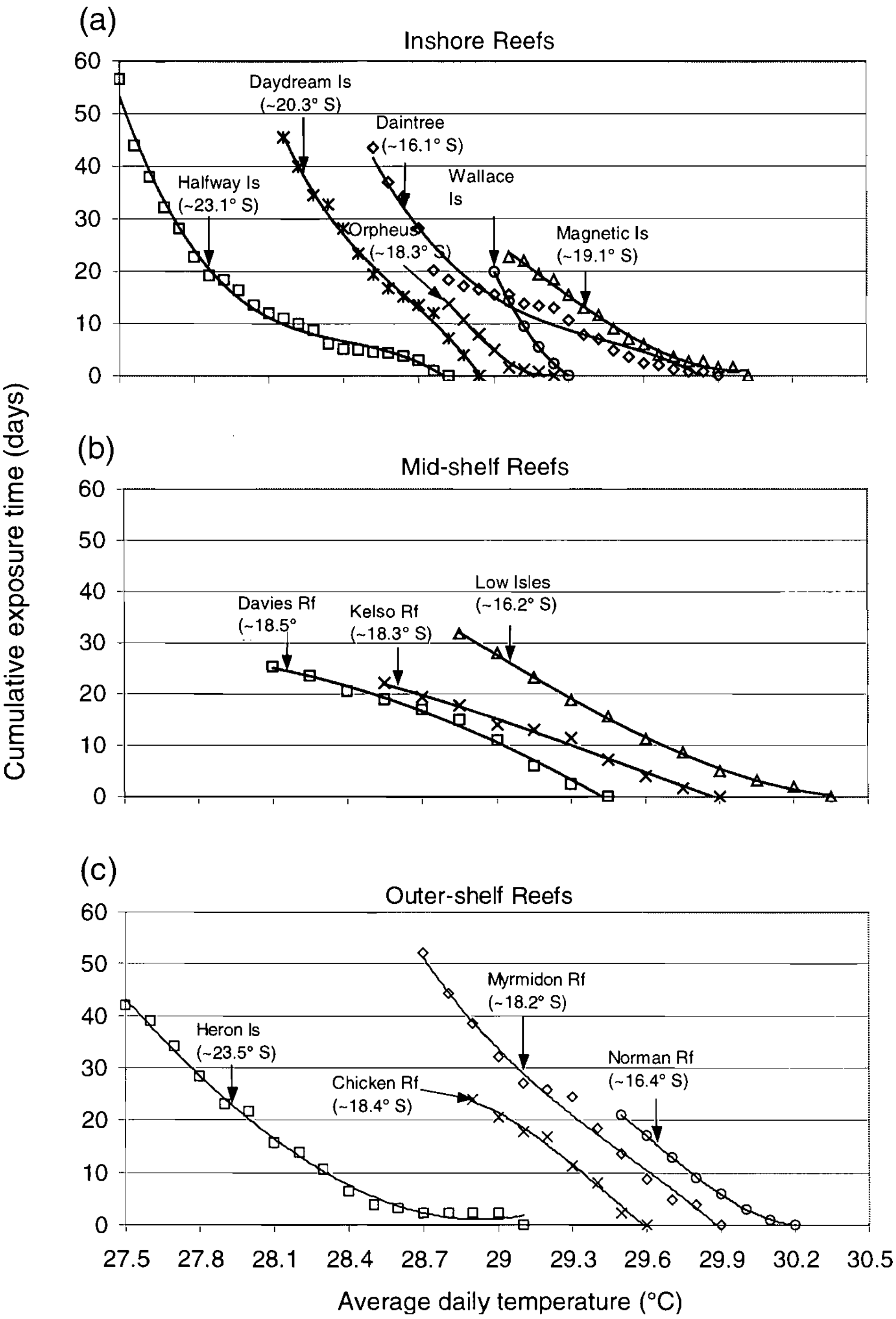


Fig 6.6. Latitudinal comparison of predicted bleaching threshold curves for inshore, mid-shelf and outer-shelf reefs.

The predicted bleaching threshold curves showed considerable variation in shape and intercepts over scales of 10s to 100s of kilometers. For predictive (and site-specific) purposes, these curves can be modeled using cubic polynomial equations (Figs 6.5, 6.6). The shapes of the curves were more variable for inshore reefs than for mid-shelf and outer-shelf reefs (Fig 6.6a - c). Bleaching threshold curves also showed considerable separation even for relatively close reefs. For example, the slope (linear component) and the intercept for Magnetic Island on the inshore GBR, were remarkably different from those of Orpheus Island less than 75km to the north.

Distinct spatial trends in the bleaching curves were revealed when the slopes and intercepts of individual bleaching curves were regressed against latitude. Linear model intercepts (temperature axis) showed a significant curvilinear trend with latitude (Fig 6.7a) with a plateau towards low latitudes and a sharp decline towards higher latitudes (model fit $r^2 = 0.44$; regression ANOVA of latitude (transformed by it's quadratic function, Fig 6.7a) $F = 29.54$, df $_{1,11}$, $p<0.01$). In contrast, model slopes showed no significant trend with latitude (regression ANOVA $F = 0.54$, $df_{1,11}$, $p = 0.477$, Fig 6.7b). The slopes and intercepts of Magnetic Island and the Daintree coast were clear outliers, a symptom of their geography (see Discussion). When they were excluded from the above analyses the model fit for the curve intercepts on latitude increased to $r^2 = 0.85$ and became more significant. However, the trend for curve slopes with latitude remained non-significant and the model fit did not improve.

The relationship between exposure temperature above a critical level (T_t) and accumulated heat stress, expressed as 'degree-days', was approximated by a negative quadratic function (Fig 6.8). These curves represent lines of equal stress on corals at increasing temperatures above a threshold temperature. Because 'degree-days' is calculated by multiplying time by temperature above threshold, a small amount of temperature above threshold for a large number of days, or a number of days at a high temperature above threshold, both give a relatively small number of 'degree-days'. However, median levels of temperature above threshold for a median period of time yields the largest value of 'degree-days'. The shape of the curves is a function of the rate at which the area under the bleaching threshold curve accumulates at increasing temperatures. Furthermore, the curve shape implies that on the left side of the curve, time is the dominant integrating factor, while on the right side of the curve, temperature is the dominant integrating factor.

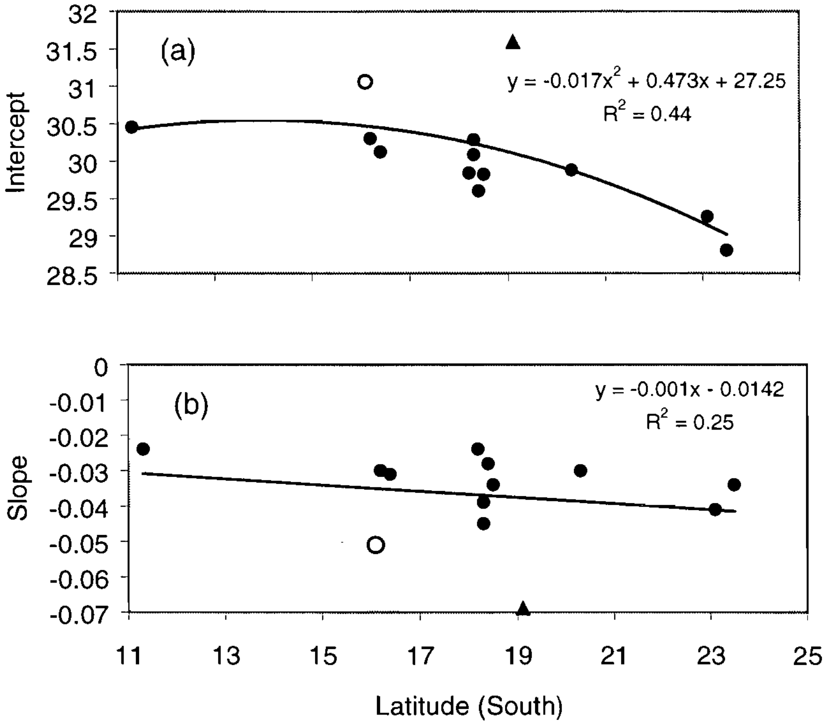


Fig 6.7. Latitudinal trend in (a) intercepts and (b) slopes of predicted bleaching curves modeled by linear regression. Magnetic Island (π) and the Daintree coast (▨) are outliers, but have been included in the analysis.

