

Major bleaching events can lead to increased thermal tolerance in corals

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Abstract Climate change is a major threat to coral reef ecosystems worldwide. A key determinant of the fate of reef corals in a warming climate is their capacity to tolerate increasing thermal stress. Here, an increase in thermal tolerance is demonstrated for three major coral genera (*Acropora*, *Pocillopora* and *Porites*) following the extensive mass bleaching event that occurred on the Great Barrier Reef (Australia) in 1998. During the subsequent and more severe thermal stress event in 2002, bleaching severity was 30–100% lower than predicted from the relationship between severity and thermal stress in 1998, despite higher solar irradiances during the 2002 thermal event. Coral genera most susceptible to thermal stress (*Pocillopora* and *Acropora*) showed the greatest increase in tolerance. Although bleaching was severe in 1998, whole-colony mortality was low at most study sites. Therefore, observed increases in thermal tolerance cannot be

explained by selective mortality alone, suggesting a capacity for acclimatization or adaptation. Although the vulnerability of coral reefs remains largely dependent on the rate and extent of climate change, such increase in thermal tolerance may delay the onset of mass coral mortalities in time for the implementation of low-emission scenarios and effective management.

Introduction

Coral reef ecosystems provide for the livelihoods of millions of people throughout the tropics (Hoegh-Guldberg 2004). The Great Barrier Reef alone supports a tourism industry worth \$6.9 billion worth of economic activity along with incalculable social values (Access 2007). Yet, coral reef ecosystems are among the most vulnerable to global climate change (Pittock 2003). Anomalously high sea temperatures cause coral bleaching (reductions in chlorophyll and/or densities of symbiotic dinoflagellates), leading to mortality when the temperature stress is severe or prolonged (Hoegh-Guldberg 1999). In 1998, more than 16% of the world's tropical coral reefs were seriously degraded by bleaching, with 50–90% mortality in some regions (Wilkinson 2002). Climate-change models predict a 1.8–4°C increase in temperatures for tropical regions over the next century (IPCC 2007), which are likely to result in more frequent and more severe mass bleaching events. Recent observations and projections of future change have given rise to grave concerns about the future of the world's coral reefs (Hoegh-Guldberg et al. 2007; Hoegh-Guldberg 1999; Knowlton 2001; Wilkinson 2002; Hughes et al. 2003).

The extent to which a coral reef crisis will unfold depends on the rate of climate change and the resilience of

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corals to these changes. A key component of reef resilience is the capacity of corals to adapt or acclimatize with the rate of change (Kennedy et al. 2002; Hoegh-Guldberg 2004). Adaptation requires selective mortality of less thermally tolerant individuals or differential reproductive success, and provides a genetic basis for a change in tolerance. Acclimatization can result from conditioning to past exposure to thermal stress, both acute and chronic (Gates and Edmunds 1999; Brown et al. 2002). Acclimatization in corals can take the form of a change in the physiology of the host (Garrett and Mundt 1999), as well as a change in the relative proportion of symbiont types in the host (Baker 2001; Coles and Brown 2003; Baker et al. 2004; Fautin and Buddemeier 2004; Rowan 2004).

To date, our ability to gauge the vulnerability of coral reefs to global warming has been limited by our lack of knowledge about the capacity for coral symbioses to adapt or acclimatize to thermal stress over ecological time frames (Coles and Brown 2003; Hoegh-Guldberg 2004). Major stress events, such as the mass coral-bleaching event in 1998, are likely to impose strong selective pressures on coral populations, and potentially trigger mechanisms of adaptation, physiological acclimatization or change in genotype–phenotype interactions in the surviving coral symbioses. Indeed, increases in thermal tolerance have been demonstrated between bleaching events in Central and South America (Podesta and Glynn 2001; Glynn et al. 2001), but, to our knowledge, not from a field-based study on Indo-Pacific reefs where genera-level bleaching and mortality patterns are included.

Here, the bleaching responses of three common coral genera are compared between two major thermal stress events on the Great Barrier Reef (GBR): the 1998 mass bleaching event, which was unprecedented in severity (Baird and Marshall 1998; Lough 2000), and the subsequent, even more severe event in 2002 (see Berkelmans et al. 2004). In this paper, it is demonstrated that, over a timeframe of only 4 years, a major bleaching event can lead to enhanced thermal tolerance of surviving coral assemblages without extensive mortality.

