Corals escape bleaching in regions that recently and historically experienced frequent thermal stress

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The response of coral-reef ecosystems to contemporary thermal stress may be in part a consequence of recent or historical sea-surface temperature (SST) variability. To test this hypothesis, we examined whether: (i) there was a relationship between the historical frequency of SST variability and stress experienced during the most recent thermal-stress events (in 1998 and 2005–2006) and (ii) coral reefs that historically experienced frequent thermal anomalies were less likely to experience coral bleaching during these recent thermal-stress events. Examination of nine detrended coral $\delta^{18}\text{O}$ and Sr/Ca anomaly records revealed a high- (5.7-year) and low-frequency (>54-year) mode of SST variability. There was a positive relationship between the historical frequency of SST anomalies and recent thermal stress; sites historically dominated by the high-frequency mode experienced greater thermal stress than other sites during both events, and showed extensive coral bleaching in 1998. Nonetheless, in 2005–2006, corals at sites dominated by high-frequency variability showed reduced bleaching, despite experiencing high thermal stress. This bleaching resistance was most likely a consequence of rapid directional selection that followed the extreme thermal event of 1998. However, the benefits of regional resistance could come at the considerable cost of shifts in coral species composition.

Keywords: climate change; coral bleaching; sea-surface temperature variability; El Niño-southern oscillation; adaptation

1. INTRODUCTION

Coral populations are highly responsive to thermal stress, often resulting in considerable bleaching and subsequent mortality (Glynn 1993; Brown 1997a,b). Coral bleaching is the general response of corals to stress, resulting in the loss of coral pigment and often the expulsion of their symbiotic dinoflagellates. Coral-bleaching events have become more frequent and intense in response to recent climate-change-related temperature anomalies (Glynn 1993; Hoegh-Guldberg 1999; Donner *et al.* 2007). Bleaching events will probably become even more intense and severe, as temperatures are projected to continue to rise under the scenarios for future climate change (IPCC 2007). Yet, regional differences in bleaching responses during past thermal events raise several questions: (i) did the differential response patterns result from regional differences in temperature and irradiance stress? (Mumby *et al.* 2001; Kleypas *et al.* 2008), (ii) did the different regions support different species, with different tolerances to elevated temperatures? (Loya *et al.* 2001; van Woesik 2001) or (iii) did the regions, which support similar coral communities, adjust differently to thermal stress because of recent and/or historical circumstances? (Glynn *et al.* 2001; Brown

et al. 2002; Berkelmans & van Oppen 2006; Baird *et al.* 2008).

The first objective of this study was to determine the strength of the dominant modes of SST variability on a global scale, allowing us to test whether there was a positive relationship between the relative strength of the high- and low-frequency modes of temperature variance and the severity of stress experienced during recent temperature anomalies. The second objective was to examine whether the frequency of anomalous SST events in the past influenced the ability of corals to resist bleaching during the 1998 and the 2005–2006 thermal-stress events. Directional-selective pressure and/or long-term acclimatization may have allowed adjustment to thermal stress in regions dominated by high-frequency variability, either historically or recently (Baird *et al.* 2008; Edmunds & Gates 2008; Maynard *et al.* 2008). If so, then the relative strength of high- and low-frequency SST variability may be a useful proxy to predict contemporary coral-bleaching responses. To test these hypotheses we: (i) determined the historical frequency of SST variability at each site based on the relative strength of the high- and low-frequency modes of variability; (ii) tested the relationship between the severity of recent thermal stress and the historical frequency of SST variability; (iii) determined if there was an association between the historical frequency of SST variability and bleaching severity in 1998; and (iv) compared the 1998 response with subsequent bleaching in 2005–2006.

