

Limiting global warming to 2 °C is unlikely to save most coral reefs

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Mass coral bleaching events have become a widespread phenomenon causing serious concerns with regard to the survival of corals. Triggered by high ocean temperatures, bleaching events are projected to increase in frequency and intensity. Here, we provide a comprehensive global study of coral bleaching in terms of global mean temperature change, based on an extended set of emissions scenarios and models. We show that preserving >10% of coral reefs worldwide would require limiting warming to below 1.5 °C (atmosphere-ocean general circulation models (AOGCMs) range: 1.3–1.8 °C) relative to pre-industrial levels. Even under optimistic assumptions regarding corals' thermal adaptation, one-third (9–60%, 68% uncertainty range) of the world's coral reefs are projected to be subject to long-term degradation under the most optimistic new IPCC emissions scenario, RCP3-PD. Under RCP4.5 this fraction increases to two-thirds (30–88%, 68% uncertainty range). Possible effects of ocean acidification reducing thermal tolerance are assessed within a sensitivity experiment.

Coral reef ecosystems provide habitat for over a million species and are important for the socio-economic well-being of approximately 500 million people¹. At present, reef-building corals persist only within relatively narrow environmental conditions associated with shallow, sunlit and alkaline waters of tropical coastal areas. The carbonate reef structures that result from their calcium carbonate skeletons commonly build up in regions where temperatures exceed 18 °C in winter and aragonite saturation states are greater than 3.3 Ω_{ara} (ref. 2), although high calcification rates are also found in individual locations with aragonite saturation levels of only about 2.85. However, these values belong to the lowest values observed within coral reef ecosystems³. Local stressors such as overfishing, pollution, disease and declining coastal water quality are thought to be a major driver of the decrease in living coral cover on reefs over the past several decades⁴.

Coral reefs are sensitive to elevated sea temperatures⁵, resulting in coral bleaching, which involves the breakdown of the symbiosis between corals and the dinoflagellate symbionts residing in coral tissue. Mass coral bleaching and mortality events have been observed worldwide since the early 1980s and have affected reefs at regional scales (see, for example, ref. 6). For example, during 1997 and 1998, mass coral bleaching events affected coral reefs in almost every part of the world and caused mortality of approximately 16% of reef-building corals¹. Although corals can re-establish themselves after mass bleaching events, in some cases it takes one to two decades for the ecosystem to return to the pre-bleaching state⁷. An increase in the frequency and severity of mass coral bleaching could overwhelm the ability of coral reefs to recover between events. If this happens, coral reef ecosystems would shift towards systems that are dominated by other organisms such as cyanobacteria and algae.

A common method for predicting mass coral bleaching and mortality is the accumulation of thermal stress, in the form of degree heating weeks (DHW), computed from *in situ* or satellite-derived sea surface temperature (SST) data^{8,9}. Future projections of coral

bleaching using the output of AOGCMs have been made using a similar degree heating months (DHM) metric, which is better suited to the monthly data provided by AOGCMs. The DHM value is the accumulated SSTs above the mean of maximal monthly temperatures (MMM_{max}) from a climatological base period¹⁰. A DHM total of 1 °C × month was used as the best indicator for the lower bleaching threshold ($\text{DHW} > 4 \text{ °C} \times \text{week}$) whereas a DHM value $> 2 \text{ °C} \times \text{month}$ was associated with an upper, or severe, bleaching threshold ($\text{DHW} > 8 \text{ °C} \times \text{week}$; ref. 11).

Study design

We provide a comprehensive global analysis of bleaching under different levels of global warming using the DHM method (Fig. 1). This analysis provides three key advances on previous work. First, we take advantage of the close relationship, quasi-independent of the future scenario, between mean regional and global warming levels computed by AOGCMs (ref. 12) to calculate the fraction of coral reef cells at risk of high thermal stress in terms of the global mean surface air temperature change, rather than the time period in a particular emissions scenario. This allows us to derive an essentially scenario-independent description of coral reef response to different levels of global warming. So far, bleaching indicators at different levels of global warming were also considered in ref. 13 for the Caribbean region and two individual AOGCMs.