Materials and methods

Study taxa

To represent some of the quantitatively and functionally most important coral taxa on the Great Barrier Reef, the following three genera were included: *Pocillopora*, *Acropora* and *Porites*. These groups represent a wide range of general susceptibilities to thermal stress, *Pocillopora* and *Acropora* being among the most susceptible genera and *Porites* among the most tolerant over a large spatial scale

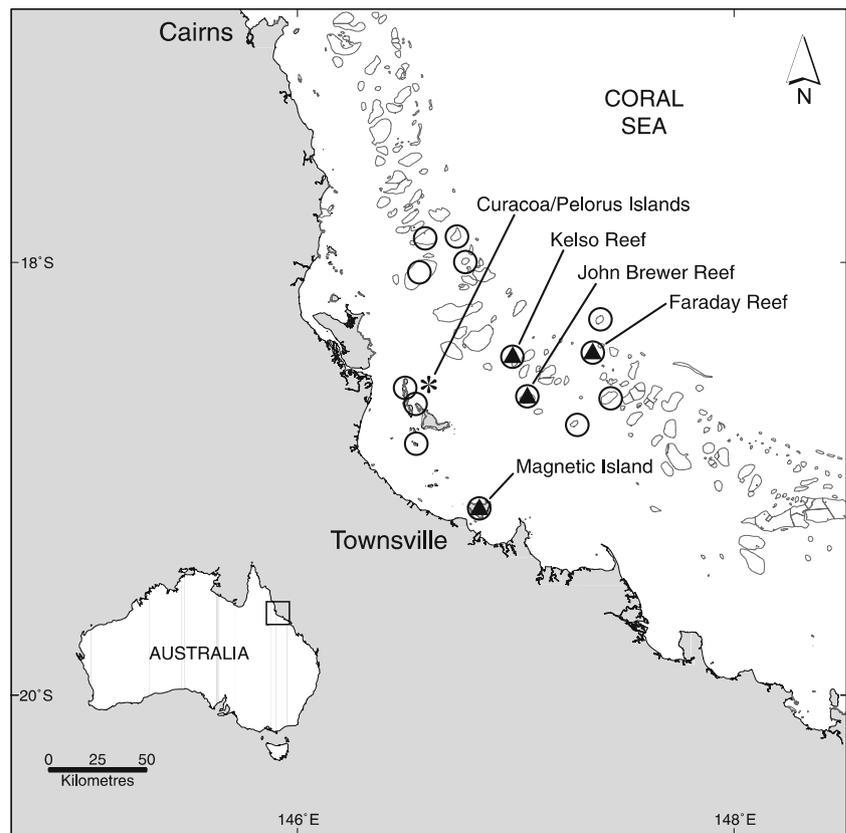
(McClanahan et al. 2004). At all sites, the genus *Pocillopora* was represented up to 95% by *P. damicornis*. *Acropora* was generally represented by more than 80% branching and tabular species, which have comparable bleaching susceptibilities (Marshall and Baird 2000). *Porites* was represented by more than 80% by the massive species *P. lutea* and *P. australiensis*.

Field surveys and video analysis

Analyses of bleaching severity were based on underwater video surveys by the Great Barrier Reef Marine Park Authority (GBRMPA) and the Australian Institute of Marine Science of sites on the central Great Barrier Reef (GBR) in late February and March of 1998 and 2002 (Fig. 1). As part of the early warning system of the GBRMPA's Coral Bleaching Response Plan, a network of observers report regularly on reef condition as part of 'BleachWatch'. Surveys were undertaken when BleachWatch participants at each of the sites reported bleaching to be at its most severe, i.e. the thermal anomalies had peaked and bleaching severity at the community level had not worsened for a week. All sites were located in the central section of the Great Barrier Reef. In 1998, 14 sites were used to estimate the relationship between accumulated thermal stress and bleaching severity. Five of these sites (Faraday Reef, Kelso Reef, John Brewer Reef, Magnetic Island Reef, and Curacoa/Pelorus Islands) were re-surveyed in 2002 to evaluate any changes in bleaching severity and potential changes in thermal tolerance of the study genera between 1998 and 2002. Bleaching was observed during both years, although the strength and spatial distribution of thermal anomalies in the GBR lagoon differed between 1998 and 2002 (Berkelmans et al. 2004). At each site, six random, replicate, video belt transects (45 × 1 m) were recorded on the upper reef slope/reef crest zone (2–6 m) using SCUBA. The video transects were analyzed for generic composition of the coral community using standard methods (English et al. 2004).

Bleaching severity (S) of each genus was estimated as the frequency of colonies on transects showing visual signs of bleaching, i.e. including colonies within the range pale to recently dead. For analyses, bleaching severity was scored as the proportion of colonies affected (i.e. bleached or recently dead) versus unaffected. According to the results of previous studies (e.g., Baird and Marshall 2002; Anthony et al. 2007) the survivorship of bleached corals will decline over time, but corals that are not visibly bleached during, or in the weeks immediately following, a thermal anomaly event are unlikely to subsequently become visibly bleached or die due to the event.

