# Global assessment of coral bleaching and required rates of adaptation under climate change

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### Abstract

**Elevated ocean temperatures can cause coral bleaching, the loss of colour from reef-building corals because of a breakdown of the symbiosis with the dinoflagellate *Symbiodinium*. Recent studies have warned that global climate change could increase the frequency of coral bleaching and threaten the long-term viability of coral reefs. These assertions are based on projecting the coarse output from atmosphere–ocean general circulation models (GCMs) to the local conditions around representative coral reefs.**

**Here, we conduct the first comprehensive global assessment of coral bleaching under climate change by adapting the NOAA Coral Reef Watch bleaching prediction method to the output of a low- and high-climate sensitivity GCM. First, we develop and test algorithms for predicting mass coral bleaching with GCM-resolution sea surface temperatures for thousands of coral reefs, using a global coral reef map and 1985–2002 bleaching prediction data. We then use the algorithms to determine the frequency of coral bleaching and required thermal adaptation by corals and their endosymbionts under two different emissions scenarios.**

**The results indicate that bleaching could become an annual or biannual event for the vast majority of the world's coral reefs in the next 30–50 years without an increase in thermal tolerance of 0.2–1.0 °C per decade. The geographic variability in required thermal adaptation found in each model and emissions scenario suggests that coral reefs in some regions, like Micronesia and western Polynesia, may be particularly vulnerable to climate change. Advances in modelling and monitoring will refine the forecast for individual reefs, but this assessment concludes that the global prognosis is unlikely to change without an accelerated effort to stabilize atmospheric greenhouse gas concentrations.**

*Keywords:* adaptation, bleaching, climate change, coral reefs, general circulation model, ocean warming, symbiosis

## Introduction

Coral reefs appear to be among the most vulnerable ecosystems to future climate change. Sea temperatures of only 1 °C warmer than the usual summer maxima can cause the syndrome known as coral bleaching, because of the breakdown of the endosymbiosis between corals and the dinoflagellate protist *Symbiodinium*. During coral bleaching, the brown pigments of

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the symbionts are lost causing corals to pale in colour. Field and laboratory evidence has shown that frequent or severe bleaching can lead to a reduction in the reproductive capacity, growth, disease resistance and/or survivorship of affected corals at large geographic scales (Hoegh-Guldberg, 1999; Douglas, 2003). Incidences of mass coral bleaching in recent decades have been attributed to rising near-surface ocean temperatures and led many to speculate that future climate change could lead to the long-term degradation of many coral reefs (Glynn, 1991; Brown, 1997; Hoegh-Guldber, 1999; Wellington *et al.*, 2001; Sheppard, 2003).

The variable response of many coral species to temperature stress both within reefs and across the tropical oceans suggests some potential for corals and their endosymbionts to adapt or acclimate to warming ocean temperatures (Douglas, 2003; Hughes *et al.*, 2003). Corals may be capable of adapting to thermal stress by shifting to symbioses with more temperature-tolerant species of *Symbiodinium* (Brown *et al.*, 2002; Baker *et al.*, 2004; Rowan, 2004), although the strength of the evidence is still a matter of debate (Hoegh-Guldberg *et al.*, 2002; Hoegh-Guldberg, 2005). Identifying both the thermal stress that coral reefs worldwide may experience because of climate change and the level of thermal adaptation which may be required to avoid frequent coral bleaching in the future is vital both to the conservation of coral reefs (West & Salm, 2003) and the design of global climate policy (O'Neill & Oppenheimer, 2002; O'Neill & Oppenheimer, 2004).

Previous studies have estimated the impact of climate change on coral bleaching by the relating projected future sea surface temperatures (SST) from atmosphere–ocean general circulation models (GCMs) to the conditions on selected reefs or regions (Hoegh-Guldberg, 1999; Sheppard, 2003). The key source of uncertainty in such projections is the large difference between the horizontal scale of individual coral reefs ($10^1$–$10^3$ m) and the horizontal scale of coupled atmosphere–ocean GCMs used to project future climate ($10^4$–$10^5$ m). The coarse spatial and temporal resolution of the current GCMs can be sufficient for describing the average conditions of an area of ocean that contains coral reefs, but not for describing the fine-scale hydrodynamics around the individual coral reefs themselves. For example, the resolution limits the representation of some regional currents that influence SST around reef complexes, any localized upwelling of cool, deeper ocean waters or the heating of shallow waters on reef flats (Skirving & Guinotte, 2001; Wooldridge & Done, 2004). The direct GCM output is better suited to represent the average thermal environment of an area containing coral reefs rather than the temperature that would be recorded at an observing station on a specific reef.

The mass coral bleaching prediction system developed by the NOAA Coral Reef Watch project provides an ideal framework for bridging the gap in scale. The system tracks anomalously warm water that may lead to coral bleaching in a region via satellite (Liu *et al.*, 2003; Skirving *et al.*, 2004a, in press). The accumulation of degree heating weeks (DHWs), a measure of thermal stress, has proven effective at identifying the occurrence of coral bleaching in each $36 \text{ km} \times 36 \text{ km}$ grid cell defined by the satellite dataset (Liu *et al.*, 2003; Skirving *et al.*, 2004a, in press). The real-time bleaching warnings are routinely used by scientists, marine reserve officials and recreational dive operators worldwide and are increasingly incorporated in studies of the response of coral communities to thermal stress (e.g., Wellington *et al.*, 2001; Liu *et al.*, 2003). The bleaching prediction system is a reliable way to evaluate whether GCMs can represent the thermal stress that leads to coral bleaching events and assess the stress facing reefs worldwide under a warmer climate.

In this study, we take advantage of the NOAA Coral Reef Watch historical satellite data and a global coral reef map to develop and test algorithms for projecting the likelihood of coral bleaching from the output of two GCMs. We then forecast the frequency of mass coral bleaching and the increase in thermal tolerance necessary to ensure long-term survival for thousands of coral reefs in two future emissions scenarios. The results identify the range in thermal stress that coral reefs worldwide may face because of climate change and the adaptive response required to avoid dangerously frequent bleaching events.

## Materials and methods

### Input data

Historical SST and annual DHW values for 1985–2002 at $36 \text{ km} \times 36 \text{ km}$ spatial resolution were derived from the AVHRR SST Pathfinder data (Skirving *et al.*, 2004a, in press). The Pathfinder SST dataset is a retrospective analysis conducted to account for any sensor drift and atmospheric attenuation issues via comparisons of the satellite-derived SST with the *in situ* SST monitored by a network of buoys (http://www.nodc.noaa.gov/sog/pathfinder4 km/). The resultant composite SST product is calibrated to 1 m depth and produced twice weekly.

The annual accumulation of DHWs is determined from the twice weekly SST data. One DHW is equal to a week of SSTs that are one degree greater than the mean temperature of the warmest month in the climatology (i.e. the historical mean for February on parts of the Great Barrier Reef). The total DHW accumulation for a given year is the accumulation of positive SST anomalies over a rolling 12-week time period; only anomalies in excess of $1 \,^\circ\text{C}$ are included, because smaller SST spikes are believed to be insufficient to cause stress on corals (i.e. consecutive weekly anomalies of 1.0, 1.5 and 0.8 results in total DHW value of 2.5, because the third value is less than 1). The extent of bleaching and likelihood of coral mortality tends to increase with the level of heat stress. Independent coral bleaching reports have consistently indicated that some coral bleaching occurs in a region when the DHW value exceeds four, and severe bleaching with coral mortality

occurs when the DHW value exceeds eight (Liu *et al.*, 2003; Skirving *et al.*, 2004a, in press).