Second, we employ more than 32,000 model years derived from seven scenarios (twentieth century, three Special Report on Emissions Scenarios (SRES), the commitment scenario (COMMIT) and two idealized CO₂-only scenarios) and up to five ensemble members per scenario by 19 AOGCMs that provided output to the comprehensive multi-model CMIP3 (Coupled Model Intercomparison Project phase 3) archive (see Supplementary Section S1) to capture the uncertainty in projected regional SST. This allows for a more robust representation of uncertainty than any previous study. A regional study¹⁴ also followed a multi-model

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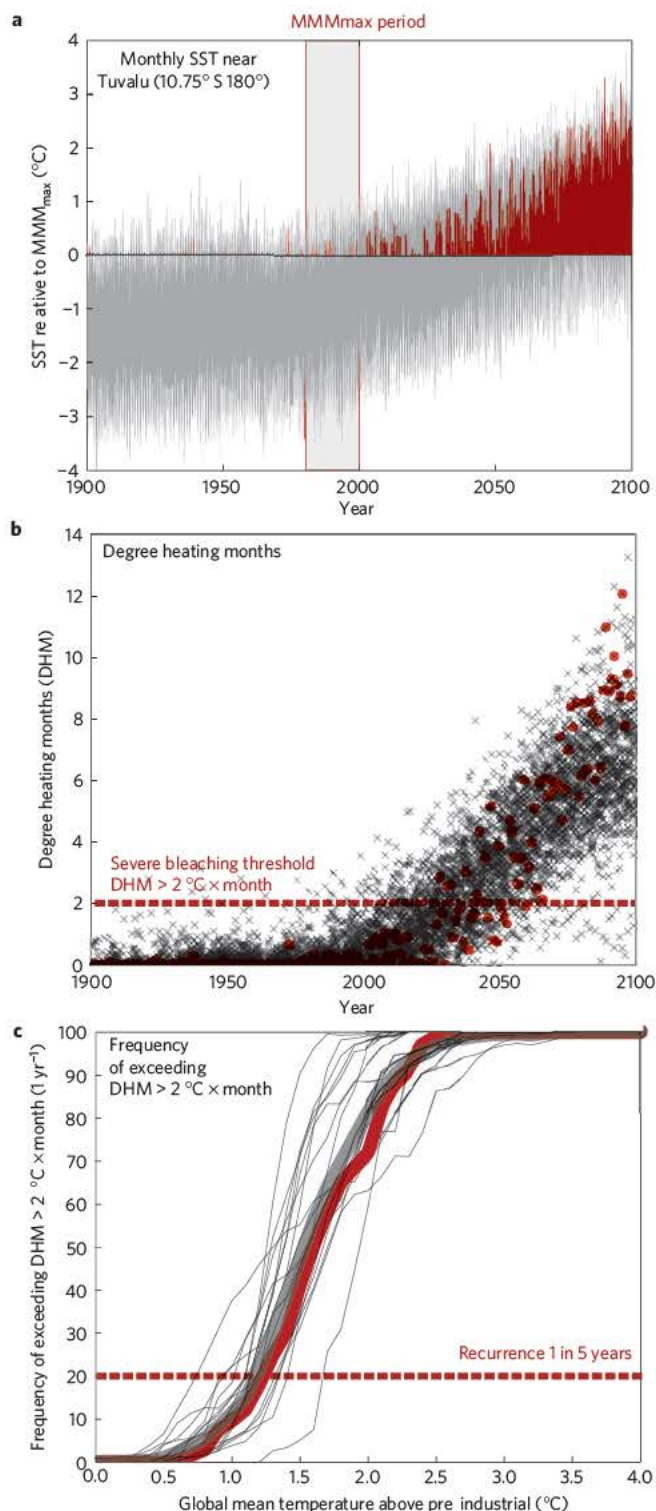