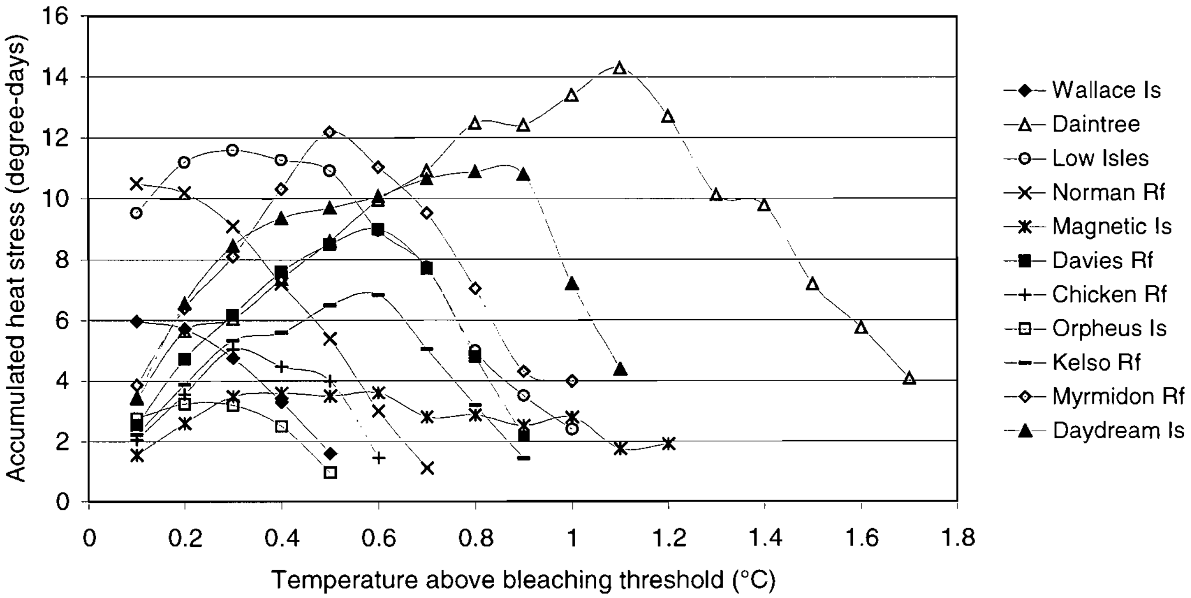


Fig 6.8. Predicted bleaching threshold curves recalculated as accumulated heat stress (degree-days) indicating the relationship between 'degree-days' and the exceedence of daily threshold temperature (°C). Resulting curves represent lines of equal thermal stress at various combinations of exposure time and temperature.

6.5. DISCUSSION

Sea temperature is strongly associated with coral bleaching and its wide availability through cheap data loggers and satellites makes this variable an extremely useful and widely applicable predictor of coral bleaching. Although calm wind conditions, and high solar radiation may be important but secondary co-factors during coral bleaching (Dennis and Wicklund 1993, Drollet et al. 1994), the results presented here suggest that these variables by themselves do not correlate with widespread coral bleaching and their effect on bleaching may only become relevant at high temperatures (see Jokiel and Coles 1990). In this study, this is demonstrated by high light intensities in the absence of high water temperatures at Hardy Reef (January 1992) and Myrmidon Reef (March 1993) without causing widespread bleaching (Figs 6.2, 6.3). Light levels during these months approached the highest theoretical surface light intensities for these locations (Kirk 1983), yet no bleaching was observed. Light has been suggested as the primary stress factor in a natural bleaching event at Lizard Island in 1982 (Harriott, 1985), but these conclusions were reached using "sunshine hours" as a proxy for light intensity and while sea temperatures were clearly elevated between December 1981 and April 1982 compared to other years (Fig 3 in Harriott, 1985). Fitt et al. (2001) argue that the concept of a "bleaching threshold temperature" is not meaningful to either corals or humans because the pigment state in corals is naturally variable and can result from many combinations of temperature, light and exposure time. Thus, any reduction in pigment cannot be attributed to any one environmental parameter (such as temperature). However, while high light intensities (at various wavelengths, including photosynthetically active radiation, UV-A and UV-B) may confound the interpretation of the bleaching state of corals in the field (especially over small spatial scales (< 1 – 100's of metres), the evidence remains that elevated temperature is the primary stress factor in wide-spread 'natural' bleaching events. While light levels may alter the final bleaching state of corals, its effects are secondary (Jones et al. 1998). The physiological mechanism proposed by Jones et al. (1998) to explain the secondary effect of light in bleaching, is that temperature damages the biochemical pathway leading to carbon fixation (via the Calvin - Benson Cycle) in the zooxanthellae. The blocking of the photochemical pathway in turn results in an overwhelming of Photosystem II with light and the production of reactive oxygen species (Jones et al. 1998, Hoegh-Guldberg 1999). However, because light levels are almost always high at the time of bleaching events (solar radiation drives sea temperature increases), over large spatial scales (1 -100's of km), the effect of light intensity in causing variable bleaching responses is effectively a constant. Thus, at appropriate scales, temperature is a useful and appropriate parameter for modeling bleaching thresholds.

The predicted bleaching curves presented here define for the first time the relationship between stress temperature and exposure time for a range of reefs on the Great Barrier Reef. Despite inherent inaccuracies due to the limited number of years of in-situ temperature data available, these curves are nevertheless defined within relatively narrow limits and can be more precisely defined as more temperature and bleaching data become available. Although these curves are expressed in terms of thermal criteria, they do in fact incorporate a light component, because they are based on in-situ bleaching observations, as discussed above. Variation in ambient light regimes and other physico-chemical factors at the time of bleaching between sites and between years may also influence the precise position of the curve. Nevertheless, the temporal consistency of these curves at locations that have experienced multiple bleaching events is encouraging and consistent with the notion that temperature is an adequate predictor of bleaching at the scale of reefs and above. At Magnetic Island for example, the time-temperature curves for the bleaching years of 1992, 1994 and 1998 were all higher than the warmest non-bleaching year in 1995. Similarly at Orpheus Island, the bleaching years of 1994 and 1998 were consistently warmer than the warmest non-bleaching year in 1999. The predicted bleaching curves at Magnetic and Orpheus Island also showed close agreement with one another regardless of the bleaching year used in the calculation. At Magnetic Island for example, the predicted bleaching curve estimated from temperatures in 1995 (when no bleaching occurred) and 1994 (when mild bleaching occurred) is very similar to the calculated exposure times and temperatures estimated from temperatures in 1995 and 1998 (when very heavy bleaching occurred, Fig 5i). At Orpheus Island, the bleaching curves estimated from weighted 1994/1999 and 1998/1999 data deviate only at higher exposure temperatures (Fig 5f). Winter et al. (1998) found similar consistency in the exposure times and temperatures during four severe coral bleaching events in Puerto Rico using in-situ SST data spanning 30 years. The temporal consistency of the bleaching response of coral communities also indicates that no discernable thermal acclimatization or adaptation response (at least in terms of bleaching) has taken place over this time period.

By contrast, the results from the present study suggest that substantial thermal adaptation may have occurred over a number of spatial scales. This is evidenced by the spatial variation in the bleaching curves of reefs spanning ~1600km and over 12 degrees in latitude. This variation in thermal sensitivity mirrors the latitudinal gradient of mid- and outer-shelf reefs, but for inshore reefs the situation is more complex. The relative position of the bleaching threshold curves for the inshore reefs of Magnetic Island (central GBR) and the Daintree coast fringing reefs (northern GBR) are higher than would be predicted by latitude alone (Fig 6.6a). Local-scale oceanographic features (enclosed embayments, shallow coastal waters) have resulted in warmer and more variable SST regimes on some inshore fringing reefs compared with offshore reefs and between neighboring coastal waters. The lack of consistency in thermal regimes with latitude at inshore locations has also resulted in more variable shapes in the bleaching curves for inshore reefs compared with mid- and outer-shelf reefs. The former are best modeled as polynomials which feature variable regression slopes, whereas curves for mid- and outer-shelf reefs are well modeled by linear regression featuring relatively consistent regression slopes.

Spatial differences in bleaching curves across the GBR shelf are consistent with shelf position at three latitudes investigated (~16, 18 and 23°S) with ‘warmer’ curves inshore and ‘cooler’ curves offshore. The most striking difference occurs in the central GBR where there is no overlap of exposure temperatures and times between Magnetic Island and either Kelso Reef or Myrmidon Reef (Fig 6.6a - c). These cross-shelf trends reflect the trend to deeper water and more stable temperatures near the Coral Sea (Wolanski 1994).

Aside from gaining an understanding of spatial variation in upper thermal limits and thermal sensitivity of populations, the predicted bleaching curves presented here also have application in providing near-real time warning of coral bleaching. Used in conjunction with automatic weather stations or temperature buoys, the predicted bleaching curves can be incorporated into expert-system computer programs to generate automated warnings of conditions likely to be conducive to bleaching (e.g. Hendee et al. 1998). Such systems compliment broad-scale early warning systems such as the satellite-based 'Hotspot' system (e.g. Strong et al. 1997), which is spatially comprehensive, but lacks fine temporal and spatial resolution. In-situ monitoring buoys and weather stations also provide more accurate SSTs at local-scales.

The geographic variation in bleaching curves implies that there may also be patterns in the vulnerability of reefs to climate change. Assessing these patterns of risk is of particular interest to reef-based industries, especially tourism, where investment and growth require long-term planning. The predicted bleaching curves derived in this study represent sub-lethal stress limits of thermally sensitive corals. Among the most sensitive corals are the *Acropora* species (Oliver 1985; Baird and Marshall 1998; Marshall and Baird 2000), which also make up by far the highest coral cover and three dimensional complexity of Indo-Pacific reefs (e.g. Wallace 2000). On the Great Barrier Reef, tabulate and corymbose *Acropora sp.* dominated coral cover in 14 of 15 groups of reefs in 1998/99, covering inshore, mid-shelf and outer-shelf reefs between Cooktown and the bottom of the GBR (Fig 6.1, Sweatman et al. 2000). The bleaching curves thus reflect the bleaching thresholds of the most important living structural element of reefs. In conjunction with regional-scale climate models these threshold curves can be used to assess how often threshold temperatures may be exceeded in various climate change scenarios (Charles et al. 1999; Hoegh-Guldberg 1999).