Fig. 1 Map of sites in the central section of the Great Barrier Reef surveyed by GBRMPA and AIMS for coral bleaching severity 4–8 weeks after the thermal stress events in 1998 (*open circles*) and in 2002 (*triangles*). The asterisk refers to Curacao and Pelorus Islands. These were used in the analyses comparing 1998 and 2002, are in the same island chain and experienced similar thermal regimes in both event years



Environmental data

Historical records of the temperature regime at each site were obtained using remotely sensed sea surface temperatures (SST). These were measured by Advanced Very High Resolution Radiometer (AVHRR) from the satellite platforms of the US National Oceanic and Atmospheric Administration (NOAA, Gleeson and Strong 1995) and calibrated to ships and drift buoys within the central GBR region. During the 1998 and 2002 events, remotely sensed temperature data values used were consistently within 0.25°C of values recorded by in situ loggers positioned at 3 m depth at each of the five sites used in comparisons of thermal tolerance (Maynard 2004). This demonstrates that remotely sensed temperature values accurately reflect those experienced by corals at the study sites during 1998 and 2002, and that the rates and extent of vertical mixing during each event were similar at these sites. SST data were compiled for the central GBR region (~4 km res), for the 14 years preceding the 2002 event (1988–2002), to produce a temperature climatology as a basis for calculating thermal anomalies at each site. Average temperatures for the austral summer (1st December–28th February), were calculated as the grand mean of SSTs for summers during this period.

Solar irradiance is an important covariate in the coral bleaching response by two means. First, high light intensity can exacerbate the thermal stress response (Fitt et al. 2001). Second, high light levels prior to a thermal stress event can trigger the onset of photo-protective defense mechanisms, thereby increasing thermal tolerance during the thermal anomaly (Dunne and Brown 2001). To account for differences in solar radiation between the summers of 1998 and 2002 and among sites, remotely sensed estimates of surface irradiance were obtained using an approach modified from that of Pinker and Laszlo (1991). Briefly, this method produces a map (1.25 km resolution) of solar irradiance using a Streamer Radiative Transfer algorithm, and, to limit influence of cloudiness, a 5-day averaging period that assesses and omits highly anomalous data (for details see Masiri et al. 2008). Model validation indicated a mean error of 2.3% for the area of the Great Barrier Reef that includes the study sites. Surface irradiance values were derived for each of the five revisited sites during the month preceding (15th November–30th December) and during the period of the thermal anomaly (15th December–28th February) in each of the years 1997/1998 and 2001/2002. Underwater data on irradiance is not available for our study sites during 1998 and 2002. However, except for Magnetic Island, these sites are mid-shelf reefs and characterized by clear water. It is, therefore, unlikely that differences in

mixing processes (e.g., wave action) and turbidity would have led to strong variation in light attenuation, and hence benthic irradiance, among sites and between years (Anthony et al. 2004).

Data analysis

To examine shifts in patterns of thermal tolerance between 1998 and 2002, observed bleaching severities in 2002 were compared at the five re-surveyed sites with those predicted based on the linear relationship between bleaching severity and thermal stress for the 14 sites measured in 1998. Thermal stress was calculated as the accumulated amount of heating (as degree heating days, DHD, °C days) during each thermal anomaly; specifically the summed positive deviations of daily average sea surface temperatures (T_{Heating}) from historical summer mean temperatures (T_{Hist}) (see also Berkelmans et al. 2004). Historical mean temperatures were calculated from the ten summers prior to 1998 (1988–1997).

$$\text{DHD} = \sum (T_{\text{Heating}} - T_{\text{Hist}}) \quad (1)$$

To account for variation in bleaching susceptibility among sites due to potential local acclimatization/adaptation (e.g., inshore vs. offshore reefs, Berkelmans and Oliver 1999), the historical summer mean temperature (T_{Hist}) at each site was included as a covariate. As the functional relationship between bleaching severity, thermal stress and thermal history is unknown, bleaching severity during each event year was modeled as a simple linear system and analysed as a multiple regression:

$$S_{(1998/2002)} = a(\text{DHD} - \text{DHD}_{\text{mean}}) + b(T_{\text{Hist}} - T_{\text{Hist,mean}}) + S_0 \quad (2)$$

where DHD_{mean} is the average number of DHDs across all sites, $T_{\text{Hist, mean}}$ is the historical mean temperature averaged across all sites, a and b are regression coefficients, and S_0 is the intercept. DHD_{mean} and T_{Hist} are here used to centralize the thermal variables so that S_0 represents the mean bleaching severity rather than a negative value. Equation 2 was fit to the 1998 dataset for each of the three genera using multiple regression (Statistica, Release 7, Statsoft). To account for the autocorrelation of before versus after comparisons of bleaching severities in 1998 and 2002 at each site, predicted bleaching severity in 2002 (PS_{2002}) was calculated as:

$$PS_{2002} = a\Delta\text{DHD} + b\Delta T_{\text{Hist}} + S_{1998} \quad (3)$$

where ΔDHD is the change in thermal stress and ΔT_{Hist} is the change in average historical temperatures between 1998 and 2002, and S_{1998} is the observed bleaching severity in 1998. Confidence intervals for S_{2002} were determined by Monte Carlo analysis in which the parameters a and b were

sampled from within their normal distributions established by their mean \pm standard deviations. Each Monte Carlo analysis (simulation) was run 1,000 times using the analytical package PopTools (version 2.7.5., www.cse.csiro.au/poptools) written for MS Excel.