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2. MATERIAL AND METHODS

(a) *Past climate variability*

Multi-channel singular spectrum analysis (M-SSA) is a multivariate method that reveals the dominant spatio-temporal patterns of variability by using a sliding window (width M) to obtain overlapping views of a spatially distributed network of time series. The individual time series at each site that make up the network are known as channels. Stable oxygen isotope ($\delta^{18}\text{O}$) and Sr/Ca records from 18 sites were obtained from the National Climatic Data Center's (NCDC) World Data Center for Paleoclimatology (<http://www.ncdc.noaa.gov/paleo/paleo.html>) and used as proxies for sea-surface temperature (SST) and salinity (in the case of $\delta^{18}\text{O}$). We then used M-SSA on detrended $\delta^{18}\text{O}$ and Sr/Ca records ($n = 647$) from corals at nine sites (figure 1) to determine the patterns of temperature variability (given by the eigenvectors) that explain the most variance in the coral records (i.e. the top-ranked eigenvalues), subsequently referred to as modes of variability (figure 2). Chi-square and Monte Carlo significance tests were then used to determine which of these patterns of SST variability were significantly above noise (figure 2). The sites used in this analysis were Ras Umm Sidd, Madagascar, the Seychelles, the Houtman Abrolhos Islands, Ningaloo Reef, Guam, Maiana Atoll, Rarotonga and Palmyra Island (figure 1). These channels were selected from the original pool of bimonthly resolved $\delta^{18}\text{O}$ and Sr/Ca records such that all records were at least 100 years in length, uncorrelated at zero-lag and strongly inversely correlated (>0.6) with Hadley Centre Sea Ice and Sea Surface Temperature data (HadISST1.1, <http://badc.nerc.ac.uk/data/hadisst/>; Rayner *et al.* 2003). To determine the patterns of temperature variability experienced directly by the corals themselves, M-SSA was performed on the $\delta^{18}\text{O}$ and Sr/Ca records, instead of on the (1° by 1°) HadISST SST data. Correlation analyses between the M-SSA patterns and gridded HadISST SST data were then used to determine the strength of the modes of variability at sites for which no coral $\delta^{18}\text{O}$ or Sr/Ca records were available.

For the significant high- and low-frequency modes of SST variability obtained from M-SSA (see electronic supplementary material for more details), each original time series was partially reconstructed at that frequency to retain the original time interval and phase (figure 2). These reconstructed components (RCs) were then averaged across all channels to produce an average RC for the high- and low-frequency modes of variability. To determine the strength of these high- and low-frequency modes on a global scale, the high- and low-frequency RCs obtained from M-SSA were correlated with globally gridded (1° by 1°) HadISST1.1 SST data over the period common to all records (i.e. 1886–1993) (figure 2). High (positive or negative) correlation coefficients indicate that the mode of variability was strong at that location.

(b) *Coral bleaching, temperature and irradiance*

Bleaching records were obtained from the Status of the coral reefs report (Wilkinson 1998), the ReefBase data archive (<http://www.reefbase.org/>) and personal observations (R.v.W.) (see electronic supplementary material for data used in the analysis). The severity of bleaching from each of these sources was ranked into four categories: (i) no bleaching (0% of corals bleached); (ii) low bleaching (1–10% of corals bleached); (iii) medium bleaching (>10–30% of corals bleached); and (iv) high bleaching (>30% of corals bleached). The 1998 and 2005–2006 bleaching events were used for the present analysis because they were the latest, most severe and the most

extensively observed coral bleaching events on record. Although the Reefbase data have known uncertainties that stem from the multitude of data contributors, these data have been used to show useful regional stress patterns (Kleypas *et al.* 2008; Maina *et al.* 2008). The use of bleaching severity categories allowed for a more robust assessment of relative bleaching severity, because the surveyor only had to estimate an approximate range of bleaching severity, rather than estimate the per cent bleaching. In addition, at sites where data were available from multiple sources (Reefbase, Status of the coral reefs and personal observations), the estimated bleaching severities were compared, which allowed us to make additional error estimates of the bleaching approximations.

The objective of this analysis was to test whether differences in past-temperature variability, rather than differences in the degree of stress experienced during each contemporary event, was the major factor causing differential bleaching severity. Therefore, it was necessary to compare the bleaching response of corals at localities that experienced similar contemporary thermal stress. To do this, we had to first determine the amount of stress experienced at each reef site during the two contemporary bleaching events. However, determining temperature stress alone may not be sufficient because physiological studies suggest reciprocity between the effects of temperature and irradiance on photo-inhibition, paling and bleaching (Takahashi *et al.* 2004). Therefore, the combined temperature and irradiance stress experienced at each site during the event was calculated.