Accumulated heat stress has been represented by a single number (e.g. 'degree-heating-weeks'), where exposure time and temperature are integrated by adding cumulative time above a given temperature (e.g. Gleeson and Strong 1995, Podestá and Glynn 1997). This study cautions against this approach. Implicit in such a bleaching index is the assumption that there is a linear relationship between exposure time and temperature, ie. X weeks at Y °C above threshold temperature has the same effect as Y weeks at X °C above threshold temperature. The results shown here indicate that this relationship is highly non-linear and that a single 'degree-day' bleaching threshold value could indicate a broad range of accumulated heat stress (Fig 6.8). At Myrmidon Reef for example, 4 days at 3 °C (12 degree-days) above the minimum bleaching threshold would represent a far greater stress impact than 24 days at 0.5°C above threshold (also 12 degree-days; Fig 6.8). Physiologically, corals can easily stand small increases in temperature above long-term means for long periods of time. The seasonal acclimatization in thermal tolerance in *P. damicornis* is evidence of a natural protection mechanism to small temperature increases above 'normal' levels (Chapter 4, Berkelmans and Willis, 1999). However, when temperatures exceed 'normal' levels by a large amount, the coral-algal symbiosis is compromised. The inappropriateness of stress indices such as 'degree-heating-weeks' concurs with the conclusion of Winter et al. (1998) that no single temperature variable or index of cumulative heat stress adequately reflects observed temporal bleaching patterns. However, the dual-factor bleaching curves presented here provide a greatly improved representation of thermal triggers likely to cause bleaching stress in corals.

Chapter 7

General Discussion, Summary and Conclusions

Bleaching at most mid-shelf reefs in 1998 was restricted to patches of white or pale acroporids and pocilloporids. Many colonies bleached to a fluorescent pink, blue or yellow colour. Photo courtesy GBRMPA.

7.1. Documenting bleaching patterns and insights into causes

The documentation of bleaching patterns over many years and over a wide spatial scale during the severe event of 1998 (Chapter 2), in conjunction with the collection of temperature (Chapter 3) and other physical data (Chapter 6), have provided invaluable insights into the physical factors and thresholds causing bleaching. Evidence from both the temporal and spatial studies suggest that high temperature is the single most important factor leading to coral bleaching. Although temperature has previously been associated with bleaching in natural events (e.g. Glynn et al. 1988, Glynn and D'Croz 1990), this is the first study to comprehensively combine exposure times with temperatures to predict bleaching threshold curves for a variety of reefs. Consistency in the shape and magnitude of bleaching threshold curves, calculated at sites where multiple bleaching events have been recorded, support the efficacy of this modelling approach. Consistent variation in the bleaching threshold curves with both latitude and shelf location suggests that the thermal environment strongly influences the position and shape of the curve.

Evidence that bleaching thresholds determined experimentally in the absence of high light (Chapter 5) are higher than equivalent time-temperature thresholds predicted from observations of in situ bleaching (Chapter 6), suggest that light may modify coral bleaching patterns. These results corroborate laboratory studies of Jones et al. (1998), who have shown that light exacerbates bleaching when thermal damage has been incurred in the dark-reaction cycle of photosynthesis. However, although light can significantly affect the bleaching intensity of individual corals, over reef-wide and regional scales bleaching thresholds can be adequately modelled without specific consideration of light levels (Chapter 6). The limited effect of light in determining regional bleaching patterns during natural bleaching events is also evident in the strong correlation of bleaching patterns with temperature (Chapter 2). One explanation for the finding that light does not appear to drive bleaching patterns during large-scale bleaching events may be that high light intensity almost always goes hand in hand with high temperatures: high temperatures seldom occur under high cloud conditions. While clouds may be patchy in distribution after critical temperatures are reached, it takes only a few hours of high light intensity to damage the photo systems of zooxanthellae (Jones et al. 1998). The likelihood of having at least one clear day to cause permanent photo system damage is very high. However, Mumby et al. (2001) do report a case where extremely high cloud cover over the Society Island, which occurred when sea temperatures were near or just over estimated bleaching threshold, may have prevented large-scale bleaching in 1998. The fact that light does affect natural bleaching patterns over smaller scales (<1 - 100's metres) is evident from patterns of decreased bleaching with depth (e.g. Oliver 1985) and increased bleaching with increased light penetration, especially inshore as a result of decreased turbidity during calm conditions. At these scales therefore, light has the effect of causing some measure of noise around the thermal thresholds. For the most part, light is effectively a constant over regional scales and is encompassed in temperature, thus allowing bleaching to be modelled effectively by thermal criteria alone.

The results of the aerial surveys (Chapter 2) indicate that this methodology can provide a spatially comprehensive overview of bleaching as well as information on the relative intensity of bleaching from reef to reef, and region to region. To my knowledge, this is the first study where aerial survey techniques have been applied to documenting a bleaching event. Estimates of bleaching intensities from aerial surveys were generally lower than ground-truth estimates, but the bias was consistent enough to provide an overview of general patterns in bleaching. An equivalent overview of bleaching could not be practically obtained using visitor-based reports, or small-scale in-situ survey techniques. However, future use of aerial surveys for documenting bleaching must include a ground truth component to calculate the error associated with estimating the intensity of bleaching and to provide a basis for comparisons between bleaching events.

7.2. Upper thermal limits and climate sensitivity

A number of experimental studies have shown that the upper thermal limits of corals vary from place to place and from species to species (e.g. Coles et al. 1976, Glynn and D'Croz 1990), but prior to this study few data have been published on the upper thermal limits of corals on the Great Barrier Reef (GBR). I establish the 5-day bleaching thresholds for 3 common species of coral, *Pocillopora damicornis*, *Acropora formosa* and *A. elseyi,* in the central inshore GBR (Chapter 4). These bleaching thresholds were found to be equivalent to the classic physiological determination of upper thermal limits, as more than 50% bleaching corresponded to more than 50% mortality. Bleaching thresholds varied relatively little between these species (~1°C), but importantly, were only 2-4°C higher than mean summer temperatures for Orpheus Island (Chapter 3) and within 1°C of daily mean temperatures for considerable periods each summer (Chapter 4). The clear cut-off between tolerable and intolerable temperatures in these experiments, and the proximity of these temperatures to those routinely experienced in summer, confirms the precarious existence of many tropical coral populations (Jokiel and Coles 1990). Relative to mean summer temperatures, these bleaching thresholds are equivalent to those determined for *P. damicornis* at Hawaii, the Marshall Islands and the Gulf of Panama (Coles et al. 1976, Glynn and D'Croz 1990).

A novel empirical approach to quantify bleaching thresholds in terms of temperature and time at a reef-wide scale (Chapter 6) confirms that bleaching thresholds vary in a manner that correlates strongly with ambient summer temperatures (Chapter 3). Together with experimental data, these results suggest that local adaptations in upper thermal limits are inextricably linked to ambient temperature regimes. The implications of this are twofold. Firstly, upper thermal limits can be predicted fairly precisely for thermally sensitive genera like *Acropora* and *Pocillopora* based on local sea temperature climatology. This point also explains why the 'rule-of-thumb' approach in satellite 'HotSpot' predictions of bleaching, whereby predictions are based on anomalies of ≥1°C above local monthly maxima, generally works well (Strong et al. 1997). Secondly, if climate change affects all regions equally, coral populations in warm-adapted regions (e.g. Magnetic Island, central GBR) theoretically have no more advantage than those from cool-adapted regions (e.g. Halfway Island, southern GBR). However, indications to date are that different regions within the GBR are not warming at equal rates. Over the period 1903-1994, yearly average temperatures in the southern GBR (latitude 23.5°S) rose by an average of 0.8°C, whereas those in the northern GBR (latitude 11.5°S) rose by <0.3°C (Lough 1999). If temperature anomalies follow annual mean trends, the southern GBR is likely to be at greater risk from climate warming than the northern GBR.

In addition to a north-south gradient in the risk of reefs to temperature anomalies associated with climate warming (Pittock 1999), I also found evidence of an inshore-offshore risk gradient. The patterns exhibited in six mass bleaching events on the GBR, including a detailed aerial survey during the 1998 event, indicates that inshore reefs have a greater propensity to bleach than offshore reefs (Chapter 2). This effect may be due to greater and more rapid warming of inshore compared to offshore waters during bleaching events (Chapter 3). During the 1998 bleaching event, Magnetic Island daily mean temperatures were 2 – 2.5°C warmer than Kelso and Myrmidon Reef offshore, whereas temperature differences were only 1 – 1.5°C for the three-week period prior to the bleaching event. Such amplified temperature differences are most likely the result of shallow inshore waters having a much smaller thermal inertia than deeper offshore waters causing them to warm up more rapidly and to a greater extent than offshore waters.