Differences between predicted and observed bleaching response severity at the re-surveyed sites in 2002 were analysed using Welch's approximate t , a deviation of Student's t -test that overcomes having uneven sample sizes.

To determine the extent to which changes in observed bleaching severity between events could be attributed to mortality in 1998, the difference between predicted and observed bleaching severity in 2002 (S_{diff}) was calculated. A simple linear regression was then used to relate S_{diff} to mortality in 1998, defined as the proportion of colonies recently dead due to bleaching, for each of the three genera. If bleaching severity in 2002 were partly driven by selective mortality in 1998, S_{diff} would be expected to increase with rates of mortality associated with the 1998 bleaching event.

Results

Bleaching severity at the central GBR sites in 1998 was almost exclusively a function of degree heating days (DHD, Fig. 2). In the multiple regression analysis (Eq. 2), the regression coefficient for thermal history (parameter b) was not significantly different from zero in any of the genera in 1998, meaning that thermal history, at the study sites used here, was not a significant predictor of bleaching severity in 1998 (Table 1). A simple linear regression of bleaching severity versus thermal stress in 1998 (i.e. excluding the term for thermal history) explained 54–64% of the variation in bleaching severity. This allowed us to make reasonable predictions of bleaching severity of the three species at the five re-surveyed sites in 2002 based on degree heating days only.

Observed bleaching severities of *Acropora*, *Pocillopora*, and *Porites* in 2002 at the five sites were significantly lower ($P < 0.001$, see Table 2) than predicted for all comparisons (Fig. 3). Specifically, for *Acropora*, bleaching severities in 2002 were less than 50% of those predicted for all sites. This pattern was similar for *Pocillopora* at Faraday and Kelso Reefs, and very strong at John Brewer Reef, Magnetic and Curacao/Pelorus Islands where no colonies were observed to bleach in 2002. Bleaching severities of *Porites* were also substantially lower than predicted except at Kelso Reef. Similar to the results for *Pocillopora*, 100% of the colonies at Magnetic Island were predicted to bleach in 2002, but none was observed to undergo bleaching. These results are striking, given that the amount of accumulated thermal stress (as degree heating days, DHD) in

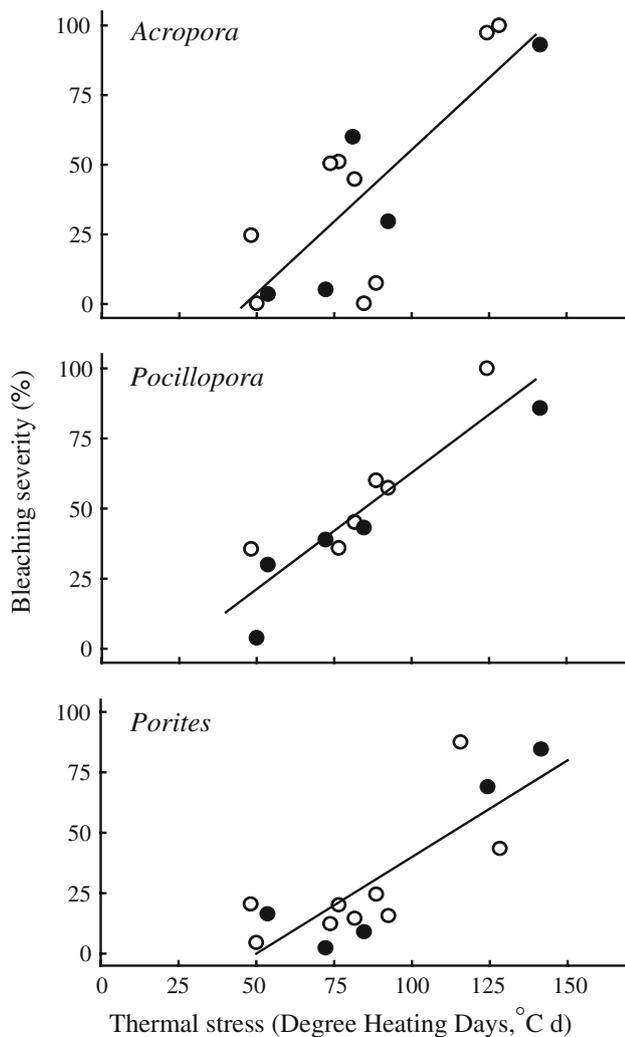


Fig. 2 Relationship between observed bleaching severity and accumulated heat stress (degree heating days, DHD) for the three study genera following the major bleaching event on the Great Barrier Reef in 1998. Bleaching data are from visual surveys at 15 sites in the central Great Barrier Reef and sea surface temperatures are obtained from NOAA satellite data. Filled-in circles represent sites surveyed during both the 1998 and 2002 event years. A simple linear regression model (Model B, Table 1) provided the best fit to the data. Centered DHD data (lower x-axis) are used as input variable in Eq. 2

2002 was more than double that in 1998 at four of the five sites. Importantly, increases in thermal tolerance could not be explained by variation in light regimes. In fact, average surface irradiance during the 2002 thermal anomaly was 15.6–18.9% higher than during the 1998 anomaly (Table 3), suggesting that calculated increases in thermal tolerance in 2002 are underestimates. In addition, irradiance values prior to the 2002 thermal anomaly were only marginally higher (5.5–7.7%) than those prior to the 1998 anomaly (Table 3). Therefore, light/temperature stress conditions were more conducive to widespread bleaching in 2002 than in 1998, yet bleaching responses were far less severe than predicted.