Monthly SST data, for 137 years (from 1870 to 2007), were extracted from the global HadISST1.1 dataset for each 1° latitude by 1° longitude grid box that contained a coral bleaching record for the 1998 and/or 2005–2006 event(s). The mean of SSTs in the adjacent gridboxes was used for coral sites at the edge of two or more gridboxes. Monthly photosynthetically active radiation (PAR) data for the two bleaching periods were obtained for the nearest 90 km by 90 km grid box from the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) on the OrbView-2 platform (<http://oceancolor.gsfc.nasa.gov/cgi/>). Because the objective of this study was to address differences in bleaching severity at a regional scale, grid cells of 100 km by 100 km (for HadISST1.1) and 90 km by 90 km (for PAR) were sufficient for this analysis. Although differences in temperature and PAR exist at sub-grid scales, the resolutions of the data sets were sufficient to estimate the difference in temperature variability and stress experienced between bleaching sites located in separate grid cells. In addition, although the PAR data from the SeaWiFS sensor may be biased because of high diurnal variability in cloud cover at some sites (Dunne 2008), the monthly weighted average of the daily PAR values was sufficient to estimate the relative irradiance stress experienced by reefs during the regional bleaching events.

Studies have demonstrated that corals respond most severely to prolonged temperature and irradiance stress (Gleeson & Strong 1995; Podestá & Glynn 1997; Winter *et al.* 1998). Therefore, the degree of stress experienced by each reef site was calculated as the product of the cumulative PAR integral 2 months prior to, and the cumulative SST anomaly integral 1 month prior to, the observed bleaching. Because of high-cloud cover, the Society Islands (149.5° W, 17.5° S) did not experience bleaching during the 1998 event (Mumby *et al.* 2001). Therefore, the product of the cumulative SST and PAR integrals at the Society Islands was used as a bleaching threshold. All sites with a product of the cumulative SST and PAR integrals less than

Figure 1. Sites of the nine detrended $\delta^{18}\text{O}$ and Sr/Ca records (channels) used in M-SSA to determine the significant modes of SST variability: 1. Ras Umm Sidd (-0.812); 2. Madagascar (-0.907); 3. the Seychelles (-0.726); 4. the Houtman Abrolhos Islands (-0.732); 5. Ningaloo Reef (-0.798); 6. Guam (-0.677); 7. Maiana Atoll (-0.637); 8. Rarotonga (-0.783); 9. Palmyra Island (-0.797). The values next to each site represent the correlation coefficients (r_s) between the $\delta^{18}\text{O}$ or Sr/Ca records and local HadISST SSTs.

Figure 2. Flow chart summarizing the methodology used to analyse the association between the relative strength of the high- and low-frequency modes of sea-surface temperature (SST) variability in the past and bleaching severity during the 1998 and 2005–2006 bleaching events, where RCs are the reconstructed components from the M-SSA of coral $\delta^{18}\text{O}$ and Sr/Ca records.

that of the Society Islands in 1998 were excluded from the analysis, because corals at these sites were unlikely to have experienced enough stress to drive a strong bleaching response, either because they were protected by high-cloud cover or because they were not experiencing high temperature anomalies (figure 2). Therefore, this threshold selection criterion removed bleaching data from the times of the year when corals were not stressed by high temperature and high irradiance. We note that the same bleaching patterns were observed if only observations from the peak

bleaching months were utilized (peak bleaching months were defined based on the latitude of observation: January, February and March at latitudes south of 10°S ; April, May and June between 10°N and 10°S ; and July, August and September at latitudes north of 10°N). Because the results were similar, only the results using the quantitative stress-threshold were reported, so that the relationship between the frequency of temperature anomalies in the past and stress experienced during these contemporary events could be assessed. To remove sites at which the attenuation of

irradiance with depth reduced stress (Dunne 2008), coastal and offshore observations at depths greater than 15 and 25 m, respectively, were removed from the dataset (figure 2). Furthermore, any records with unknown or ambiguous information about the month, depth, PAR, SST or severity of the bleaching observation were excluded. Finally, to avoid pseudoreplication, only one bleaching observation per severity class was randomly selected for each HadISST gridbox (figure 2). These randomly selected observations were then used to test whether the frequency of temperature anomalies in the past caused differential bleaching during contemporary stress events despite similar modern temperature and irradiance stress (see electronic supplementary material, tables S1 and S2, for the bleaching observations analysed for the 1998 and 2005–2006 events, respectively). To test the sensitivity of the results to the selection of bleaching observations, additional analyses were performed on random subsets of the data and on the data with only one bleaching observation per grid box. Again, the results were the same regardless of the way the data sets were selected.