7.3. The Potential for Acclimation and Adaptation

The time-temperature curves presented in Chapter 6 suggest that considerable adaptation in the bleaching thresholds of coral populations and assemblages may have taken place over cross-shelf and latitudinal gradients. Inshore reefs generally have 'warmer' curves than offshore reefs at the same latitude and northern (low latitude) reefs have 'warmer' curves than southern (high latitude) reefs. Bleaching threshold curves for coral assemblages at Magnetic Island and the Daintree coast are exceptions to the inshore latitudinal pattern, most likely because of their unusually warm thermal regimes. It is not known how long it has taken for this adaptation to take place nor the rapidity of the temperature rise to which corals were exposed, but such differences in bleaching threshold curves indicate that adaptation to different thermal environments has occurred within the Great Barrier Reef region.

Seasonal shifts in the upper thermal limits of *P. damicornis* (Chapter 4) indicate that resistance acclimatisation can take place in corals. However, this does not indicate that existing summer limits can be extended. An experiment to test the possibility of pushing the summer thermal boundaries in *P. damicornis* and *Porites cylindrica* over a 10-day period was unsuccessful (Chapter 5). No acclimatory ability was displayed by either species. The time needed for most organisms to acclimate to high temperatures is relatively short (e.g. less than 24 hours for bullfish (Brett 1956, Crawshaw 1975); 4 days to full capacity acclimation for crayfish (Bullock 1954)). Based on the rate of acclimation in these and other studies (e.g. Prosser 1973), the 10-day acclimation time afforded to corals in my experiments, should have been adequate to solicit an acclimation response, if one existed. The lack of resistance acclimation in these corals contrasts with an impressive acclimation response in many fishes. Goldfish (*Carassius auratus*) for example, can change their upper thermal limits from 29° to 39°C and the bullfish, *Ameiurus nebulosus*, from 27° to 37°C (Brett 1956). The acclimation responses in these fish correlate with seasonal and/or diurnal temperature ranges which occur in their natural environment. However, despite the large diurnal variation in temperature experienced on the reef flat compared to the reef slope at Orpheus Island (Chapter 3), I found no discernable difference in the upper thermal limits between these two habitats in two species of coral (Chapter 4). Although these results are only from one location and for a few species, they are not encouraging with respect to the potential of corals to adapt to rapid climate change. However, an acclimation response in corals over longer time periods may still occur as indicated by the increased survival times of *Montipora verrucosa* after 56 days of exposure to higher temperatures (Coles and Jokiel 1978). A small acclimation response of even 1°C would make a big difference to current predictions of climate change effects on reefs (Hoegh-Guldberg 1999). Longer-term studies involving both controlled acclimation and field acclimatization of corals are required to evaluate the potential of corals to cope with temperature rises over short timeframes.

7.4 Relevance to management

Climate change looms as the biggest medium-term (30-50 years) threat to reefs globally (Hoegh-Guldberg 1999). As climate change is a global-scale threat, little can be done by reef management agencies. However, at local and regional scales, reef management agencies can work to minimize additional impacts from anthropogenic activities. Sediment, nutrients, herbicides, pesticides and other pollutants carried into the sea by rivers have the potential to adversely affect reef communities (Haynes and Michalek-Wagner 2000). These pollutants could cause chronic long-term stress to reefs and make them less resilient to disturbances such bleaching events. Over-extraction of herbivorous fish, sea urchins and other grazers could hinder recovery of reefs affected by bleaching further (e.g. Hughes 1994). As inshore reefs are at greater risk of bleaching than offshore reefs on the GBR, and inshore reefs are also under greater influence of river runoff, the need for good land management practices and prudent fisheries management is especially important.

Information on the scale, intensity and patterns of disturbances such as coral bleaching are important to reef managers. These data provide a background against which to measure changes which may be human-induced and help understand the processes controlling the abundance and distribution of organisms (Andrew and Mapstone 1987). However, there may also be a public and political demand for information on large-scale disturbances that reef managers need to satisfy. Coral bleaching is controversial and has a high profile in the public domain. High quality information on bleaching disturbances is essential to keep public debate focussed and in perspective. Equally important, this information must be available within short time frames (weeks) to be of value in public debate. The aerial survey method used to document the 1998 coral bleaching event was quick (10 flying days spread over one month), comprehensive and cost effective (<$10,000 in aircraft charter). A preliminary assessment on the scale and intensity of the bleaching event was available within days of the aerial survey. Such a high quality and rapid overview of bleaching could not have been obtained using conventional in-situ video or manta tow surveys, or by soliciting bleaching reports from reef visitors. Unfortunately aerial surveys, or any remote sensing methods, cannot provide reliable information on mortality as a result of coral bleaching. This level of information is of equal (if not greater) importance than the bleaching information itself. In-situ methods, such as video or line transects, to estimate coral cover before (or during) bleaching and after recovery, remain the most viable options. Despite the need for lengthy and costly follow up surveys to quantify bleaching related mortality, the aerial surveys satisfied an important and urgent need of the Great Barrier Reef Marine Park Authority for information at the time of the 1998 bleaching event.

7.5. Summary and conclusions

1. A review of historical mass bleaching events based on visitor reports, and a dedicated aerial survey of a recent bleaching event, indicates that inshore reefs have a greater propensity to bleach than offshore reefs. Climate trends in sea temperature on the GBR over most of the 20th century also indicate that the southern GBR is warming at a greater rate than the northern GBR. Hence inshore, southern reefs may be at greater risk of temperature anomalies due to climate change than other areas on the GBR.
2. The aerial survey method of documenting coral bleaching provides a cost-effective, but conservative, overview of the extent and relative intensity of bleaching over large spatial scales.
3. Recovery after the 1998 bleaching event on the GBR was generally good, especially at offshore reefs. Only a few inshore reefs in the Palm Island and Whitsunday island areas suffered moderate to high mortality.
4. Reef flat environments experience much greater temperature variation (both daily and seasonal) than reef slope environments, although mean daily temperatures are nearly identical at most times.
5. The maximum upper thermal limits of three species of corals are defined for Orpheus Island. No variation in the upper thermal limits of corals were found between the reef slope and flat, or between sites 3km apart. Winter upper thermal limits were 1°C lower than summer limits in one species.
6. A 'delayed' response in bleaching was evident in 2 separate experimental studies whereby the condition of corals deteriorated for up to six weeks after removal of thermal stress. This has implications for the timing of bleaching

surveys after temperature stress. The duration of bleaching also implies that an additional mechanism (over and above the effect of heat on the dark-reaction cycle in zooxanthellae) may be associated with the breakdown of coral-algal symbiosis.

7. No increase in the thermal resistance of two coral species from Orpheus Island was found after short-term (10-day) acclimation.
8. A method is proposed to define bleaching thresholds for reefs that takes into account both the magnitude and duration of thermal stress. These time-integrated bleaching thresholds helped identify an erroneous assumption in commonly used indices of accumulated heat stress, such as ‘degree-days’ or ‘degree-heating-weeks’, that time and temperature contribute equally to thermal stress.
9. Time-temperature curves for coral bleaching indicate that spatial trends exist in the bleaching thresholds of reefs over a wide geographical area. These trends correlate generally with latitude, but more specifically with local environmental temperature regimes, and suggest that thermal adaptation has taken place over small (10’s km) and large (100’s – 1000’s km) spatial scales.

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Appendix A. Records of coral bleaching on the Great Barrier Reef obtained from reported observations (1980 – 1994) predominantly by scientists and reef managers and aerial survey data (1998). Blank spaces denote no information.

Reef	Reef Id	Latitude (S)	Longitude (E)	1980	1982	1987	1992	1994	1998
North Ledge Rf	10-325	10.68	142.74						bleached
South Ledge Rf	10-327	10.70	142.73						bleached
Wyborne Rf	10-336	10.82	142.76						bleached
Unnamed	10-338	10.80	142.98						bleached
Turtle Is	10-340	10.89	142.70						bleached
Arnold Is	11-001	11.01	142.99						bleached
Unnamed	11-008	11.25	142.82						bleached
Bushy Is	11-009	11.26	142.87						bleached
Caircross Islets	11-010	11.25	142.93						bleached
Halfway Is	11-013	11.39	142.97						bleached
Unnamed	11-025	11.07	143.09						bleached
Sinclair Is	11-026	11.11	143.02						bleached
Unnamed	11-034	11.17	143.10						bleached
Aplin Islet	11-035	11.18	143.03						bleached
Douglas islet	11-038	11.24	143.00						bleached
Cholmondeley Islet	11-052	11.39	143.07						bleached
Wallace Is	11-055	11.46	143.04						bleached
Little Boydong	11-061	11.49	143.04						bleached
Unnamed	11-091	11.40	143.96						unbleached
Hunter Rf	11-132	11.51	142.87						bleached
Hannibal Is	11-136	11.60	142.94						bleached
Macarthur Is	11-138	11.73	142.99						bleached
Unnamed	11-139	11.76	142.97						bleached
Unnamed	11-142	11.77	142.94						bleached
Nigger Head	11-146	11.80	142.94						bleached
Unnamed	11-150	11.84	142.94						bleached
Wizard Rf	11-156	11.55	143.02						bleached
Viking Rf	11-161	11.60	143.01						bleached
Bird Is	11-167	11.77	143.08						bleached
Cockburn Is	11-173	11.82	143.36						unbleached
Unnamed	11-175	11.87	143.30						unbleached
Rodney Is	11-176	11.90	143.11						bleached
Nob Is	11-185	11.95	143.27						bleached
Unnamed	11-186	11.96	143.27						bleached
Hicks Is	11-191	11.99	143.26						bleached
Yule Detached Rf	11-240	11.95	143.99						unbleached
Raine Is	11-243	11.59	144.04						unbleached
Haggerstone Is	12-001	12.03	143.30						bleached
Moodey Rf	12-004	12.10	143.26						bleached
Laurel Rf	12-006	12.14	143.27						unbleached
Nomad Rf	12-007	12.14	143.37						bleached