The difference between predicted and observed bleaching severity in 2002 for all three genera was not significantly correlated to mortality levels of any of the genera in 1998 (*Acropora*: $F_4 = 1.64$, $P = 0.330$; *Pocillopora*: $F_4 = 2.62$, $P = 0.250$; *Porites*: $F_4 = 9.19$, $P = 0.090$). This indicates that differences in thermal tolerance levels between years could only be accounted for partly by mortality in 1998, which, except for Magnetic Island and Curacao/Pelorus Islands, was lower than 15% for all genera (Table 4).

Discussion and conclusions

The results presented here demonstrate an increase in thermal tolerance for all three coral genera between the 1998 and 2002 bleaching events, suggesting that thermal acclimatization or adaptation by some mechanism occurred between these major events. At all five sites, thermal stress in 2002 (expressed as degree heating days) was at least double that during the 1998 thermal event and solar irradiance, a key secondary bleaching factor, was more than 15% higher in 2002 at the study sites than in 1998. The 2002 bleaching event was more severe than that of 1998 (Berkelmans et al. 2004) but not nearly as severe as the relationship, shown here, between the accumulation of heat stress, calculated as degree heating days, and bleaching severity suggests it should have been. Admittedly, the degree heating days index has known weaknesses (Berkelmans et al. 2004; Maynard 2004) in that short periods of really high temperatures can, using the degree heating days metric, equate to longer periods of only slightly elevated temperature—the physiological implications for the corals being clearly different. Even so, a better metric for predicting spatial patterns in bleaching responses of communities on the GBR, the ‘heating rate’ (see Maynard 2004), cannot explain as much variance in population-level bleaching response patterns as degree heating days does (Maynard 2004). Most importantly, coral populations at the study sites in 2002 demonstrate increases in tolerance, relative to 1998, to major increases in both temperature and light. And the findings presented here are, though over a shorter timeframe, consistent with previous studies documenting an increase in thermal tolerance between bleaching events (1982–1983 vs. 1997–1998) in the Galapagos Islands (Podesta and Glynn 2001), the Gulf of Chiriqui, the Gulf of Panama (Glynn et al. 2001), and on Costa Rican reefs (Jimenez et al. 2001).

Because the study of specific mechanisms of thermal tolerance is beyond the scope of this study, a list of possible mechanisms is discussed here rather than presenting arguments for a specific process. The observed increase in thermal tolerance in 2002 could be due to the involvement

Table 1 Summary of parameter estimates for (A) multiple regression analysis using thermal stress (1998 event) and thermal history (1992–1998) as variables, and (B) a simple linear regression model using thermal stress as the only input variable

Model	Parameter	<i>Acropora</i>		<i>Pocillopora</i>		<i>Porites</i>	
		Estimate	<i>P</i> -value	Estimate	<i>P</i> -value	Estimate	<i>P</i> -value
A	a (°C ⁻¹ d ⁻¹)	1.12 (0.26)	<0.001	0.87 (0.19)	<0.001	0.73 (0.22)	0.007
	b (°C ⁻¹)	24.4 (31.4)	0.453	21.4 (20.8)	0.328	-7.4 (16.1)	0.653
	S ₀	40.3 (6.7)	<0.001	53.5 (4.6)	<0.001	32.5 (5.4)	<0.001
	R ² (adjusted)	0.66		0.65		0.51	
B	a (°C ⁻¹ d ⁻¹)	1.03 (0.22)	<0.001	0.79 (0.17)	<0.001	0.78 (0.19)	0.001
	S ₀	40.6 (6.1)	<0.001	55.1 (4.4)	<0.001	32.8 (5.2)	<0.001
	R ² (adjusted)	0.64		0.64		0.54	

Both analyses were based on bleaching survey data for 14 sites on the central Great Barrier Reef in 1998. Parameter *a* is a coefficient for the accumulated amount of thermal stress during the 1998 event (degree heating days), and parameter *b* is a coefficient for the term for thermal history (grand mean of summer mean temperatures since 1992). Standard errors associated with parameter estimates are in parentheses

of (1) the triggering of photo-protective mechanisms prior to the 2002 event, (2) selective holobiont mortality of susceptible genotypes in 1998, (3) adaptation through the shuffling of symbiont clades, and (4) rapid evolution of algal symbionts and/or the coral host, (5) greater energy reserves prior to the 2002 event and/or great access to heterotrophic resources, and/or (5) long-term physiological memory of past events (i.e. acclimatization).