The simulated monthly surface 'skin' temperature for 1980–2100 were obtained from simulations of the US National Center for Atmospheric Research's PCM (http://www.cgd.ucar.edu/pcm/main.html) and the UK Hadley Centre's HadCM3 (http://www.meto. gov.uk/research/hadleycentre/models/HadCM3.html) under the SRES A2a and B2a scenarios conducted from the third IPCC assessment (Cubasch *et al.*, 2001). Previous analyses of the impact of climate change on coral bleaching employed output from one model under one future scenario (Sheppard, 2003) or from an earlier IPCC assessment (Hoegh-Guldberg, 1999). Here, the models and emissions scenarios were selected to reflect the range of possible futures. HadCM3 has a spatial resolution of $2.5° \times 3.75°$ and a climate sensitivity of $3.0°C$ (increase in global surface temperature from a doubling of atmospheric $CO_2$). The climate sensitivity is slightly above average for the models employed in the IPCC assessments. PCM has a resolution of $2.8125° \times 2.8125°$ and a climate sensitivity of only $1.7°C$, lowest of the models used in the 3rd IPCC assessment (McAvaney *et al.*, 2001). It is used here to represent a lower bound for projected ocean warming under the emissions scenarios.

The SRES future emissions scenarios were designed to reflect different paths of future economic development and energy use (Nakicenovic *et al.*, 2000). The SRES A2 emission scenario is commonly used for 'business as usual' impact studies, projecting a $3°C$ increase in surface air temperature by 2100 (on average across all the IPCC models). The less energy-intensive SRES B2 scenario features a lower emission path, projecting a $2.2°C$ temperature increase on average across all models. These two scenarios played a central role in the 3rd IPCC assessment (Cubasch *et al.*, 2001) and are commonly used in climate impact studies (e.g., Parry *et al.*, 2004). The projected warming in this study could be considered conservative or optimistic, as the more fossil fuel intensive emissions scenarios (e.g. SRES A1F) and the GCMs with greater climate sensitivity (e.g., GFDL R15a, CCCMA) were excluded.

The surface 'skin' temperature from GCMs is the closest proxy for the satellite-derived SST and has been employed in previous coral bleaching studies (Hoegh-Guldberg, 1999; Sheppard, 2003). In the future projections, the monthly SST was estimated as the sum of the GCM monthly SST anomalies (future minus today) and the monthly satellite data averaged to the GCM resolution. For example, the projected average SST for January 2030 equals the sum of mean for January in the historical satellite data and the difference between the GCM-simulated value for January 2030 and the GCM-simulated mean January in today's climate (represented by 1980–1999 in the SRES scenarios).

The distribution of the world's coral reefs was derived from a $1° \times 1°$ resolution map of the world's coral reefs developed by the World Resource Institute's Reefs at Risk project (Bryant *et al.*, 1998), and updated with observations from Reefbase (see http://www.reefbase.org). The map was used to determine if coral reefs are present in each $36\,km \times 36\,km$ grid cell represented by the satellite SST data. The number of coral reef grid cells included in the future projections depends on the ocean definition employed by the particular GCM. There are 3579 coral reef grid cells with the HadCM3 ocean mask and 2098 reef cells with the PCM ocean mask, which excludes waters in the Caribbean and around Southeast Asia.

## Evaluating limits posed by model resolution

The ability to project thermal stress on coral reefs from GCM output is limited by the coarse spatial resolution of the models and the temporal resolution of archived model output. In order to best adapt the DHW bleaching prediction methodology for use with GCM output, we first carefully evaluated how the coarse spatial and temporal resolution of the GCM output limits the ability to project regional coral bleaching. We examined how the spatial and temporal resolution may limit the ability to predict mass bleaching events by contrasting the prediction of historical bleaching events using the existing satellite data, known to be a reliable but conservative measure of mass thermal coral bleaching (Skirving *et al.*, 2004a, in press), and the satellite data interpolated to the GCM resolution.

First, we evaluated whether the temperatures in the relatively shallow coral reef environments can be realistically represented at the spatial scale of existing GCMs by examining the difference between the range of observed shallow, coastal SSTs and observed open ocean SSTs within the region defined by a GCM grid cell. The area-averaged observed SST for all $36\,km$ grid cells, the shallow $36\,km$ grid cells ($<200\,m$) and the deep $36\,km$ grid cells ($>200\,m$) within each GCM-resolution ocean grid cell containing coral reefs (for both models) were calculated using the 1985–2002 satellite SST dataset, the global reef map and bathymetry data derived from the ETOPO5 dataset (available at http://www.ngdc.noaa.gov/mgg/global/seltopo.html). We focused on the warmest month in the climatology in each GCM-resolution grid cell since that is when coral bleaching is most likely to develop (i.e. February for the Great Barrier Reef).

The annual mean shallow and deep water SSTs for the warmest month are very similar within the large

majority of the GCM grid cells. At the HadCM3 resolution, the values for the average shallow and deep water SSTs are the same for 57% of the 339 grid cells containing reefs; only 9% of the grid cells had a difference of greater than 0.25 °C and only one grid cell had a difference of greater than 0.5 °C. The results are similar at the different PCM spatial resolution, with the average shallow and deep water SSTs being the same for 45% of the 414 grid cells containing reefs; only 11% of the grid cells had a difference of greater than 0.25 °C and only two had a difference of greater than 0.5 °C. It is worth noting that although the PCM employs a higher spatial resolution than HadCM3, many coral reefs are excluded from the analysis because the model's land mask excludes parts of the Caribbean and waters around SE Asia.

A few isolated regions show a slightly greater variation between shallow and open ocean SSTs in the warmest years, when the conditions for bleaching were present. At the HadCM3 resolution, 52% of the 339 grid cells containing reefs had no difference between shallow and deep SSTs in the warmest year, while 3% had a difference of greater than 0.5 °C. Predictably, the large difference occurs in GCM-resolution grid cells with only small areas of shallow water or reefs. While not surprising, this result is nevertheless important for predicting the thermal stress that can lead to bleaching. It indicates that the SST simulated by the GCM is only influenced by the coastal SSTs in regions with large shallow areas, either continental shelves or large reef complexes. In these locations, knowledge of subgrid heterogeneity in SST is necessary to extrapolate GCM-simulated temperatures to reef conditions. In more open ocean reef environments, where the shallow coastal area represents only a small fraction of the region defined by a GCM grid cell, it is less likely the GCM output can be directly representative of the reef conditions.

## Development of a monthly bleaching index

The accuracy of bleaching forecasts tends to improve using SST data with shorter time steps that can better describe the spikes in SSTs that lead to the onset of bleaching (Berkelmans, 2002). The historical DHW data are estimated from twice weekly SST observations, while most GCM output to date has been archived at monthly time steps. Previous studies have used monthly data to predict the frequency of bleaching events, assuming that monthly average temperatures that are 1 °C greater than the maximum of the monthly mean SST climatology will lead to bleaching (Hoegh-Guldberg, 1999; Sheppard, 2003). We evaluated the impact of using monthly, rather than the daily or weekly, data on the predicted occurrence of thermal stress that can lead to bleaching in the 1985–2002 satellite data.

The annual accumulation of degree heating month (DHM) values in each of the 36 km grid cells containing reefs was calculated from the 1985–2002 observed data. A DHM is equal to 1 month of SST that is 1 °C greater than the maximum in the monthly climatology for that grid cell. We determined that annual DHM total of 1 °C was the best proxy for the lower intensity bleaching threshold (DHW > 4) and an annual DHM total of 2 °C as the higher threshold, for severe coral bleaching with more associated coral mortality (DHW > 8). The monthly method agrees with 68% of bleaching events predicted using the weekly method from 1985 to 2002, and predicts 8% more total bleaching events overall. The agreement is poorer for the higher bleaching threshold; the monthly method predicts 35% more occurrences of severe bleaching in the historical record. Any positive or negative changes in the DHM thresholds decreased the agreement on specific occurrences of bleaching with the weekly method.