Reef	Reef Id	Latitude (S)	Longitude (E)	1980	1982	1987	1992	1994	1998
Wishbone Rf	12-037	12.08	143.97						unbleached
Mantis Rf	12-056	12.27	143.92						unbleached
Lloyd Is	12-084	12.75	143.40						bleached
May Rf	12-086	12.086	12.78			bleached			
Burke Rf	12-105	12.64	143.56						bleached
Ape Rf	12-112	12.71	143.61						bleached
Zennith Rf	12-115	12.77	143.61						bleached
Bligh Rf	12-118	12.83	143.84						unbleached
Wye rf	12-119	12.81	143.61						bleached
Ham Rf	13-005	13.04	143.87						unbleached
Unnamed	13-016	13.08	143.91						unbleached
Tijou Rf	13-028	13.14	143.95						unbleached
Unnamed	13-040	13.27	143.94						unbleached
Unnamed	13-077	13.56	143.84						unbleached
Unnamed	13-078	13.64	143.92						unbleached
Lytton Rf	13-088	13.74	143.91						unbleached
Hedge Rf	13-108	13.91	143.95						unbleached
Grub Rf	14-003	14.01	143.98						unbleached
Corbett Rf	14-016	13.98	144.11						unbleached
Clack Rf	14-017	14.07	144.24						unbleached
King Is	14-018	14.10	144.32						bleached
Unnamed	14-053	14.31	144.79						unbleached
Stapleton Islet	14-054	14.32	144.86						unbleached
Combe Rf	14-063	14.42	144.95						unbleached
Cresent Rf	14-082	14.42	145.10						unbleached
Parke Rf	14-083	14.42	145.32						unbleached
Hilder Rf	14-085	14.45	145.41						unbleached
Hicks Rf	14-086	14.45	145.48						unbleached
Day Rf	14-089	14.50	145.54						unbleached
Petricola Shoal	14-113	14.63	145.48						unbleached
MacGillivray Rf	14-114	14.65	145.49						unbleached
Nymph Is	14-115	14.66	145.25						unbleached
Lizard Is, Palfrey Is	14-116	14.66	145.47						unbleached
Lizard Is	14-116	14.66	145.45		bleached	bleached	unbleached		unbleached
Lizard Is, South Is	14-116	14.68	145.47						unbleached
Eyrie Rf	14-118	14.71	145.38						unbleached
Turtle Rf	14-120	14.72	145.19						bleached
Turtle Rf	14-120	14.73	145.18						bleached
Turtle Rf	14-120	14.73	145.19						bleached
Turtle Rf	14-120	14.74	145.20						bleached
Decapolis Rf	14-131	14.85	145.27	bleached	bleached				bleached
No Name	14-133	14.92	145.51						unbleached
Helsdon Rf	14-135	14.94	145.48						unbleached
Carter Rf	14-137	14.55	145.59						unbleached
Yonge Rf	14-138	14.60	145.62						unbleached

Reef	Reef Id	Latitude (S)	Longitude (E)	1980	1982	1987	1992	1994	1998
No Name Rf	14-139	14.65	145.65						unbleached
North Direction Is	14-143	14.74	145.51				unbleached		unbleached
Ribbon No 10	14-146	14.83	145.70				unbleached		
South Direction Is	14-147	14.81	145.52						unbleached
South Direction Is	14-147	14.82	145.52						unbleached
No Name	14-150	14.88	145.56						unbleached
Unnamed	14-151	14.92	145.69						unbleached
Unnamed	14-152	14.93	145.68						unbleached
Ribbon No 9	14-154	14.99	145.70				unbleached		unbleached
Two Islands	15-002	15.02	145.44						bleached
Low Wooded Is	15-003	15.10	145.38						bleached
Three Islands	15-005	15.11	145.42						bleached
Conical Rock, east	15-006	15.14	145.32						bleached
Conical Rock, west	15-006	15.14	145.32						bleached
Beor Rf	15-008	15.16	145.27						bleached
Boulder Rf	15-012	15.41	145.43						bleached
Egret Rf	15-013	15.47	145.42				unbleached		bleached
Pasco Rf	15-018	15.05	145.53						unbleached
Long Rf	15-019	15.05	145.57						unbleached
Ribbon No 8	15-021	15.08	145.72						unbleached
Makay Rf	15-024	15.14	145.58						unbleached
Harrier Rf	15-025	15.14	154.70				unbleached		
Marx Rf	15-027	15.20	145.62						unbleached
Startle Rf	15-028	15.21	145.56				unbleached		unbleached
Swinger	15-030	15.24	145.54				unbleached		
Pullen Rf	15-031	15.25	145.58						unbleached
Ribbon No 7	15-032	15.28	145.75						unbleached
No Name	15-035	15.32	145.64						unbleached
No Name	15-036	15.33	145.65						unbleached
Ribbon No 5	15-038	15.37	145.78				unbleached		
Williamson	15-039	15.36	145.58						unbleached
No Name	15-043	15.43	145.51				unbleached		
No Name	15-044	15.43	145.61						unbleached
No Name	15-047	15.46	145.68				unbleached		unbleached
No Name	15-048	15.49	145.65						unbleached
Gubbins Rf	15-063	15.71	145.39						bleached
West Hope Is	15-064	15.74	145.44						bleached
East Hope Is	15-065	15.74	145.46						bleached
No Name	15-066	15.94	145.40						bleached
No Name	15-069	16.00	145.44						bleached
No Name	15-070	15.50	145.62				unbleached		unbleached
No Name	15-077	15.56	145.65						unbleached
Rosser Rf	15-081	15.61	145.51				unbleached		
Emily Rf	15-082	15.61	145.63						unbleached
Cairns Rf, NE side	15-086	15.69	145.50						bleached

Reef	Reef Id	Latitude (S)	Longitude (E)	1980	1982	1987	1992	1994	1998
Cairns Rf, SE side	15-086	15.69	145.50						bleached
Ruby Rf	15-088	15.75	145.78				unbleached		
Endeavour Rf	15-089	15.78	145.58				unbleached		bleached
Andersen Rf	15-090	15.79	145.80				unbleached		
Pickersgill Rf	15-093	15.88	145.57						unbleached
Escape Rf	15-094	15.88	145.79				unbleached		
Evening Rf	15-095	15.91	145.66						unbleached
Agincourt No 4	15-096	15.95	145.82				bleached		
Agincourt No 2	15-099	16.02	145.85			bleached			
Agincourt No 1	15-099	16.05	145.86				unbleached		
No Name	16-002	16.06	145.47					unbleached	bleached
No Name	16-003	16.10	145.47			bleached			
Snapper Is, N side	16-006	16.30	145.50						bleached
Snapper Is, S side	16-006	16.30	145.50						bleached
Unnamed	16-013	16.10	145.47						
Unnamed	16-014	16.03	145.71						bleached
Unnamed	16-017	16.08	145.72					unbleached	
St Crispins Rf	16-019	16.11	145.84						bleached
Undine Rf	16-020	16.13	145.67					unbleached	unbleached
Rudder Rf	16-023	16.19	145.70						unbleached
Opal Rf	16-025	16.22	145.89				unbleached		
Low Isles	16-028	16.39	145.56				bleached		bleached
Batt Rf	16-029	16.42	145.77						bleached
Norman Rf	16-030	16.43	145.99			bleached		unbleached	bleached
Saxon Rf	16-032	16.47	145.99					unbleached	
Egmont Rf	16-038	16.53	145.54						bleached
Alexandra Rf	16-039	16.55	145.50						bleached
No Name	16-041	16.55	145.95					unbleached	
No Name	16-042	16.58	145.98					unbleached	
Oyster Rf	16-043	16.64	145.93					unbleached	
Middle Cay	16-044	16.65	145.98					unbleached	
Upolo Cay	16-046	16.67	145.94					unbleached	bleached
Double Is	16-047	16.73	145.68						bleached
Green Is, NW side	16-049	16.77	145.99	bleached			unbleached	unbleached	bleached
Green Is, NE side	16-049	16.77	145.99						bleached
Fitzroy Is	16-055	16.92	146.00						bleached
Hastings Rf	16-057	16.52	146.01	bleached			unbleached	unbleached	
No Name	16-059	16.52	146.01					unbleached	
Michaelmas Rf	16-060	16.58	146.02	bleached			unbleached	unbleached	
Pretty Patches	16-062	16.62	146.04					unbleached	
Euston Rf	16-063	16.69	146.25						bleached
Arlington Rf,SE and S side	16-064	16.70	146.05					unbleached	bleached
Arlington Rf, SW side	16-064	16.70	146.05					unbleached	bleached
Flynn Rf	16-065	16.74	146.27					unbleached	
Milne Rf	16-067	16.79	146.27					unbleached	