(c) Effect of past climate variability on bleaching severity

The strength of high- and low-frequency SST variability in the past, obtained from correlations of local HadISST SSTs with the high- and low-frequency components from M-SSA, was used to examine the influence of past SST variability on the capacity of modern coral populations to resist bleaching. As the relative strength of high- and low-frequency SST variability may influence the bleaching response observed at any given site, the difference between the absolute strength of the high- and low-frequency modes was used as the independent predictor variable (i.e. the bleaching predictor):

$$|r_{s(\text{high-frequency})}| - |r_{s(\text{low-frequency})}|$$

where $r_{s(\text{high-frequency})}$ and $r_{s(\text{low-frequency})}$ represent the Spearman's rank correlation coefficients between the high- and low-frequency modes of variability (obtained through M-SSA) and HadISST SSTs at that site (figure 2). The absolute value of the correlation coefficients was used because the coral responses are influenced by the strength of these modes of variability, regardless of whether the variance is in-phase (i.e. positive correlation) or out-of-phase (i.e. negative correlation) with variability in the rest of the domain. Less bleaching was expected at localities dominated by high-frequency SST variability (i.e. $|r_{s,\text{high-frequency}}| - |r_{s,\text{low-frequency}}| > 0$), because corals at these sites have most likely adjusted to frequent thermal stress. To test this prediction, a contingency table analysis was used to determine if there was a significant association between the relative strength of these modes of SST variability in the past and bleaching severity during contemporary bleaching events (figure 2). More formally, the analysis examined the influence of the relative strength of the high- and low-frequency modes of variability ($|r_{s,\text{high-frequency}}| - |r_{s,\text{low-frequency}}| < 0$ at low-frequency dominated sites and $|r_{s,\text{high-frequency}}| - |r_{s,\text{low-frequency}}| > 0$ at high-frequency dominated sites) on bleaching severity (no, low, medium and high) during the 1998 and 2005–2006 mass bleaching events. The frequency of sites within each bleaching severity class, for regions in which the high- and low-frequency modes were dominant, was compared with the expected random, Chi-square distribution. Correlation analyses were also performed to determine whether there was an association between

the relative strength of these modes of variability and the severity of stress experienced during the 1998 and 2005–2006 events.

3. RESULTS

(a) Global patterns of SST variability

The nine detrended coral $\delta^{18}\text{O}$ and Sr/Ca records revealed two dominant modes of variability, with periods of > 54 and 5.7 years (see electronic supplementary material, figure S4), which represent the main low- and high-frequency SST variability experienced by reefs globally (Mantua *et al.* 1997; Zhang *et al.* 1998; Power *et al.* 1999). The eigenvalues of these first two reconstructed modes (RC1 and RC2) were significant against a red noise null hypothesis (Ghil *et al.* 2002) and together explained approximately 13 per cent of the variance in the coral $\delta^{18}\text{O}$ and Sr/Ca network. Correlation of the low-frequency mode (RC1) with globally gridded HadISST SST data (figure 3) revealed that this component was evident outside the tropics (i.e. extratropics), particularly within the North Pacific, North Atlantic and Southern Ocean basins. This mode was also evident within the Caribbean Sea and in the central and southern Indian Ocean. The high-frequency mode (RC2_3) displayed the characteristic pattern of the El Niño–Southern Oscillation (ENSO) within the Pacific Ocean basin, with high-frequency SST variability in the eastern Pacific Ocean, and high-frequency variability of the opposite sign in the western, northern and southern portions of the Pacific basin (figure 4). This mode was also evident in much of the tropical and subtropical Indian Ocean.