There are two primary explanations for the difference in prediction of bleaching events with the two methods. First, if some weekly temperatures are in excess of the maximum in the monthly climatology, but the monthly average is not, there will an accumulation of DHWs but not of DHMs. This causes some disagreement on specific occurrences of bleaching. Second, in the NOAA methodology, the accumulation of DHWs does not commence until the weekly SST reaches 1 °C greater than the maximum in the monthly climatology (i.e. the minimum DHM value is 1). This causes the monthly method to predict slighter more frequent exceedence of the bleaching thresholds. Experiments with a minimum threshold for accumulating DHMs did not improve results; for example, with a minimum threshold of 0.25 °C greater than the max month SST, the monthly method predicts fewer (only 62%) of the bleaching events described by the weekly method.

The annual DHM value is employed as a measure of accumulated thermal stress in the future scenarios, as it proved to be a reasonable proxy for DHW value. The projected annual DHM value at the GCM resolution for 2010–2099 in each scenario are determined from the projected monthly SSTs (sum of the GCM anomaly and mean in the historical satellite data). The warmest month in the satellite climatology serves as the minimum threshold (e.g. the February mean for the Great Barrier Reef).

## Statistical downscaling of GCM output

Evaluating the regional impacts of climate change often requires increasing the resolution of GCM climate projections using dynamical (i.e. regional climate models) or statistical 'downscaling' (Murphy, 1999).

Hydrodynamic models, the oceanic equivalents of atmospheric regional climate models, can be used to simulate temperatures around a particular coral reef at higher resolution than currently possible with a GCM, but this technique is impractical for a global assessment. Statistical downscaling of GCM output based on historical observations of SST patterns can increase the resolution of global coral bleaching projections. We developed a method of statistically interpolating SSTs from the coarse GCM resolutions to the resolution of the satellite data.

Detailed analysis of observed SSTs at a subset of coral reef locations across the tropical oceans confirmed that the relationship between the annual observed SST at 36 km resolution and the spatially averaged SST for the region within the relevant GCM grid cell was best described by a linear regression. We developed a linear regression between the local SST and the GCM-resolution SST the warmest month in the climatology (e.g. February on parts of the Great Barrier Reef) using the 18 years of satellite data for each 36 km coral reef cells. The goodness of fit from the linear regressions indicated that the GCM-resolution SST was a strong predictor of 36 km SST for almost all the coral reef grid cells. For example, at the HadCM3 resolution, $r > 0.8$ for 3114 of the 3579 coral reef cells; at the PCM resolution, $r > 0.8$ for 1972 of the 2098 coral reef cells. The few coral reef cells – 28 using HadCM3, five using PCM – with regressions not significant at the 98% level ($r > 0.542$ for two-tailed test with 16 degrees of freedom) were omitted from the study.

We further evaluated the goodness of fit of each downscaling relationship by testing whether linear regressions could predict the monthly SST in the 2 warmest years of the satellite record. To be applicable under the warmer climate scenarios, the downscaling relationships must not exhibit a bias at high SSTs. The absolute error (predicted−observed) in SST downscaled from the HadCM3 resolution was less than $0.25\,^{\circ}\mathrm{C}$ in 73% of the grid cells and less than $0.5\,^{\circ}\mathrm{C}$ in 96% of the 36 km grid cells for both the warmest and second warmest years (Fig. 1). The results were similar for SSTs downscaled from the PCM resolution; over 77% of the grid cells had prediction errors of less than $0.25\,^{\circ}\mathrm{C}$ in the 2 warmest years. For both models, the errors were normally distributed about zero for both model resolutions, indicating no systematic positive or negative bias. The 36 km grid cells with prediction error greater than $0.5\,^{\circ}\mathrm{C}$ in the first and/or the second warmest year – 172 for HadCM3 and 70 for PCM – were omitted from this study. In total, the statistical analysis developed acceptable downscaling relationships for 3379 coral reef cells using HadCM3 resolution and 2023 coral reef cells using the PCM resolution.

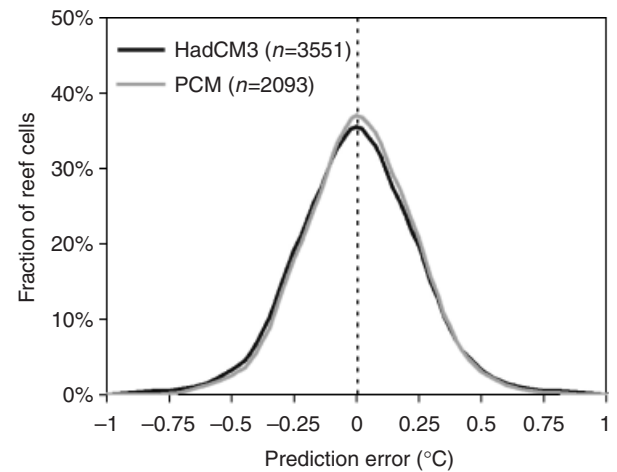The impact of downscaling on bleaching predictions was further tested by estimating the annual DHM



**Fig. 1** Frequency distribution of prediction errors from the downscaling relationships. The prediction error for a given reef is the difference (in $^{\circ}\mathrm{C}$) between peak monthly sea surface temperatures (SST) for the warmest year in the satellite record predicted by the regression relationship for that grid cell and the observed SST. Grid cells where the regression resulted in prediction error $> |0.5\,^{\circ}\mathrm{C}|$ for the 20 warmest years were omitted from this study.

values for 1985–2002 in each reef cell using 36 km SST data directly, the 36 km data averaged to GCM resolutions, and the 36 km data averaged to the GCM resolutions and interpolated back to the 36 km resolution using the linear downscaling regression developed for the particular grid cell. The three methods agree as to whether or not bleaching occurred in 93% of the cases in the 1985–2002 record (each reef cell, each year) and agreement as to whether or not severe bleaching occurred in 98% of the cases. The downscaled DHMs predict slightly fewer total occurrences of low-intensity bleaching than the DHMs averaged to the GCM resolution (2% at HadCM3 resolution, 1% at PCM resolution) and also slight differences in total occurrences of severe bleaching (2% more at HadCM3 resolution, 3% less at PCM resolution). The analysis suggests that statistically interpolating the GCM-simulated SSTs to the satellite data resolution should have a relatively minor impact on the projected occurrence of thermal stress in the majority of locations. The method was applied in hopes of best representing projected bleaching frequency and particularly the possible spatial variability in required adaptation rates.

## Results

### Projected thermal stress and frequency of coral bleaching

The models project an increase in annual accumulation of thermal stress across the tropical oceans over the next

50 years in the SRES A2 and B2 emission scenarios. The mean annual DHM value exceeds one or two across much of the world's tropical oceans by 2030s in HadCM3 in both SRES scenarios (Fig. 2a, b). Warming is less extensive in the PCM but has a similar geographical pattern. In both models, the highest mean annual DHM values in the next several decades are projected for the central Pacific, the eastern Indian Ocean and the lower in the Atlantic Ocean. This pattern generally reflects the projected increase in mean sea surface warming noted for the models in the IPCC assessment (Cubasch *et al.*, 2001) and climate impact studies (e.g. Sarmiento *et al.*, 2004). In HadCM3, the projected DHMs exceed four in much of the central Pacific by the 2030s since the model predicts conditions similar to El Nino will prevail in a warmer climate (Cubasch *et al.*, 2001). In contrast to HadCM3 and most GCMs, the projected Pacific warming is more uniform in PCM (Washington *et al.*, 2000).