Reef	Reef Id	Latitude (S)	Longitude (E)	1980	1982	1987	1992	1994	1998
Thedford Rf	16-068	16.80	146.18					unbleached	
Moore Rf	16-071	16.87	146.21					unbleached	unbleached
Elford Rf	16-073	16.92	146.25					unbleached	unbleached
Briggs Rf, NW side	16-074	16.94	146.21					unbleached	bleached
Briggs Rf, SE side	16-074	16.94	146.21						bleached
Korea Rf	16-080	16.56	145.55						bleached
Sudbury Rf	17-001	17.02	146.22						bleached
Scott Rf, SW side	17-004	17.07	146.18						bleached
Scott Rf, lagoon	17-004	17.07	146.18						bleached
Scott Rf, SE side	17-004	17.07	146.18						bleached
High Is, east	17-009	17.15	146.01						bleached
High Is, south	17-009	17.15	146.01						bleached
Flora Rf	17-010	17.19	146.29						bleached
Coats Rf	17-011	17.20	146.37						bleached
Franklins, Mabel Is west	17-012	17.22	146.08						bleached
Franklins, Normanby Is east	17-012	17.21	146.08						bleached
Franklins, Normanby Is west	17-012	17.21	146.08						bleached
Franklins, Round Is west	17-013	17.23	146.09						bleached
Franklins, Russel Is east	17-013	17.23	146.09						bleached
Franklins, Russel Is west	17-013	17.23	146.09						bleached
Hedleys Rf	17-014	17.23	146.48					unbleached	
Gibson Rf, on reef edge	17-017	17.30	146.36						bleached
Gibson Rf, bommies on east side	17-017	17.30	146.36						bleached
Howie Rf, east side	17-018	17.40	146.40						bleached
Howie Rf, lagoon	17-018	17.38	146.42						bleached
Peart Rf	17-024	17.49	146.39						bleached
Wardle Rf	17-032	17.43	146.54					unbleached	
Feather Rf	17-034	17.53	146.38					unbleached	bleached
Nathan Rf, NW side	17-035	17.53	146.52						bleached
Nathan Rf, east side	17-035	17.53	146.52						bleached
Hall-Thompson Rf	17-037	17.61	146.45						bleached
Adelaide Rf	17-042	17.66	146.47						bleached
North Barnard, Hutchison Is	17-043	17.68	146.17						bleached
North Barnard, Linquist Is	17-043	17.67	146.17						bleached
North Barnard, Kent Is	17-043	17.68	146.18						bleached
Ellison Rf, NE bommies	17-044	17.72	146.39					unbleached	bleached
Ellison Rf, SE edge	17-044	17.72	146.39						bleached
South Barnard Is, Sister Is	17-046	17.75	146.15						bleached
South Barnard Is, Stevens Is	17-046	17.75	146.15						bleached
South Barnard Is, main reef on east	17-046	17.75	146.15						bleached
Eddy Rf	17-047	17.77	146.44						bleached
King Rf	17-048	17.77	146.12						bleached

Reef	Reef Id	Latitude (S)	Longitude (E)	1980	1982	1987	1992	1994	1998
Beaver Rf	17-051	17.85	146.49					unbleached	bleached
Dunk Is, SE side	17-053	17.96	146.15						bleached
Dunk Is, NE side	17-053	17.96	146.15						bleached
Dunk Is, S side	17-053	17.96	146.15						bleached
Unnamed shoal	17-054	17.97	146.14						bleached
Thorpe Is	17-055	17.98	146.13						bleached
Potter Rf	17-059	17.70	146.54						bleached
No Name	17-060	17.74	146.50						unbleached
Farquharson Rf, east side	17-063	17.79	146.52						unbleached
Farquharson Rf, lagoon	17-063	17.79	146.52						bleached
Taylor Rf	17-064	17.83	146.55						unbleached
No Name	17-066	17.89	146.59						bleached
Moss Rf	17-068	17.95	146.80						bleached
No Name	17-069	18.00	146.77						bleached
Coombe Is	18- 004	18.00	146.18						bleached
Richards Is	18-001	18.01	146.15						bleached
Wheeler Is	18-003	18.02	146.17						bleached
Smith Is	18-005	18.04	146.20						bleached
Hudson Is	18-006	18.05	146.20						bleached
Bowden Is	18-006	18.05	146.21						bleached
Kennedy Shoal	18-007	18.08	146.45						bleached
Brook Is, Middle Is	18-008	18.15	146.29					bleached	bleached
Brook Is, Tween Is	18-008	18.15	146.29						bleached
Brook Is, South Is	18-008	18.15	146.29						bleached
Brook Is, North Is, south side	18-008	18.15	146.29						bleached
Brook Is, North Is, north side	18-008	18.15	146.29						bleached
Goold Is, east side	18-010	18.17	146.15						bleached
Goold Is, Hayman Point	18-010	18.17	146.15						bleached
Goold Is, south side	18-010	18.17	146.15						bleached
Eva Rock	18-013	18.24	146.32						bleached
No Name	18-017	18.04	146.79						bleached
Otter Rf	18-018	18.05	146.56					unbleached	bleached
Duncan Rf	18-020	18.10	146.80						bleached
No Name	18-023	18.14	146.97						bleached
Britomart Rf	18-024	18.23	146.73	bleached	bleached				unbleached
No Name	18-026	18.32	146.74					unbleached	unbleached
Trunk Rf	18-027	18.35	146.83						bleached
Bramble Rf, S side	18-029	18.41	146.71						bleached
Bramble Rf, SE side	18-029	18.41	146.71						bleached
Kelso Rf	18-030	18.43	146.99					unbleached	bleached
Little Kelso	18-031	18.47	146.99						unbleached
Rib Rf	18-032	18.48	146.87		bleached	unbleached			bleached
Myrmidon Rf	18-034	18.27	147.39		bleached	unbleached			bleached
Dip Rf	18-039	18.41	147.45		bleached				unbleached

Reef	Reef Id	Latitude (S)	Longitude (E)	1980	1982	1987	1992	1994	1998
Faraday Rf	18-041	18.42	147.35						unbleached
Coil Rf	18-046	18.44	147.52						unbleached
Pelorus Is, South side	18-048	18.56	146.49						bleached
Pelorus Is, East side	18-048	18.56	146.49						bleached
Pelorus Is, West side	18-048	18.56	146.49			bleached			bleached
Orpheus Is, NE Reef	18-049	18.59	146.50					bleached	bleached
Orpheus Is, Harrier Point	18-049	18.66	146.49					bleached	bleached
Orpheus Is, Pioneer Bay	18-049	18.60	146.49					bleached	bleached
Orpheus Is, Hazard Bay	18-049	18.64	146.49					bleached	bleached
Orpheus Is, SE side	18-049	18.64	146.50					bleached	bleached
Pandora Rf	18-051	18.81	146.43		bleached	unbleached		bleached	bleached
Curacao Is, NE side	18-052	18.67	146.56						bleached
Curacao Is, SW side	18-052	18.68	146.55						bleached
Fantome Is	18-053	16.68	146.51					bleached	
Great Palm, NE Bay	18-054	18.74	146.64						bleached
Great Palm, Sinballa Point	18-054	18.68	146.58						bleached
Great Palm, unnamed bay	18-054	18.70	146.60						bleached
Great Palm, Coolgaree Bay	18-054	18.72	146.58						bleached
Great Palm, Hayman Rock	18-054	18.74	146.69						bleached
Eclipse Is	18-058	18.77	146.55		bleached				bleached
Esk Is	18-059	18.78	146.52						bleached
Falcon Is	18-062	18.78	146.53						bleached
Fly Is	18-064	18.83	146.52						bleached
Havanna Is	18-065	18.84	146.54						bleached
Acheron Is, north	18-066	18.97	146.63						bleached
Acheron Is, south	18-066	18.97	146.63						bleached
Yankee Rf	18-074	18.57	147.49						bleached
John Brewer Rf	18-075	18.63	147.05			unbleached	unbleached		unbleached
Helix Rf	18-076	18.63	147.29				unbleached		
Lodestone Rf	18-078	18.70	147.10			unbleached			bleached
Keeper Rf	18-079	18.75	147.27						bleached
Bowl Rf	18-080	18.51	147.54						unbleached
Cup Rf	18-084	18.62	147.61						unbleached
Cup Rf	18-084	18.64	147.59						unbleached
Cup Rf	18-084	18.66	147.60						unbleached
Centipede Rf	18-088	18.73	147.54						bleached
No Name	18-090	18.73	147.84						bleached
Lynch's Rf	18-091	18.77	147.71						bleached
No Name	18-094	18.78	147.87						bleached
Wheeler Rf	18-095	18.80	147.53						unbleached
Davies Rf	19-096	18.82	147.65		bleached	unbleached		unbleached	
No Name	18-099	18.86	147.89						bleached
Big Broadhurst Rf	18-100	18.92	147.74		bleached				unbleached
Big Broadhurst, north side	18-100	18.87	147.72						bleached