Triggering of photo-protective mechanisms

Dunne and Brown (2001) found similar results to those presented here in the Andaman Sea, in that bleaching severity was far reduced in 1998 compared to 1995 despite sea-temperature and light conditions being more conducive to widespread bleaching in 1998. These authors presented evidence that the observed increase in tolerance involved a stimulation of the photo-protective defenses in both host coral and algae in the period prior to the stress event coincident with much higher-than-normal daily doses of photosynthetically active radiation (PAR) during this time, and that the tolerance then persisted during the maximum combined light/temperature stress. However, in this study, average surface solar irradiance prior to the 2002 thermal anomaly, was only marginally higher than prior to the 1998 anomaly, making it unlikely that photoprotective defense mechanisms could explain the increase in thermal tolerance in 2002.

Selective mortality

The severe 1998 mass bleaching event was likely to represent a selective pressure on the coral assemblages with the consequent removal of at least some of the least tolerant genotypes. Therefore, the recovery and growth of the more thermally tolerant surviving genotypes, and/or a

reduction in the light/temperature stress interaction in 2002, could work to explain bleaching responses being less severe in 2002 than predicted. However, the poor correlation between the shifts in thermal tolerance (as the difference in observed and predicted bleaching severity in 2002) and rates of mortality in 1998 suggests that the observed increase in tolerance is not driven entirely by selective mortality in 1998. In fact, although a large proportion of colonies at the surveyed sites bleached in 1998, whole-colony mortality levels were low (<15%) except at Magnetic Island and Curacao/Pelorus Islands, and therefore unlikely to explain a significant proportion of the increases in thermal tolerance observed in 2002.

Symbiont shuffling

Shifts in the relative proportion of thermally tolerant symbionts could also be a potential mechanism to explain the observed increase in tolerance (Baird et al. 2007; Baker 2003; Brown 1997; review in Coles and Brown 2003). Recently, Berkelmans and van Oppen (2006) showed that *Acropora millepora* in laboratory experiments could acquire increased thermal tolerance and that this was a result of a shuffling from dominance of symbiont (*Symbiodinium*) type C to dominance of type D, the latter normally present at low background levels.

Greater energy reserves and/or heterotrophic resources

Energy acquisition by the coral–algal symbiosis is determined by two processes: rate of photosynthetic carbon fixation and energy transfer by symbionts (Spencer-Davies 1984; Muscatine 1990) and heterotrophy by the host (Ferrier-Pages et al. 1998; Anthony and Fabricius 2000). Bleaching (symbiont or photo-pigment loss) will, as a result, have varying impacts on the coral energy balance

Table 2 Summary of Student's *t*-test results comparing predicted bleaching response severity from model runs ($n = 1,000$) to observed bleaching severity ($n = 6$) in 2002

Site		Mean	SE	df	<i>t</i>	<i>P</i>
<i>Acropora</i>						
Faraday Reef	pred	51	0.72	5	54.82	$P < 0.001$
	obs	18	2.04			
Kelso Reef	pred	62	0.81	5	53.15	$P < 0.001$
	obs	27	2.45			
John Brewer Reef	pred	83	1.01	5	110.61	$P < 0.001$
	obs	25	1.22			
Magnetic Island	pred	100	0.32	5	78.19	$P < 0.001$
	obs	46	2.86			
Curacoa/Pelorus Islands	pred	100	0	N/	A	N/A
	obs	N/A	0			
<i>Pocillopora</i>						
Faraday Reef	pred	74.7	0.70	5	15.33	$P < 0.001$
	obs	50	3.67			
Kelso Reef	pred	77.9	0.67	5	70.29	$P < 0.001$
	obs	20	3.67			
John Brewer Reef	pred	86.3	0.69	999	2,978	$P < 0.001$
	obs	0	0			
Magnetic Island	pred	100	0.32	999	5,623	$P < 0.001$
	obs	0	0			
Curacoa/Pelorus Islands	pred	95	0.21	999	6,556	$P < 0.001$
	obs	0	0			
<i>Porites</i>						
Faraday Reef	pred	39.7	0.60	5	75.31	$P < 0.001$
	obs	4	1.22			
Kelso Reef	pred	49.3	0.57	5	16.25	$P < 0.001$
	obs	32	3.27			
John Brewer Reef	pred	66.6	0.81	5	73.48	$P < 0.001$
	obs	13	2.45			
Magnetic Island	pred	100	1.58	999	2,490	$P < 0.001$
	obs	1	0			
Curacoa/Pelorus Islands	pred	98	0	5	94.56	$P < 0.001$
	obs	20	4.08			

The test could not be run for *Acropora* at the Curacoa/Pelorus Island sites but the difference between predicted and observed was significant ($P < 0.001$) at all other sites for all three genera