(b) Coral bleaching

Contingency table analysis of bleaching observations for the 1998 thermal event revealed a significant association between the relative strength of the high- and low-frequency modes of SST variability ($|r_{s,\text{RC2}_3}| - |r_{s,\text{RC1}}| < 0$ or > 0) and bleaching severity during the event ($\chi^2 = 8.69 > 7.81$, $\text{df} = 3$, $p < 0.05$). However, high-frequency dominated regions showed significantly more 'high' bleaching than expected in 1998 (figure 5) ($\chi^2 = 4.17 > 3.84$, $\text{df} = 1$, $p < 0.05$). This deviation from the expected frequencies can be attributed to a positive correlation between the relative strength of the high- and low-frequency modes of variability ($|r_{s,\text{RC2}_3}| - |r_{s,\text{RC1}}|$) and the severity of stress experienced during the 1998 thermal event ($r_s = 0.373$, $n = 76$, $p < 0.05$) (figure 6). Therefore, in regions dominated by high-frequency SST variability, corals were more likely to experience high stress during the 1998 event, resulting in 'high' bleaching. This same pattern of bleaching severity (i.e. more sites observed than expected displaying high bleaching at high-frequency dominated sites) was also observed when: (i) random subsets of the bleaching observations were sampled; (ii) when only one observation per grid box was selected; and (iii) when only peak bleaching observations were used, suggesting that these results were not a consequence of a sampling bias. Therefore, contrary to our expectation, corals at high-frequency dominated sites were more likely to experience high bleaching severity during the 1998 event.

Contingency-table analysis revealed that there was no significant association between the relative strength of

Figure 3. Correlation of the annual mean of the low-frequency (>54-year) component (reconstructed component 1, RC1, which explained 5.5% of the variance) with the detrended, annually resolved 1° by 1° globally gridded HadISST1.1 sea-surface temperature data over the common time period (1886–1993), where shading represents the strength of the correlation and contours mask out correlations that were not significant at the 95 per cent confidence level (map created using climate explorer, <http://climexp.knmi.nl/start.cgi?someone@somewhere>).

Figure 4. Correlation of the annual mean of the high-frequency (>5.7-year) component (reconstructed component 2_3 RC2_3, which explained 7.2% of the variance) with the detrended, annually resolved 1° by 1° globally gridded HadISST1.1 sea-surface temperature data over the common time period (1886–1993), where shading represents the strength of the correlation and contours mask out correlations that were not significant at the 95 per cent confidence level (map created using climate explorer, <http://climexp.knmi.nl/start.cgi?someone@somewhere>).

the high- and low-frequency modes of variability ($|r_{s,RC2\_3}| - |r_{s,RC1}| < \text{or} > 0$) and bleaching severity during the 2005–2006 event ($\chi^2 = 2.45 < 7.81$, $df = 3$,

$p > 0.05$). However, unlike during the 1998 event, regions dominated by the high-frequency mode showed less ‘medium’ and ‘high’ bleaching than expected in

Figure 5. (a) Observed and expected (random, Chi-square) frequencies of sites displaying no (0% of corals bleached), low (1–10%), medium (>10–30%) and high (>30%) coral bleaching during the 1998 event in regions dominated by (i) low- and (ii) high-frequency SST variability. (b) Same as (a) but for the 2005–2006 bleaching event.

2005–2006 (figure 5). There were also more sites observed than expected displaying ‘no’ bleaching in these regions dominated by high-frequency SST variability (figure 5). As in 1998, these results were obtained regardless of the sampling protocol. The contrasting pattern in 2005–2006 occurred despite a positive correlation between the relative strength of the high- and low-frequency modes of variability and the severity of stress experienced ($r_s = 0.396$, $n = 49$, $p < 0.05$; figure 6). Therefore, despite experiencing greater stress than other sites, corals in regions dominated by high-frequency SST variability were less likely to severely bleach in 2005 and 2006.

4. DISCUSSION

Multi-channel singular spectrum analysis (M-SSA) of the nine detrended coral $\delta^{18}\text{O}$ and Sr/Ca records revealed two dominant modes of variability, characterized by spectral peaks at periods greater than 54 years and at 5.7 years. The tropical Pacific Ocean was dominated by the high-frequency (5.7-year) mode of SST variability, while the low-frequency (> 54-year) mode was dominant in the Atlantic Ocean. The Indian Ocean displayed an intermediate pattern, with much of the tropical portion of the basin dominated by the high-frequency mode, while the central and southern portions were dominated by the low-frequency mode.