Reef	Reef Id	Latitude (S)	Longitude (E)	1980	1982	1987	1992	1994	1998
No Name, NE side	18-101	18.90	147.96						bleached
No Name, SE side	18-101	18.90	147.96						bleached
Little Broadhurst rf	18-106	18.97	147.70						unbleached
Shrimp Rf	18-118	18.95	148.08						bleached
Herald Is	19-002	19.03	146.63						bleached
Paluma Shoals	19-005	19.10	146.56						bleached
Geoffrey Bay	19-009	19.16	146.87	bleached	bleached		bleached	bleached	bleached
Nelly Bay	19-009	19.17	146.85	bleached	bleached		bleached	bleached	bleached
Picnic Bay	19-010	19.19	146.84						bleached
Middle Reef	19-011	19.20	146.81					bleached	bleached
Virago Shoal	19-012	19.21	146.80						bleached
Salamander Rf	19-013	19.18	147.06						bleached
Bowden Rf	19-019	19.04	147.93						unbleached
Prawn Rf	19-024	19.02	148.11						bleached
Caster Rf	19-025	19.02	148.32						unbleached
Shell Rf	19-028	19.07	148.18						unbleached
Mid Rf	19-029	19.07	148.08						unbleached
Dingo Rf, north	19-038	19.13	148.47						unbleached
Dingo Rf, south	19-038	19.18	148.38						bleached
Darley Rf	19-043	19.21	148.17						bleached
Faith Rf	19-044	19.28	148.35						bleached
Stanley Rf	19-045	19.30	148.08						unbleached
Hope Rf	19-046	19.32	148.43						bleached
Charity Rf	19-047	19.37	148.34						bleached
Old Rf	19-048	19.39	148.09		bleached				unbleached
Tiger Rf	19-054	19.21	148.54						bleached
Kangaroo Rf	19-063	19.26	148.55						unbleached
Kangaroo Rf	19-063	19.26	148.63						bleached
No Name	19-066	19.34	148.63						bleached
No Name	19-067	19.36	148.64						bleached
Wallaby Rf	19-071	19.43	148.66						unbleached
Gould Rf	19-072	19.50	148.74						bleached
Gould Rf	19-072	19.50	148.78						bleached
Gould Rf	19-072	19.40	148.78						unbleached
Cobham Rf	19-074	19.40	148.87						unbleached
Martin Rf	19-075	19.48	148.82						unbleached
Showers Rf	19-076	19.49	148.90						unbleached
Cape Upstart, middle	19-101	19.73	147.76						bleached
Cape Upstart, Windy Point	19-101	19.73	147.76						bleached
Camp Is	19-102	19.86	147.89						bleached
Holbourne Is	19-103	19.73	148.36			bleached			unbleached
Seagull Rf	19-107	19.53	148.98						unbleached
No Name	19-108	19.53	148.88						unbleached
Fairey Rf	19-109	19.56	148.93						unbleached
Fairey Rf	19-109	19.54	148.94						unbleached

Reef	Reef Id	Latitude (S)	Longitude (E)	1980	1982	1987	1992	1994	1998
Rattray Is	19-110	20.00	148.56						bleached
Line Rf	19-128	19.69	149.19						unbleached
No Name	19-129	19.75	149.31						unbleached
No Name	19-131	19.76	149.37					unbleached	unbleached
Black Rf	19-132	19.76	149.40						unbleached
Sinker Rf	19-133	19.72	149.20						unbleached
Black Rf East	19-134	19.75	149.49						unbleached
Hardy Rf	19-135	19.76	149.23			bleached		unbleached	unbleached
Hook Rf	19-136	19.80	149.20						bleached
Hook Rf	19-136	19.82	149.12						bleached
Bait Rf	19-137	19.81	149.07					unbleached	bleached
No Name	19-138	19.80	149.42					unbleached	
Plaster Rf	19-147	19.63	149.67					unbleached	
Ross Rf	19-197	19.88	149.58					unbleached	unbleached
Tydeway Rf	19-205	20.01	149.72						unbleached
Hyde Rf	19-207	19.75	150.08					unbleached	
Rebe rf	19-209	19.80	150.15					unbleached	
Unnamed Rf	20-001	20.01	148.27						bleached
Unnamed Rf	20-002	20.02	148.27						bleached
Stone Is, north side	20-004	20.04	148.28						bleached
Dingo Bch, north of Champayne Bay	20-010	20.08	148.49						bleached
Dingo Bch, Champayne Bay	20-010	20.08	148.49						bleached
Dingo Bch, Nelly Bay	20-010	20.08	148.49				bleached		bleached
Eshelby Is	20-012	20.02	148.62						bleached
Hayman Is, north	20-014	20.07	148.89						bleached
Hayman Is, Blue Pearl Bay	20-014	20.07	148.89					unbleached	bleached
Hayman Is, Akhurst Is	20-014	20.07	148.89						bleached
Saddleback Is, east	20-015	20.07	148.54						bleached
Saddleback Is, north	20-015	20.07	148.54						bleached
Olden Is	20-021	20.11	148.57						bleached
Armit Is, south	20-022	20.11	148.65						bleached
Armit Is, north	20-022	20.11	148.65						bleached
Grassy Is, north	20-027	20.13	148.61						bleached
Hook Is	20-028	20.07	148.93			bleached			bleached
Hook Is	20-028	20.07	148.95						bleached
Hook Is, NE side	20-028	20.08	148.96						bleached
Hook Is	20-028	20.07	148.93						bleached
Hook Is, NE tip	20-028	20.07	148.96						bleached
Grassy Is, south	20-030	20.15	148.61						bleached
North Molle Is	20-033	20.22	148.81						unbleached
West Molle Is (Daydream Is)	20-035	20.26	148.81						unbleached
South Molle Is	20-042	20.26	148.84					unbleached	unbleached
Henning Is	20-053	20.32	148.93						unbleached
Dent Is	20-058	20.34	148.93						unbleached

Reef	Reef Id	Latitude (S)	Longitude (E)	1980	1982	1987	1992	1994	1998
Hamilton Is, south	20-059	20.36	148.96						unbleached
Hamilton Is, north	20-059	20.34	148.97						unbleached
Hamilton Is, east	20-059	20.37	148.96						unbleached
Border Is, SW side	20-067	20.17	149.03					unbleached	bleached
Border Is, north	20-067	20.16	149.03					unbleached	bleached
Dumbell Is	20-068	20.17	149.01						bleached
Harold Is	20-074	20.24	149.15						unbleached
Hazelwood Is	20-078	20.26	149.11						unbleached
Lupton Is	20-078	20.28	149.11						unbleached
Hazelwood Is	20-078	20.28	149.10						unbleached
Deloraine Is	20-089	20.16	149.07						bleached
Comston Is	20-093	20.46	149.10						unbleached
Lindeman Is, south	20-095	20.44	149.03						unbleached
Lindeman Is, east	20-095	20.48	149.05						unbleached
Little Lindeman Is	20-099	20.42	149.03						unbleached
Shaw Is, SE side	20-102	20.51	149.05						unbleached
Shaw Is, north	20-102	20.43	149.08						unbleached
Shaw Is	20-102	20.46	149.08						unbleached
Shaw Is	20-102	20.51	149.05						unbleached
No Name	20-104	20.03	149.69					unbleached	
Ben Rf	20-113	20.00	150.32					unbleached	
Edgell Rf	20-112	20.13	149.94					unbleached	unbleached
No Name	20-128	20.12	150.01						unbleached
No Name	20-129	20.19	150.08						unbleached
Hunt Rf	20-134	20.30	150.10						unbleached
No Name	20-135	20.34	150.13						unbleached
No Name	20-136	20.35	150.07						unbleached
Robertson Rf	20-137	20.35	150.10						unbleached
Bax Rf	20-138	20.35	150.20						unbleached
No Name	20-142	20.40	150.24						unbleached
No Name	20-143	20.45	150.24						unbleached
Packer Rf	20-145	20.47	150.21					unbleached	
Boulton Rf	20-146	20.47	150.29						unbleached
Thomas Is, east	20-234	20.54	149.11						unbleached
Thomas Is, west	20-234	20.54	149.11						unbleached
Goldsmith Is	20-237	20.67	149.16						unbleached
Goldsmith Is	20-237	20.69	149.14						unbleached
Locksmith Is	20-248	20.66	149.15						bleached
Tinsmith Is	20-254	20.70	149.20						bleached
Wigton Is	20-262	20.74	149.48						bleached
Silloth Rocks	20-263	20.77	149.43						bleached
Cockermouth Is	20-269	20.78	149.39						bleached
Brampton Is	20-270	20.82	149.27			bleached			bleached
Keswick Is	20-277	20.91	149.39						bleached
St Bees Is	20-279	20.93	149.43						unbleached