There is greater difference in projected accumulation of thermal stress between the models than between the emissions scenarios. The magnitude and geographical pattern of the mean annual DHM is similar in the SRES A2 and B2 scenarios in both models (Fig. 2a, b). Although the projected increase in radiative forcing and global surface temperature is greater in SRES A2 over the century, it does not surpass that in SRES B2
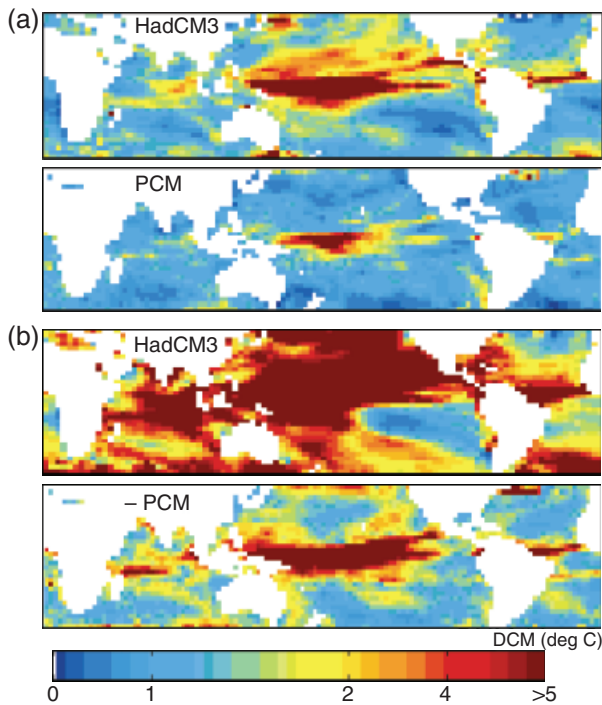
until midway through the century (Cubasch *et al.*, 2001). The annual mean DHMs in SRES A2 are slightly lower than in SRES B2 until the 2040s, particularly in the Pacific.

The frequency of thermal stress exceeding the bleaching thresholds at coral reefs worldwide was determined with projected SSTs downscaled to the 36 km resolution using the linear relationships determined for each coral reef grid cell. According to both models, low-intensity bleaching (DHM >1) occurs at the majority of world's reef areas at least every 2 years by the 2030s and almost every year by the 2050s (Fig. 3a, b). Severe bleaching (DHM > 2) occurs every 3–5 years at the majority of the world's reefs in the 2030s and becomes a biannual event
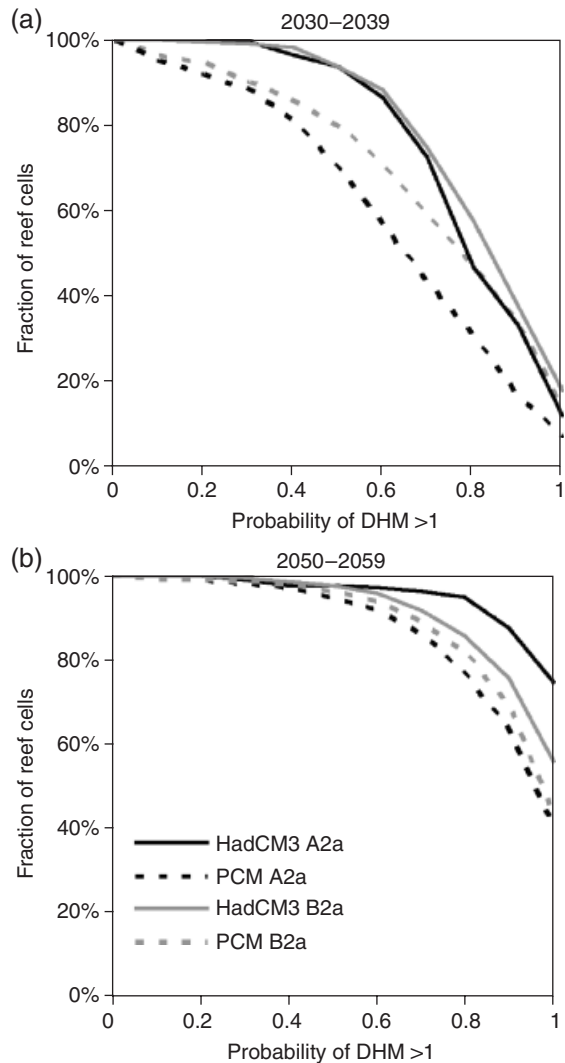
**Fig. 3** Projected frequency that the world's coral reefs during experience annual degree heating month >1 during (a) 2030–2039 and (b) 2050–2059. The results are the fraction of 36 km grid cells containing coral reefs with a given probability of exceeding threshold (e.g., $P = 0.5$ is every 2 years).
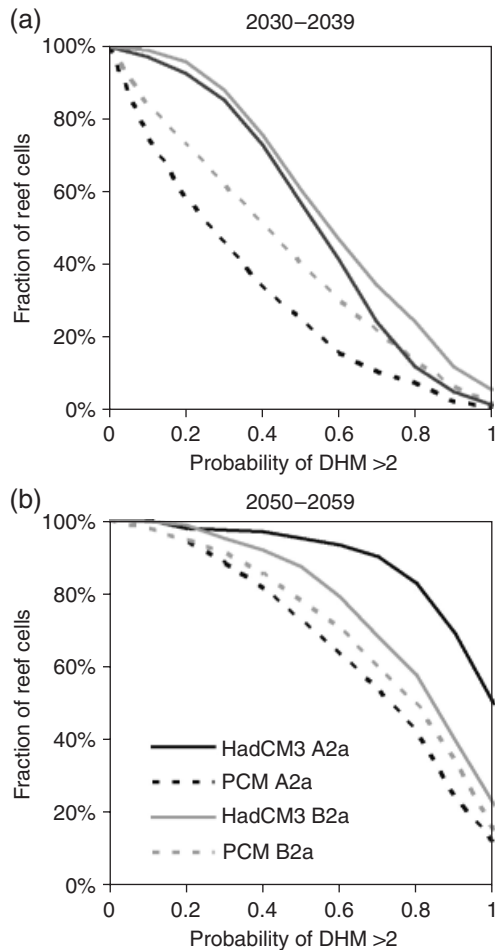
**Fig. 2** Annual mean degree heating month (DHM) values from HadCM3 and PCM–PCM in the SRES A2a scenario for (a) 2030–2039 and (b) 2050–2059.

**Fig. 4** Projected frequency that the world's coral reefs experience annual degree heating month >2 during (a) 2030–2039 and (b) 2050–2059. Results are displayed as in Fig. 3.

by the 2050s (Fig. 4a, b). The frequency of low-intensity bleaching worldwide is greater in HadCM3 than PCM in the 2030s (Fig. 3a), although the difference decreases steadily later in the century.

The noted similarity in SST in the A2 and B2 scenarios over the next 50 years causes there to be little difference in coral bleaching projections for the entire century. By the time the scenarios diverge in the 2050s, the mean annual DHMs exceed three or four across much of the tropical ocean in both models (Fig. 2a, b) and bleaching is occurring annually at many reefs (Fig. 3b). Severe bleaching is an annual or biannual event at 80–100% of the reefs worldwide by the 2080s in each model under each scenario (Fig. 4b).

The global analysis reveals large spatial variability in the future projections not noted in earlier studies restricted to a few individual sites (Figs 5–7). According to HadCM3, the frequency of bleaching events will increase the fastest around many Micronesian and Mela-

nesian islands, the northern Caribbean, the Indonesian islands and the Malaysian archipelago. The projected frequency of bleaching is lower in most regions according to PCM, although the geographical pattern is similar (excluding the Caribbean and Southeast Asia, where PCM omits large areas of coastal ocean). In all the models and scenarios, the geographic variability decreases in the latter half of the century as only a few reefs, mostly in Polynesia, are spared from at least biannual bleaching.

In summary, the models generally agree that at least low-intensity bleaching could occur at least once every 2 years on coral reefs throughout each of the major tropical ocean regions by the latter half of the century in either emissions scenario (Table 1). The PCM projections can be viewed as a lower bound as that model has the lowest climate sensitivity of the GCMs used in the last IPCC assessment (McAvaney et al., 2001). Although the rate of increase in the frequency of bleaching events over the next 50 years is slower with PCM than the more moderate HadCM3, the models agree that bleaching would become an annual event at most reefs without any increase in thermal tolerance. The exact consequences of such repeated bleaching events would depend on the composition of the coral community, the history of disturbance and a number of other factors (Fitt et al., 2001; Loya et al., 2001; Douglas, 2003,; McClanahan, 2004). The interval between bleaching events or other disturbances is crucial to successful recruitment and long-term maintenance of coral cover (Connell et al., 1997; Done, 1999). Recent evidence has shown that frequent low-intensity bleaching even with no coral mortality can lead to long-term degradation of the coral reef ecosystem by slowing coral growth, reducing coral recruitment and reducing resiliency to other disturbances (Hoegh-Guldberg, 1999; Baird & Marshall, 2002).