Calculations of modern thermal stress revealed that sites that experienced frequent thermal anomalies in the past (i.e. dominated by high-frequency SST variability) were also more likely to experience high stress during contemporary thermal-stress events (hypothesis 1). Therefore, in contrast with hypothesis 2, high-frequency dominated sites were more likely to experience high stress and severe bleaching during the 1998 thermal

event. Yet, while frequent thermal anomalies in the past did not result in less bleaching during the 1998 event, the expected results were realized during the 2005–2006 bleaching event, when corals at high-frequency dominated sites displayed less bleaching than expected despite experiencing greater stress than other sites.

Considering that different bleaching responses were observed in 1998 and 2005–2006, despite similar elevated temperatures and irradiance during the events, it would be reasonable to assume that the reduced bleaching in 2005–2006 was a consequence of acclimatization to high-irradiance stress prior to the event, as has been suggested elsewhere (Dunne & Brown 2001). However, there was no significant difference in the cumulative PAR experienced in the two months prior to bleaching in 2005–2006 between the bleaching severity classes ($H = 0.387$, $\text{df} = 3$, $p = 0.943$) (electronic supplementary material, figure S1). Similarly, there was no significant difference between bleaching-severity classes in the overall combined SST and PAR stress experienced one and two months prior to bleaching, respectively ($F = 0.339$, $\text{df} = 3$, $p = 0.797$). Therefore, the lack of bleaching at sites dominated by high-frequency variability in 2005–2006 cannot be attributed to differential PAR stress, or SST and PAR stress, prior to the bleaching event.

The result that corals at high-frequency dominated sites were less likely to severely bleach during the 2005–2006 event, despite experiencing higher thermal and irradiance stress, suggests that either (i) thermal acclimatization ‘memory’ may be as long as seven years (Maynard *et al.* 2008), that (ii) corals ‘shuffled’ symbionts to host more thermally tolerant clades (Buddemeier & Fautin 1993; Baker *et al.* 2004), that (iii) greater energy reserves, species-specific heterotrophic plasticity and/or greater access to resources allowed corals to compensate for decreased photosynthesis during the 2005–2006 event

Figure 6. (a) Scatterplot displaying the significant positive association between the stress experienced by the reef during the 1998 coral bleaching event and the relative strength of the high- and low-frequency modes of SST variability ($|r_{s, \text{RC2}_3}| - |r_{s, \text{RC1}}|$) ($r_s = 0.373$, $n = 76$, $P < 0.05$). Stress was defined as the product of the cumulative photosynthetic active radiation (PAR) integral two months prior to the observed bleaching and the cumulative SST anomaly integral one month prior to bleaching (denoted as Temp * PAR). (b) Same as (a) but for stress experienced during the 2005–2006 coral bleaching event ($r_s = 0.396$, $n = 49$, $P < 0.05$).

(Grottoli *et al.* 2004, 2006; Anthony *et al.* 2007, in press) or that (iv) differential ‘holobiont’ (i.e. coral and symbiont) mortality selected for more tolerant coral individuals, and sensitive individuals were not able to re-populate reefs dominated by high-frequency variability during the intermittent years.

Some physiological results to-date only indicate acclimatory potential over weeks to months (Brown *et al.* 2002), yet Maynard *et al.* (2008) suggest that longer-term acclimatory influences are also possible. Surveys of several reefs in the central Great Barrier Reef during two similar thermal stress events in 1998 and 2002, sampled during the peak bleaching period, demonstrated that corals in the genera *Pocillopora* and *Acropora* showed greater thermal tolerance in 2002. Maynard *et al.* (2008) suggest that this response was unlikely to be driven entirely by selection of tolerant genotypes because they recorded low mortality during their surveys. Therefore, Maynard *et al.* (2008) conclude that the corals either acclimatized or adapted. However, mortality is most likely to occur several weeks after thermal stress peaks (Jones 2008), and therefore may have been underestimated by their surveys. Furthermore, the ability of corals to ‘shuffle’ symbionts and/or increase heterotrophy in response to thermal stress is species specific, and therefore unlikely to be the main driver of these large-scale bleaching patterns (Hoegh-Guldberg *et al.* 2002). In addition, there is no evidence for increased resource availability during subsequent thermal-stress events.