Reef	Reef Id	Latitude (S)	Longitude (E)	1980	1982	1987	1992	1994	1998
St Bees Is	20-279	20.91	149.44						bleached
Credlin Rf	20-287	20.54	149.95					unbleached	unbleached
No Name	20-288	20.56	149.93						unbleached
Little Stevens Rf	20-294	20.57	150.05						unbleached
Big Stevens Rf	20-295	20.57	150.13						unbleached
Liff Rf	20-296	20.52	150.24						unbleached
Creal Rf	20-297	20.54	150.38					unbleached	unbleached
Warland Rf	20-298	20.60	150.38						unbleached
Southampton Rf	20-299	20.65	150.46						unbleached
Cole Rf	20-301	20.68	150.23						unbleached
Cole Rf	20-301	20.66	150.29						unbleached
No Name	20-302	20.70	150.18						unbleached
McIntire Rf	20-304	20.72	150.47					unbleached	unbleached
Tern Is	20-309	20.91	150.03						bleached
Bushy Is	20-310	20.96	150.08						unbleached
No Name	20-351	20.98	150.53						unbleached
No Name	20-351	20.94	150.54						unbleached
Pompey Rf	20-352	20.95	150.66						unbleached
Cockatoo Rf	20-369	20.75	151.02						unbleached
No Name	20-371	20.81	151.09						unbleached
No Name	20-374	20.80	151.16						unbleached
No Name	20-378	20.87	151.25						unbleached
No Name	20-378	20.93	151.24						unbleached
No Name	20-382	20.86	151.30						unbleached
No Name	20-385	20.94	151.32						unbleached
No Name	20-387	20.97	151.25						unbleached
No Name	20-388	20.96	151.36						unbleached
No Name	20-389	20.97	151.40						unbleached
Penrith Is	21-025	21.02	149.90						unbleached
Sandpiper Rf	21-053	21.03	150.08						unbleached
Prince Rf	21-054	21.07	150.26						unbleached
No Name	21-056	21.08	150.45						unbleached
No Name	21-056	21.05	150.51						unbleached
No Name	21-057	21.13	150.48						unbleached
No Name	21-063	21.03	150.92						unbleached
No Name	21-091	21.04	151.56						unbleached
No Name	21-109	21.13	151.08						unbleached
No Name	21-115	21.17	151.04						unbleached
No Name	21-116	21.21	151.01						unbleached
No Name	21-124	21.26	151.13						unbleached
Storm Cay	21-128	21.32	151.17						unbleached
No Name	21-130	21.34	151.28						unbleached
No Name	21-132	21.40	151.33						unbleached
No Name	21-133	21.38	151.25						unbleached
No Name	21-134	21.39	151.28						unbleached

Reef	Reef Id	Latitude (S)	Longitude (E)	1980	1982	1987	1992	1994	1998
No Name	21-136	21.39	151.42						unbleached
No Name	21-137	21.40	151.42						unbleached
No Name	21-138	21.43	151.42						unbleached
No Name	21-144	21.05	151.58						unbleached
No Name	21-146	21.08	151.65						unbleached
No Name	21-147	21.07	151.67						unbleached
No Name	21-148	21.09	151.69						unbleached
No Name	21-149	21.10	151.72						unbleached
No Name	21-150	21.11	151.74						unbleached
No Name	21-151	21.12	151.76						unbleached
No Name	21-152	21.12	151.77						unbleached
No Name	21-157	21.15	151.76						unbleached
No Name	21-158	21.16	151.78						unbleached
No Name	21-159	21.17	151.80						unbleached
No Name	21-161	21.19	151.82						unbleached
No Name	21-165	21.20	151.83						unbleached
No Name	21-166	21.21	151.99						unbleached
No Name	21-168	21.23	151.99						unbleached
Riptide Cay	21-172	21.24	151.85						unbleached
No Name	21-198	21.05	152.21						unbleached
No Name	21-199	21.07	152.19						unbleached
No Name	21-200	21.07	152.23						unbleached
No Name	21-201	21.07	152.46						unbleached
No Name	21-203	21.09	152.24						unbleached
No Name	21-204	21.09	152.28						unbleached
No Name	21-205	21.09	152.50						unbleached
Distant Cay	21-206	21.10	152.49						unbleached
No Name	21-207	21.09	152.14						unbleached
No Name	21-208	21.10	152.17						unbleached
No Name	21-209	21.10	152.26						unbleached
No Name	21-210	21.11	152.31						unbleached
No Name	21-211	21.10	152.35						unbleached
No Name	21-212	21.10	152.16						unbleached
No Name	21-213	21.10	152.20						unbleached
Zodiac Cay	21-214	21.11	152.08						unbleached
No Name	21-215	21.12	152.32						unbleached
No Name	21-216	21.12	152.39						unbleached
No Name	21-217	21.13	152.47						unbleached
No Name	21-218	21.14	152.49						unbleached
No Name	21-219	21.14	152.19						unbleached
No Name	21-222	21.16	152.31						unbleached
No Name	21-225	21.20	152.10						unbleached
No Name	21-238	21.23	152.50						unbleached
No Name	21-246	21.32	152.49						unbleached
Turner Cay	21-252	21.35	152.25						unbleached

Reef	Reef Id	Latitude (S)	Longitude (E)	1980	1982	1987	1992	1994	1998
No Name	21-256	21.36	152.48						unbleached
No Name	21-263	21.42	152.49						unbleached
No Name	21-283	21.14	152.50						unbleached
No Name	21-286	21.18	152.52						unbleached
No Name	21-290	21.20	152.52						unbleached
No Name	21-297	21.36	152.52						unbleached
No Name	21-299	21.38	152.53						unbleached
No Name	21-300	21.40	152.51						unbleached
No Name	21-303	21.47	152.52						unbleached
East Cay	21-305	21.49	152.56						unbleached
Curlew Is	21-334	21.61	149.78						bleached
Pine Peak Is	21-386	21.52	150.26						bleached
Middle Is	21-399	21.69	150.29						bleached
Howard Is	21-401	21.73	150.32						bleached
Bamborough Is	21-414	21.93	150.10						bleached
Till Shoal	21-418	21.95	150.13						bleached
Marble Is	21-423	21.98	150.19						bleached
No Name	21-558	21.56	152.54						unbleached
No Name	21-559	21.58	152.53						unbleached
No Name	21-560	21.67	152.54						unbleached
Bills Rf	21-565	21.79	152.59						unbleached
Blu Lion Rf	21-566	21.83	152.63						unbleached
Triangle Rf	21-570	21.85	152.64						unbleached
Heart Rf	21-575	21.90	152.66						unbleached
Hill Rf	21-579	21.91	152.67						unbleached
Beacon Rf	21-582	21.94	152.68						unbleached
Foller Rf	21-586	21.97	152.70						unbleached
Turtle Is	22-027	22.36	149.77	bleached	bleached				
Shields is	22-030	22.01	150.38						bleached
Collins Is	22-052	22.23	150.31						bleached
Rothbury Is	22-070	22.03	150.65						bleached
Half Moon Rf	22-103	22.01	152.73						unbleached
No Name	22-106	22.06	152.74						unbleached
Hook Rf	22-116	22.10	152.74						unbleached
Sinker Rf	22-121	22.12	152.74						unbleached
Taiwan Rf	22-124	22.15	152.76						unbleached
Sunray Rf	22-131	22.19	152.76						unbleached
Sandshoe Rf	22-133	22.21	152.75						unbleached
Sweetlip Rf	22-140	22.27	152.73						unbleached
No Name	22-142	22.30	152.73						unbleached
No Name	22-143	22.33	152.72						unbleached
Hixson Cay	22-145	22.35	152.73						unbleached
South Hixson Cay	22-147	22.36	152.69						unbleached
Conical Rocks	23-001	23.04	150.88						bleached
Corroboree Is	23-002	23.05	150.88						bleached

Reef	Reef Id	Latitude (S)	Longitude (E)	1980	1982	1987	1992	1994	1998
Outer rocks	23-003	23.98	151.77						bleached
North Keppel Is	23-004	23.08	150.89						bleached
Square Rocks	23-006	23.10	150.88						bleached
Miall Is	23-009	23.15	150.90				bleached		bleached
Middle Is	23-010	23.17	150.91			bleached	bleached		bleached
Bald Rock	23-012	23.17	150.99			bleached			bleached
Halftide Rocks	23-012	23.16	150.96			bleached			bleached
Great Keppel Is	23-012	23.19	150.96			bleached			bleached
Great Keppel Is	23-012	23.15	150.97			bleached			bleached
Halfway Is	23-014	23.20	150.97			bleached	bleached		bleached
Humpy Is	23-016	23.21	150.97				bleached		bleached
Barren Is	23-031	23.16	151.07			bleached	bleached		bleached
Egg rock	23-033	23.20	151.10				bleached		bleached
Wilson Is	23-050	23.29	151.89			bleached			
Wreck Is	23-051	23.33	151.96			bleached			
Heron Is	23-052	23.45	151.96			bleached			bleached
Wistari Rf	23-053	23.47	151.88			bleached			bleached
Sykes Rf	23-054	23.44	152.03						bleached
One Tree, lagoon	23-055	23.50	152.06						bleached
One Tree, outside	23-055	23.50	152.06						bleached
Rundle Is	23-056	23.54	151.27						bleached
Curtis Is	23-059	23.75	151.31						bleached
Pearl Ledge	23-063	23.80	151.37						bleached
Seal Rocks, south	23-067	23.96	151.48						bleached
Erskine Is	23-068	23.50	151.77			bleached			bleached
Masthead Is	23-069	23.54	151.74			bleached			bleached
Polmaise Rf	23-071	23.56	151.68						bleached
Bustard Heads	23-074	23.98	151.66						bleached
Lamont Rf	23-076	23.60	152.04						bleached
Fitzroy Rf, lagoon	23-078	23.70	152.18						bleached
Fitzroy Rf, outside	23-078	23.70	152.18						bleached
Boult Rf	23-079	23.76	152.27						unbleached
Hoskyn Is	23-080	23.81	152.29						unbleached
Fairfax Is	23-081	23.86	152.37						unbleached
Lady Musgrave Is, outside	23-082	23.91	152.41						unbleached
Lady Musgrave Is, lagoon	23-082	23.91	152.41			bleached			bleached
Clews Point	24-003	24.01	151.73						bleached
Lady Elliott Is	24-008	24.11	152.72						bleached