*Required adaptation to increased thermal stress*

Adaptation or acclimation to the projected increased thermal stress by corals and their symbionts could forestall widespread degradation of coral reefs. We determined the increase in thermal tolerance required to ensure bleaching occurs only once every five ($P = 0.1$) or 10 ($P = 0.2$) years in the projected climates under both the SRES A2 and B2 emissions scenarios. In each 36 km grid cell containing coral reefs, the threshold temperature at which DHMs accumulate was increased, with iterations of 0.05 °C, until the frequency of bleaching events in a given decade reduced to the desired level. The 5- and 10-year return intervals selected here based on a variety of evidence for the average time required for full recovery of coral cover after a bleach-
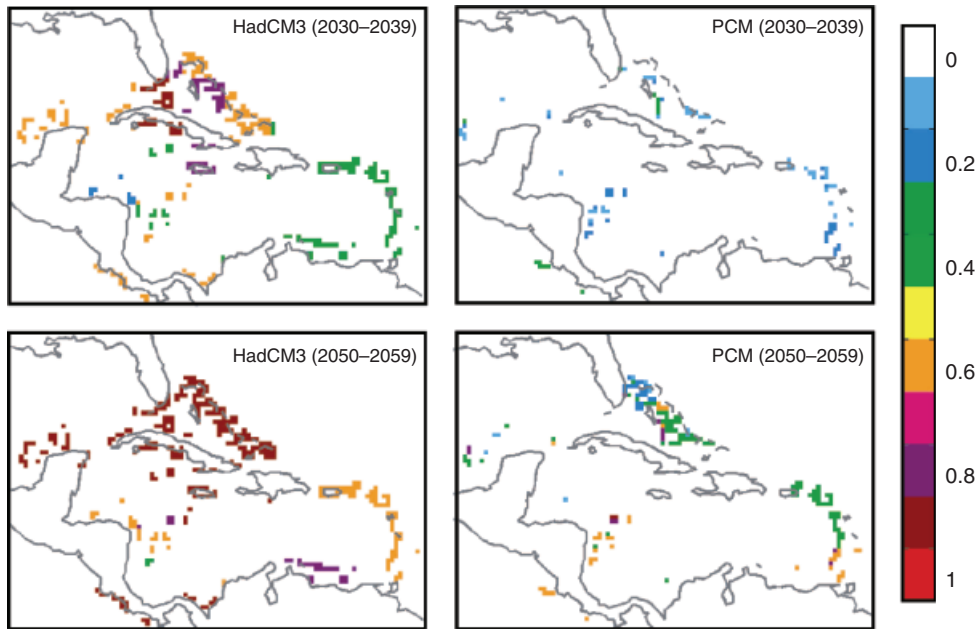
**Fig. 5** Frequency that annual degree heating month >1 during 2030–2039 and 2050–2059 for each 36 km grid cell in the Caribbean containing corals reefs, under SRES A2.

ing or disturbance event (Connell *et al.*, 1997; Done, 1999; Sheppard, 2003) and the higher confidence in the lower bleaching threshold (see Methods). The decades of 2030s and 2050s were used as possible benchmarks because the above results indicate DHMs are likely to exceed one either annually or biannually at many of the world's reefs.

The GCM output suggests that the thermal tolerance of corals and their symbionts at a majority of the world's coral reefs must increase by at least 0.5 °C by the 2030s, and at least 0.8–1.0 °C by the 2050s to ensure that low-intensity bleaching events do not occur more than once every 5 years (Table 2; Fig. 8a, b). The choice of a 5-year interval instead of a 10-year interval results in only marginally higher required adaptation rates in most grid cells. With the 2030s as a deadline, the mean of the required adaptation from all the coral reef cells is 0.80 °C (SRES A2) and 0.67 °C (SRES B2) with HadCM3, and 0.49 °C (A2) and 0.56 °C (B2) with PCM. The difference in required adaptation rates is again greater between models than between emissions scenarios in each coral reef region (Table 2).

With the 2050s as a deadline, the required adaptation differs less between models under the B2 scenario, but differs more under the A2 scenario (Fig. 8b). The mean required adaptation is 1.15 °C for the HadCM3 results under the A2 scenario, over 30% greater than the mean adaptation under the B2 scenario (0.87 °C) and the PCM results under both scenarios (0.88 °C under A2, 0.82 °C under B2). One-third (32%) of the world's coral reefs

require adaptation greater than 1.5 °C by 2050 in the A2 scenario according to HadCM3, almost three times the fraction in the HadCM3 results under the B2 scenario or PCM results under both scenarios (12–13%). This difference is because of the greater warming in the central Pacific, Indian Ocean and central Caribbean in the HadCM3 simulation of the SRES A2 scenario by the 2050s. The smaller difference in projected adaptation rates between scenarios with PCM is partly because of the exclusion of coral reefs in Southeast Asia and the Caribbean. The global distribution of required adaptation rates results from HadCM3 under the more 'business as usual' SRES A2 scenario could arguably represent a more likely future.

The results indicate substantial geographic variation in the adaptation rates, not noted in previous studies, because of the heterogeneity of projected ocean warming (Figs 9 and 10). In general, both models predict the fastest adaptation will be required in Micronesia, the Indian Ocean, western Polynesia and the Coral Sea (Table 3). The HadCM3 output indicates that many coral reefs in western Polynesia and especially Micronesia may require adaptation rates of 0.5 °C to over 1 °C per decade in the next thirty years (Fig. 10). The total adaptation required by the 2030s exceeds 1 °C per decade in 1% of the coral reef grid cells (33 cells with HadCM3, 13 with PCM, under the A2 scenario), most of which are located in the western Pacific equatorial nations of the Marshall Islands and Kiribati.
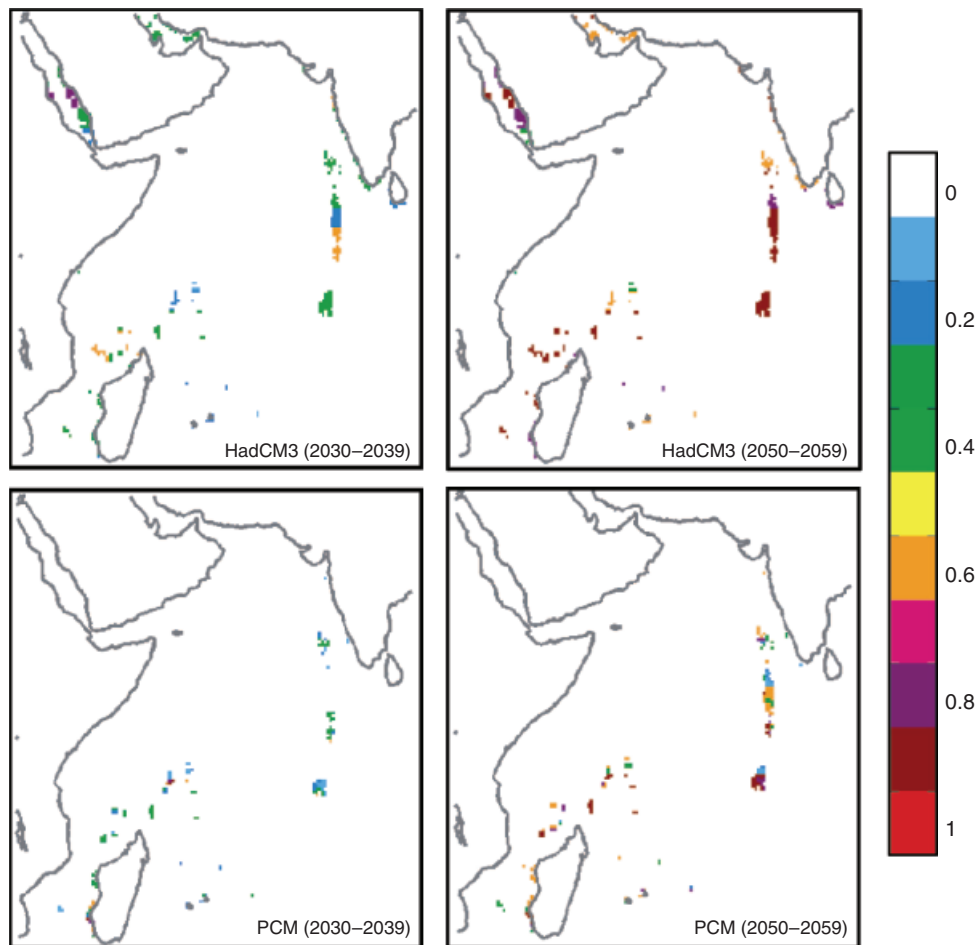
**Fig. 6** Frequency that annual degree heating month >1 during 2030–2039 and 2050–2059 for each 36 km grid cell in the Indian Ocean containing corals reefs, under SRES A2.