Therefore, although acclimatization, symbiont shuffling and heterotrophic plasticity may contribute to the adjustment of some local reef corals, the large, regional-scale adjustments in our study were most likely through differential survival of coral populations during the strong 1998 thermal anomaly (Loya *et al.* 2001), with selection against populations that were less tolerant. Indeed, recent evidence shows that tolerant host–symbiont combinations probably persisted through the 1998 event, while less tolerant individuals were selected against (Sampayo *et al.* 2008). Similarly, Glynn *et al.* (2001) found that eastern Pacific corals were more resistant to temperature stress in 1998 than in 1982–1983. Notably, while temperatures were extremely high in both 1982–1983 and 1998, Glynn *et al.* (2001) did not compare irradiance. Nonetheless, their results suggest that coral populations in the eastern Pacific may have adapted to thermal anomalies through differential survival of more tolerant genotypes.

Some authors question the capacity of corals to adapt to rapid climate change (Hoegh-Guldberg *et al.* 2002) while others extend hope for rapid evolution and adjustment (Baker 2001; Baker *et al.* 2004; Baird *et al.* 2008). Yet, all arguments are framed within the context of coral populations with longevities of years to centuries. Nevertheless, adaptation, in its strictest sense, is not simply differential survival of individuals, but also genotypic adjustment through differential reproductive rates of individuals in the populations. Corals older than 3–4 years are generally mature, with a capacity to produce

sexually recombined offspring (Wallace 1985). And since sexual reproduction is an annual event, even biannual in the tropics (Penland *et al.* 2004), (although considerably reduced or delayed by a year after a bleaching event, Baird & Marshall 2002) directional selection on the genetic constitution of coral holobionts could be rapid under the right regional circumstances. Indeed, mounting evidence shows that under rapid environmental change adaptation is highly likely (Endler 1986; Thompson 1998; Carroll *et al.* 2007), shifting ecological and evolutionary rates of change to the same time frame. Thereby, thermal stresses on reefs may open a directional-selection window and the population's genetic constitution may rapidly adjust, through forces of mutation and (sexual) recombination, particularly at reefs dominated by high-frequency variability.

However, it is still unclear how these modes of temperature variability may be altered under future climate change (Vecchi *et al.* 2008). In addition, temperature change in the oceans is only a part of global-climate change; irradiance intensity and changes in cloudiness are also essential elements influencing responses of photosynthetic organisms. For corals, low or reduced irradiance caused by high-cloud cover during times of temperature stress reduces photoinhibition, coral bleaching and coral mortality (Mumby *et al.* 2001; Takahashi *et al.* 2004). Indeed, physiological studies concur and show that a 20 per cent reduction in PAR during periods of high water temperature is sufficient to prevent photoinhibition and coral bleaching (Brown *et al.* 1994; Takahashi *et al.* 2004). Therefore, it is disturbing that rises in SST may reduce upper-level cloudiness, particularly in the tropics (Schroeder & McGuirk 1998; Bates & Jackson 2001; Lau & Wu 2003; Lau *et al.* 2005). Model simulations of doubled atmospheric CO₂ similarly predict reductions in total cloudiness, leading to greater absorption of short-wave and long-wave radiation by the oceans (Sud *et al.* 2008). High-density clouds will protect coral reefs from bleaching, while reductions in cloudiness will exacerbate thermal stress. Not negating the fact that water temperature is the primary cause of coral bleaching (Brown 1997a,b), we re-emphasize the need to examine the dynamics of temperature and cloud cover together, because bleaching refuges may occur at localities with increased high-density cloud cover (Mumby *et al.* 2001).

Future thermal stress events will again undoubtedly lead to regional differences in bleaching severity. Corals in regions dominated by high-frequency SST variability, such as the eastern and western Pacific Ocean, will probably again be the most thermally stressed, but may also experience strong selective pressures to adjust. In contrast, reefs in the Atlantic Ocean, which primarily experience low-frequency variability, may adjust more slowly to future thermal stress. Reefs in the Indian Ocean are likely to display an intermediate response to climate change, because many reefs in this region experience both strong high- and low-frequency variability. However, even though this study demonstrates that corals have a capacity to adjust to thermal stress, particularly at reefs dominated by high-frequency variability, adjustments are likely to result from differential survival (Loya *et al.* 2001). Therefore, these adjustments will probably come at the considerable cost of large changes in coral species composition on reefs worldwide.

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