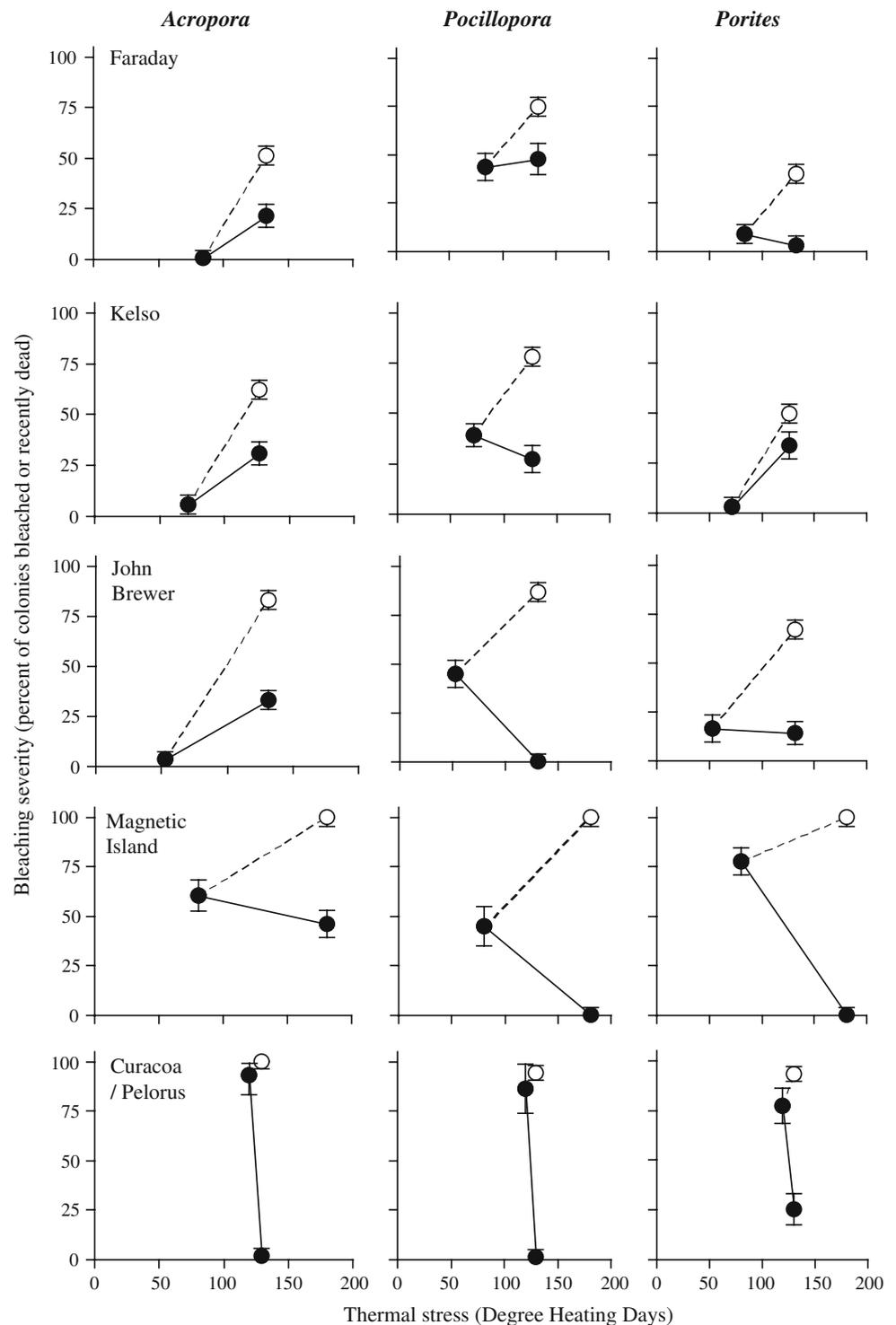
(Grottoli et al. 2004; Anthony et al. 2007), depending on the trophic plasticity of the coral species. In a recent study, Anthony et al. (in review) found that high rates of heterotrophy delayed the onset of high bleaching-induced mortalities, and can promote major increases in survivorship following bleaching episodes. Either trophic plasticity and/or greater access to resources for heterotrophic feeding in 2002, could partly explain the increases in thermal tolerance observed here.

Rapid evolution and long-term physiological memory

Other possible mechanisms include compensatory changes in the physiology of the coral host, and/or the presence of a long-term physiological memory, or rather acclimatization, of either partner. Gates and Edmunds (1999) discuss protein metabolism as a mechanism underlying acclimatization. These authors propose that differences in acclimatization capacity may be linked to rates of protein turnover, which is often higher among organisms with a high rate of metabolism. Gates and Edmunds (1999) cite evidence that there could be an inverse relationship between growth rate and metabolic rate implying that slower-growing species could acclimatize more effectively due to a higher rate of protein turnover. The results of this study, however, suggest the opposite pattern, with the fast-growing genera *Acropora* and *Pocillopora* showing a greater increase in thermal tolerance than the slow-growing *Porites*. Importantly, this also suggests that genera found to, generally, be more susceptible to bleaching (including *Acropora* and *Pocillopora*, Baird and Marshall 2002) are more likely to increase their tolerance in response to thermal stress events. The contrasting results of this study and the hypotheses raised by Gates and Edmunds (1999) highlights that the links between protein turnover, metabolic rate and coral growth rates need further study.