In summary, the models suggest the increase in thermal tolerance required to ensure sufficient time for coral reef recovery between bleaching events is at least 0.2–0.3 °C per decade in most reef cells, using either the 2030s or the 2050s as a deadline. The results further suggest that in the latter half of the century the total adaptation may become a greater challenge than the rate of adaptation. For example, HadCM3 projects that 42–65% of the world's coral reefs would need an increase thermal tolerance of over 2 °C by 2080–2089 to avoid bleaching occurring every 5 years (Table 4). As the observed post-bleaching changes in symbioses are akin to acclimation rather than genetic adaptation, the total amount of increased thermal tolerance available through such shifts in symbiont communities may be limited (Hoegh-Guldberg et al., 2002). Coral communities able to adapt over the next 30–50 years may be overwhelmed by a sustained increase in SST during the latter half of the century.

## Discussion

Our global assessment indicates that the frequency of coral bleaching at reefs worldwide could become an annual or biannual event in 30–50 years because of climate change without an increase in the thermal tolerance of corals and their symbionts. The results expand upon some previous assertions about climate change and coral bleaching, based on individual reefs or individual climate models and scenarios (Hoegh-Guldberg, 1999; Sheppard, 2003). The results also demonstrate for the first time the important geographic variation in the thermal stress facing coral reefs under projected future climates. The next generation of GCMs, featuring higher grid resolution in the tropics and higher vertical resolution in the upper ocean, and site-specific hydrodynamic models, capable of describing local upwelling and surface heating (Skirving et al., 2004b), will be crucial in refining projections for
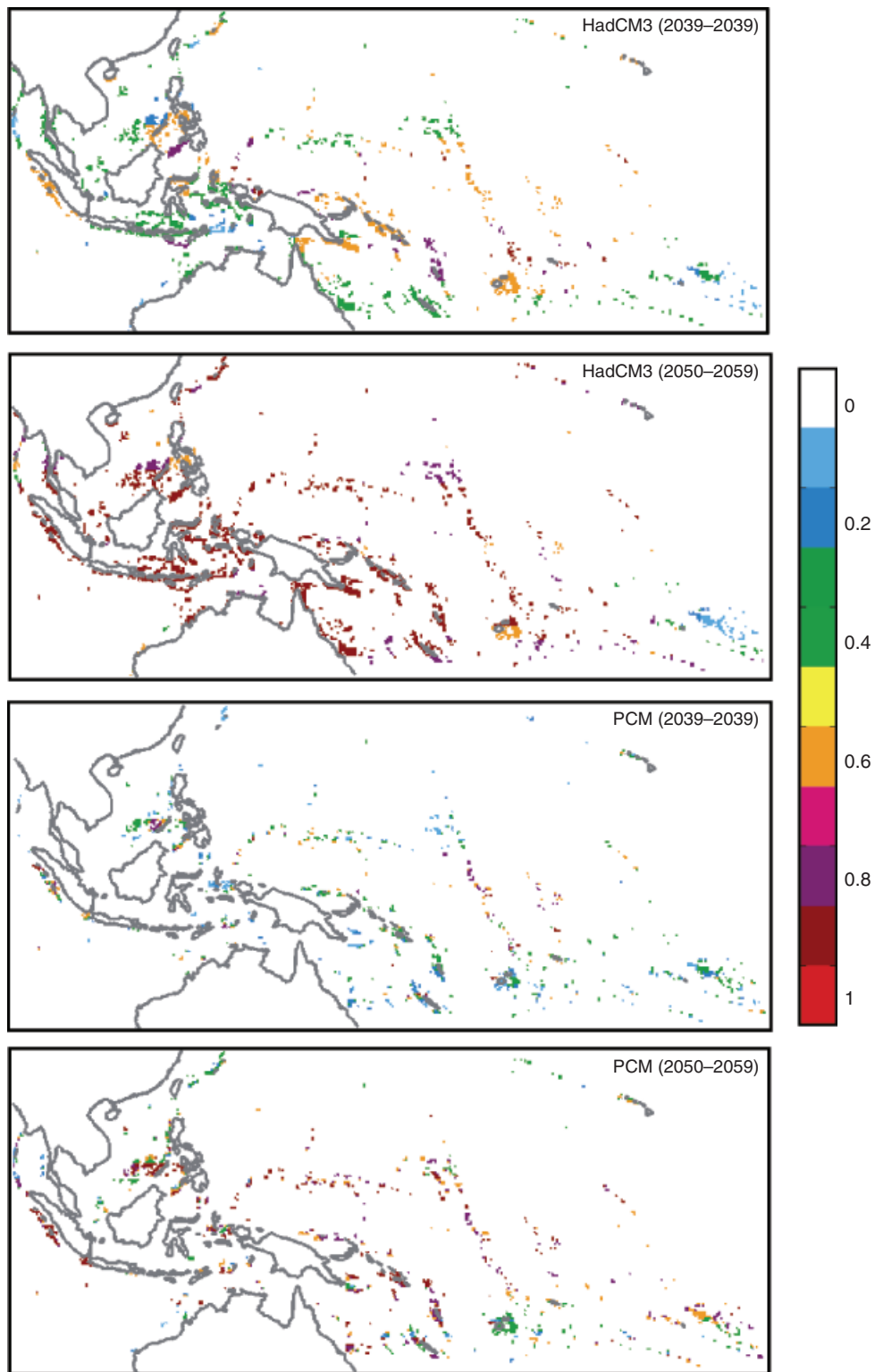
**Fig. 7** Frequency that annual degree heating month >1 during 2030–2039 and 2050–2059 for each 36 km grid cell in the Indo-Pacific (Southeast Asia, Micronesia, Coral Sea/Melanesia, Polynesia, SE Asia) containing corals reefs, under SRES A2.