With predictions of more frequent and severe thermal stress events over coming decades (Lough 2000; IPCC 2007; Hoegh-Guldberg 2004), the pressures on reef corals are likely to intensify. The range in bleaching tolerances among corals inhabiting different thermal realms suggests that at least some coral symbioses have the ability to adapt to much higher temperatures than they currently experience in the central Great Barrier Reef (Coles and Brown 2003; Riegl 1999, 2002). Further, even within reefs there is significant variability in bleaching susceptibility for many species (Edmunds 1994; Marshall and Baird 2000), suggesting some potential for a shift in thermal tolerance based on selective mortality (Glynn et al. 2001; Jimenez et al. 2001) and local population growth alone. However, adaptation of local coral populations through replacement of susceptible genotypes with more tolerant genotypes is an evolutionary process that is both uncertain and protracted. Given current knowledge about the limited range in thermal tolerances within local populations (Sheppard 2003) and connectivity between reefs in different thermal realms (Hughes and Tanner 2000), adaptation is thought by some to not proceed quickly enough to outpace predicted warming (Hoegh-Guldberg 2004). This is a contentious issue, however, and there is emerging evidence of high genetic structure within coral species (Ayre and Hughes 2004) and limited dispersal on the Great Barrier Reef (Hughes et al. 2000)

Fig. 3 Bleaching responses of the three study genera as a function of accumulated heat stress (degree heating days) at five sites in 1998 and 2002. Solid markers are observed bleaching severities in 1998 (*left markers*) and 2002 (*right markers*), respectively. Predicted bleaching severities in 2002 (*open markers*) were calculated using Eq. 3, i.e. based on the empirical relationship between bleaching severity and accumulated heat stress for 15 surveyed sites in 1998 (see Fig. 3). Confidence limits (95%) for predicted bleaching severities in 2002 were estimated using Monte Carlo analyses



suggesting that the capacity for adaptation could be greater than is currently recognized.

Given that mortality was low at the sites in 1998 (excepting at Magnetic and Curacao/Pelorus Islands), the contribution from selective mortality of more tolerant genotypes is unlikely to explain fully the increase in tolerance. Acclimatization, in contrast to adaptation, endows the

coral/zooxanthellae symbiosis the potential to adjust rapidly to changing temperature regimes without requiring high levels of mortality or selective pressures on reproductive capacity. Importantly though, bleaching events are likely to impose a range of pressures on corals, leading to a suite of responses that include selective mortality, adaptation as well as acclimatization. This suggests that further deterioration

Table 3 Surface irradiance (PAR) values for the month prior to the thermal anomaly and the weeks during the thermal anomaly at each study site

Site	Year	Surface solar irradiance			
		Month prior to thermal anomaly (MJ m ⁻² day ⁻¹)	% Difference	During thermal Anomaly (MJ m ⁻² day ⁻¹)	% Difference
John Brewer Reef	1998	27.8		26.5	
	2002	29.3	5.5	31.5	18.9
Kelso Reef	1998	27.2		26.5	
	2002	29	6.7	31.2	17.8
Faraday Reef	1998	27.4		26.8	
	2002	29.4	7.4	31.5	17.5
Magnetic Island	1998	26.8		27.1	
	2002	28.9	7.7	31.4	15.6
Curacoa/Pelorus	1998	27		27.5	
	2002	29.7	10	31.5	14.5

See text for a detailed explanation of the derivation of solar irradiance

Table 4 Coral mortality in 1998 at each of the five study sites

Site	Coral mortality in 1998 (%)		
	<i>Acropora</i>	<i>Pocillopora</i>	<i>Porites</i>
Kelso Reef	0.9	13.6	0
Faraday Reef	3.5	14.4	1.5
John Brewer Reef	2.3	23	0
Magnetic Island	48.1	89.2	22.9
Curacoa/Pelorus Islands	0	90	20.4

Mortality refers to the percentage number of colonies dead attributable to bleaching

of coral reefs in a warming climate is inevitable, but that acclimatization/adaptation might slow the onset of a coral reef crisis. Importantly though, acclimatization is far from a panacea for climate change. It is unlikely to benefit all species, and is almost certain to be limited in scope (Coles and Brown 2003). Projected temperature increases under even modest climate-change scenarios (Hoegh-Guldberg 2004; IPCC 2007) could eventually exceed the tolerance thresholds of most corals, resulting in dramatic changes in reef community assemblages. However, coral acclimatization or adaptation could buy reefs valuable time, increasing both the opportunity and the imperative for actions to lessen climate stress on coral reef ecosystems.

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