**Table 1** Percent of coral reef cells experiencing bleaching at least every 2 years

| | DHM > 1 | | DHM > 2 | |
| --- | --- | --- | --- | --- |
| Ocean region | HadCM3 | PCM | HadCM3 | PCM |
| Indian Ocean | 94–95 | 60–71 | 52–60 | 13–27 |
| | 100 | 98–99 | 90–98 | 66–77 |
| SE Asia | 90–94 | 67–77 | 49–54 | 29–35 |
| | 100 | 94–96 | 92–97 | 71–79 |
| Micronesia | 100 | 91–99 | 90–99 | 37–76 |
| | 100 | 100 | 100 | 98–99 |
| GBR/Coral Sea | 95–99 | 60–71 | 60–62 | 24–56 |
| | 99–100 | 96–98 | 85–100 | 83–85 |
| Polynesia | 75–99 | 67–84 | 50–56 | 33–34 |
| | 81 | 95–97 | 69–72 | 73 |
| Caribbean | 94–99 | 48–88 | 76–78 | 1–21 |
| | 100 | 92–95 | 90–100 | 43–65 |
| World | 93–94 | 70–80 | 57–60 | 25–39 |
| | 98 | 95–97 | 87–95 | 72–77 |

The range from the SRES A2a and B2a scenarios for 2030–2039 (top row) and 2050–2059 is displayed.
DHM, degree heating month.

**Table 2** Thermal adaptation required to limit bleaching recurrence to once every 5 or 10 years (by the 2030–2039 or 2050–2059)

| | Coral reefs (%) | | | |
| --- | --- | --- | --- | --- |
| | 2030–2039 | | 2050–2059 | |
| GCM (interval) | + 0.5 °C | + 1 °C | + 0.5 °C | + 1 °C |
| HadCM3 (5 years) | 69–71[a] | 22–33 | 74–82 | 44–68 |
| HadCM3 (10 years) | 79–81 | 27–39 | 84–90 | 51–76 |
| PCM (5 years) | 45–54 | 12–16 | 72–76 | 41–42 |
| PCM (10 years) | 50–63 | 15–19 | 84 | 47–48 |

[a]Percent of reefs requiring more than 0.5 °C increase in thermal tolerance such that bleaching occurs only once every 5 years in the 2030s. The range from the two SRES scenarios is displayed. GCM, general circulation model.

individual reefs and developing focussed conservation strategies. However, the overall projected increase in thermal stress on corals over the next 50 years is so rapid and so widespread, even in the less sensitive PCM, that the globally averaged prognosis is unlikely to change regardless of model refinements.

The flexibility of the symbiosis may help corals increase resistance to thermal stress over time and fuel the recovery of coral cover after bleaching. Higher temperature tolerance among some species of *Symbiodinium* explains why some corals survive mass bleaching events or survive in higher temperature environments (Baker *et al.*, 2004; Little *et al.*, 2004;
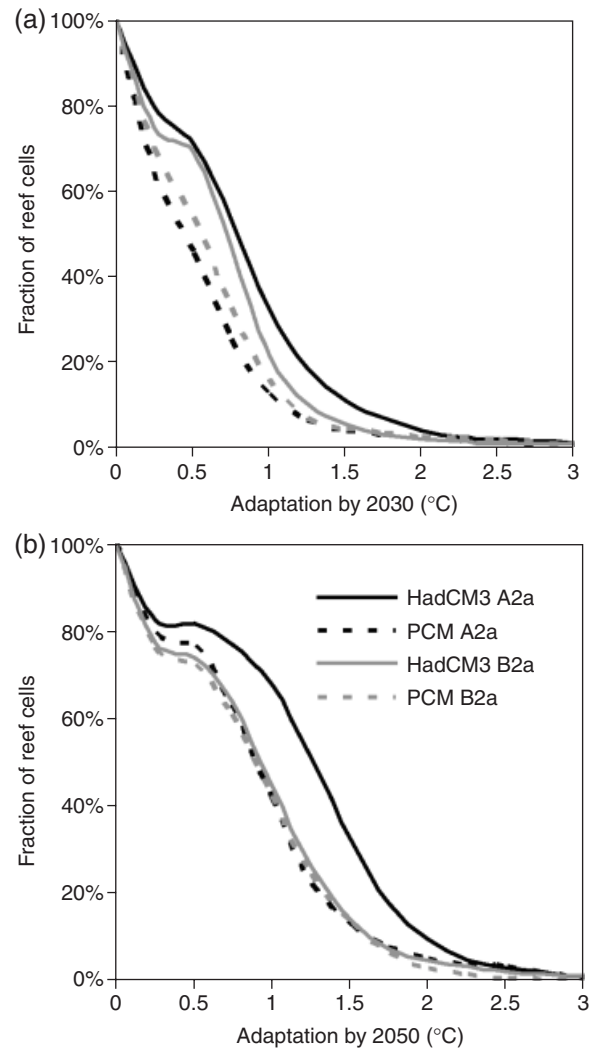


**Fig. 8** Frequency distribution of thermal adaptation to ensure low-intensity bleaching occurs only every 5 years by (a) 2030–2039 and (b) 2050–2059. The fraction of the 36 km coral reefs cells requiring an increase in thermal tolerance (°C) with HadCM3 and PCM under the SRES A2 and B2 scenarios is displayed.

Rowan, 2004). Corals may uptake a diverse assemblage of *Symbiodinium* at a young age and reshuffle the symbiosis over time in response to thermal stress (Little *et al.*, 2004) or may uptake different *Symbiodinium* from the environment in response to stress (Baker, 2003). Observed shifts to more temperature tolerant *Symbiodinium* in some coral communities after bleaching is a possible mechanism for adaptation to climate change (Baker *et al.*, 2004), although unambiguous switching to entirely novel symbioses has yet to be demonstrated (Hoegh-Guldberg *et al.*, 2002; Hoegh-Guldberg, 2005). The ability for coral communities in different regions to increase thermal tolerance at the levels presented in this study is not yet well known.
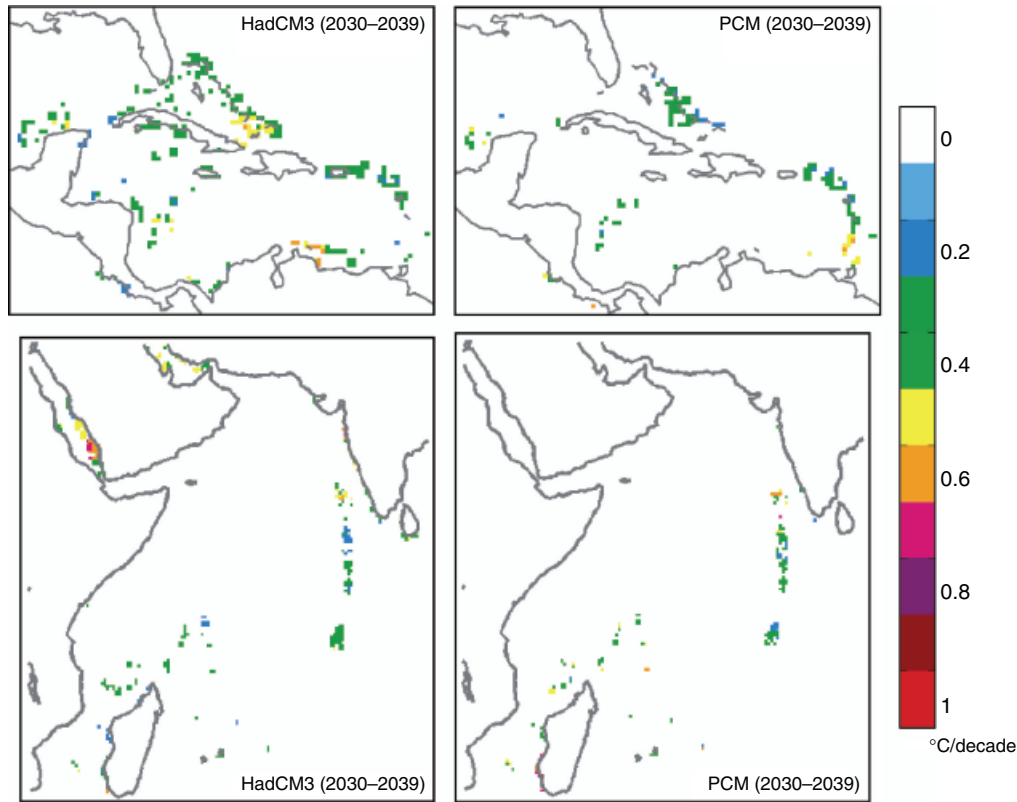
**Fig. 9** The rate of thermal adaptation (°C decade⁻¹) needed to ensure low-intensity bleaching occurs no more than once every 5 years during 2030–2039 in the SRES A2a scenario for the Caribbean and the Indian Ocean.

Adaptation to increased thermal stress would not come without changes in productivity and community structure which could reduce resilience to other stressors. First, there may be a physiological trade-off to having higher temperature tolerance. The more temperature tolerant *Symbiodinium* have lower photosynthetic rates because of higher energetic costs of enhanced photo-protective machinery, which can translate to slower and less vigorous growth (Little *et al.*, 2004). Second, the response to thermal stress and the potential for adaptation differs between coral taxa and growth forms (e.g. Loya *et al.*, 2001; Lajeunesse *et al.*, 2003; McClanahan, 2004). For example, the higher susceptibility of branching taxa, like *acropora*, than massive taxa, like some *porites*, to thermal stress causes shifts in community structure and overall decrease in coral cover after bleaching events (Loya *et al.*, 2001). Finally, the lower growth rates, reduced tissue biomass and community changes after even sublethal bleaching events may reduce resilience of coral reefs to local stresses like overfishing, nutrient loading, sedimentation and disease (Nystrom & Folke, 2001; Hughes *et al.*, 2003). In 1998, when bleaching was reported worldwide, the coral reefs that either had received high nutrient inputs or had low grazing fish populations tended to experience algal overgrowth. (Goreau *et al.*, 2000).

The potential for adaptation to climate change and the consequences for ecosystem health could depend on location. The projected variability in required thermal adaptation rates points to the greater vulnerability of corals in some regions, like Micronesia and western Polynesia. Previous research suggests the capacity for adaptation could also vary because of geographic constraints like the diversity of *Symbiodinium* (LaJeunesse *et al.*, 2003) or the connectivity between reefs (Hughes *et al.*, 2003). For example, because of a twist of geography, the more isolated coral atolls in Micronesia may face a greater threat from climate change than the more connected but heavily disturbed coral reefs in Southeast Asia. It is possible that more physically isolated coral reefs are likely to recover much more slowly from mass coral bleaching events because of lower rates of larval transport and gene flow (Hughes *et al.*, 2003; Ayre & Hughes, 2004).

The uncertainty over whether coral reefs can adapt to global climate change reveals a difficult paradox. The lag time between greenhouse gas emissions and the climate impact means that decisions made in the short term (i.e. the next decade) will commit the planet to a
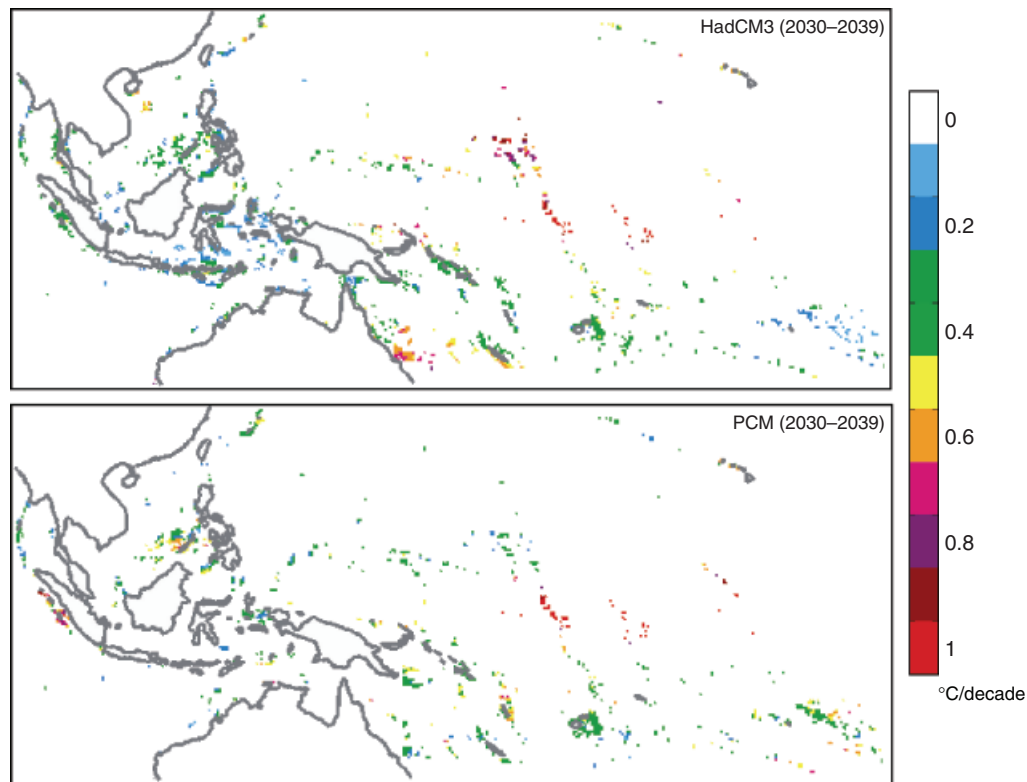
**Fig. 10** The rate of thermal adaptation ($^\circ$C decade$^{-1}$) needed to ensure low-intensity bleaching occurs no more than once every 5 years during 2030–2039 in the SRES A2a scenario for the Indo-Pacific region.

**Table 3** Range in thermal adaptation required to limit bleaching recurrence in the 2030s to once every 5 years (expressed as fraction of reef cells)

| | Coral reefs (%) | | | |
|---|---|---|---|---|
| | HadCM3 | | PCM | |
| Ocean region | + 0.5 $^\circ$C | + 1 $^\circ$C | + 0.5 $^\circ$C | + 1 $^\circ$C |
| Indian Ocean | 83–92[a] | 46–55 | 38–57 | 10–19 |
| SE Asia | 58–62 | 16–17 | 39–40 | 6–9 |
| Micronesia | 58–79 | 13–54 | 58–79 | 6–7 |
| GBR/Coral Sea | 29–67 | 7–40 | 17–53 | 4–6 |
| Polynesia | 69–81 | 24–39 | 58–82 | 19–31 |
| Caribbean | 75–78 | 22–30 | 13–40 | 0–11 |

[a]Percent of cells in the Indian Ocean requiring more than 0.5 $^\circ$C increase in thermal tolerance by the 2030s. The range from the two SRES scenarios is displayed.

**Table 4** Coral reefs requiring at least 2 $^\circ$C increase in thermal tolerance by the 2080 s (for 5-year bleaching interval).

| | Coral reefs (%) | |
|---|---|---|
| Ocean region | HadCM3 | PCM |
| Indian Ocean | 80–85 | 5–20 |
| SE Asia | 36–57 | 3–25 |
| Micronesia | 59–78 | 3–29 |
| GBR/Coral Sea | 48–60 | 2–26 |
| Polynesia | 29–83 | 8–28 |
| Caribbean | 23–55 | 0–8 |
| *World* | *42–65* | *4–24* |

minimum level of warming in the long term (i.e. the next century). The lowest estimate of projected ocean warming (PCM) indicates that corals and their symbionts must increase thermal tolerance by at least 0.5–1 $^\circ$C in the next 50 years to avoid dangerously frequent bleaching events. A moderate estimate of warming (HadCM3), the total adaptation required by most reefs may exceed 2 $^\circ$C in the latter half of the century. Despite recent findings of postbleaching shifts to symbiosis more temperature tolerant *Symbiodinium* by some corals, there is no unequivocal evidence that coral reefs worldwide can adapt to this projected warming. If emissions controls were delayed until there was a consensus on the level of warming to which coral reefs can adapt, presuming such a consensus was even possible, it may become to late to limit future warming

to that level (O'Neill & Oppenheimer, 2002, 2004). To ensure the world's coral reefs are protected from climate change, the margin for error on emission controls may be small.

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