Figure 1 | Heat stress projections at the example location of Tuvalu (10.75°S, 180°). Data from the mpi_echam5 model are shown in red whereas other AOGCM data are plotted in grey. **a**, Downscaled monthly SSTs of 19 AOGCMs (grey lines) normalized relative to their maximum monthly mean (here, MMM_{max}) level over the 1980–1999 period, shown for scenario SRES A1B. **b**, Derived degree heating months for the same location. **c**, The recurrence frequency of exceeding DHM ≥ 2 °C × months in Tuvalu relative to the global mean temperature levels. Diagnostics for 19 individually analysed AOGCMs and the ex-post AOGCM average (thick grey line) are shown; the dashed red line corresponds to recurrence 1 in 5 years.

approach but does not provide the linkage to global mean temperature changes.

Third, we employ time-variable thermal bleaching thresholds to illustrate the effect of thermal adaptation and provide exploration of the possible effect of ocean acidification on thermal sensitivity. In our thermal adaptation setting the threshold for severe bleaching events is assumed to increase linearly from 2 °C × month to DHM levels of 6 °C × months or more in 2100. This is considered to be a theoretical and ambitious level of adaptation given the long generation times of reef-building corals and the consequently slow rate at which evolutionary adaptation occurs. This level of thermal stress has also been extremely rare over the past several decades; it exceeds the maximum reached during the 2005 Caribbean bleaching event¹⁵ and has probably only been reached in the Central Equatorial Pacific during warm El Niño/Southern Oscillation events. Thermal adaptation may in particular include a shift to symbiotic species with a higher thermal tolerance, although evidence of this particular adaptation strategy is slim at best². On the community level, repeated thermal stress may shift the community towards more thermally tolerant coral species. Such a shift to more thermally tolerant coral species might be considered as a kind of reef degradation. However, there is also evidence of intra-specific variation in thermal resistance^{16–18}. Given recent debate about the issue of adaptation (for example, refs. 19–22), we explore a range of possible futures from one with no thermal adaptation over the next century to those that include a highly optimistic level of thermal adaptation. In addition to this specific assumption about adaptation, we also estimate bleaching frequencies for a whole range of different DHM thresholds to estimate the increase of the bleaching threshold necessary to protect a certain fraction of reef cells.

We also conduct a sensitivity analysis assuming that, in combination with the projected warming, ocean acidification may accelerate the degradation of coral reefs during the twenty-first century. Both experimental^{23–25} and field observations^{26–28} indicate that some but not all corals respond to ocean acidification and reduced aragonite saturation through reduced calcification rates. Once the average tropical (30°S–30°N) aragonite concentration decreases below the saturation level ($\Omega_{\text{ara}} < 1$), exposed coral skeletons start to dissolve in sea water. Although corals might be able to sustain positive calcification rates through active elevation of carbonate ion concentration within an extracellular calcifying compartment, they are still expected to be subject to severe degradation independent of temperature²⁹. Therefore, in our sensitivity experiment we assume that the present temperature-driven degradation of coral reefs will gradually turn into an acidification-driven degradation.

Consideration of thermal stress in combination with other changes such as ocean acidification is important if we are to gain a full understanding of how future ocean conditions will affect coral reef ecosystems and indeed other ecosystems. The potential effect of thermal adaptation on projected bleaching frequencies has been included in other analyses^{10,14}. In contrast, the potentially opposite effect of ocean acidification on increasing bleaching thresholds has not been considered so far in future projections.

We test different ways in which this possible transition may happen. As the means of the transition is not yet clear we make different assumptions. First we assume that the bleaching threshold linearly decreases from 2 °C × months to 0 °C × months when reaching undersaturation. This approach is based on ref. 30, in which it was proposed that CO₂ may act to create a greater sensitivity of corals to thermal stress. A similar effect was also shown for water pollution³¹. In addition, we consider transitions of the bleaching threshold from 2 °C × to 0 °C × months at other levels of aragonite saturation including a stepwise decrease as a transition not mediated by increasing temperature sensitivities, a delayed decrease starting at lower levels of tropical mean aragonite saturation, and steeper declines because at some point above $\Omega_{\text{ara}} = 1$, coral reef structures

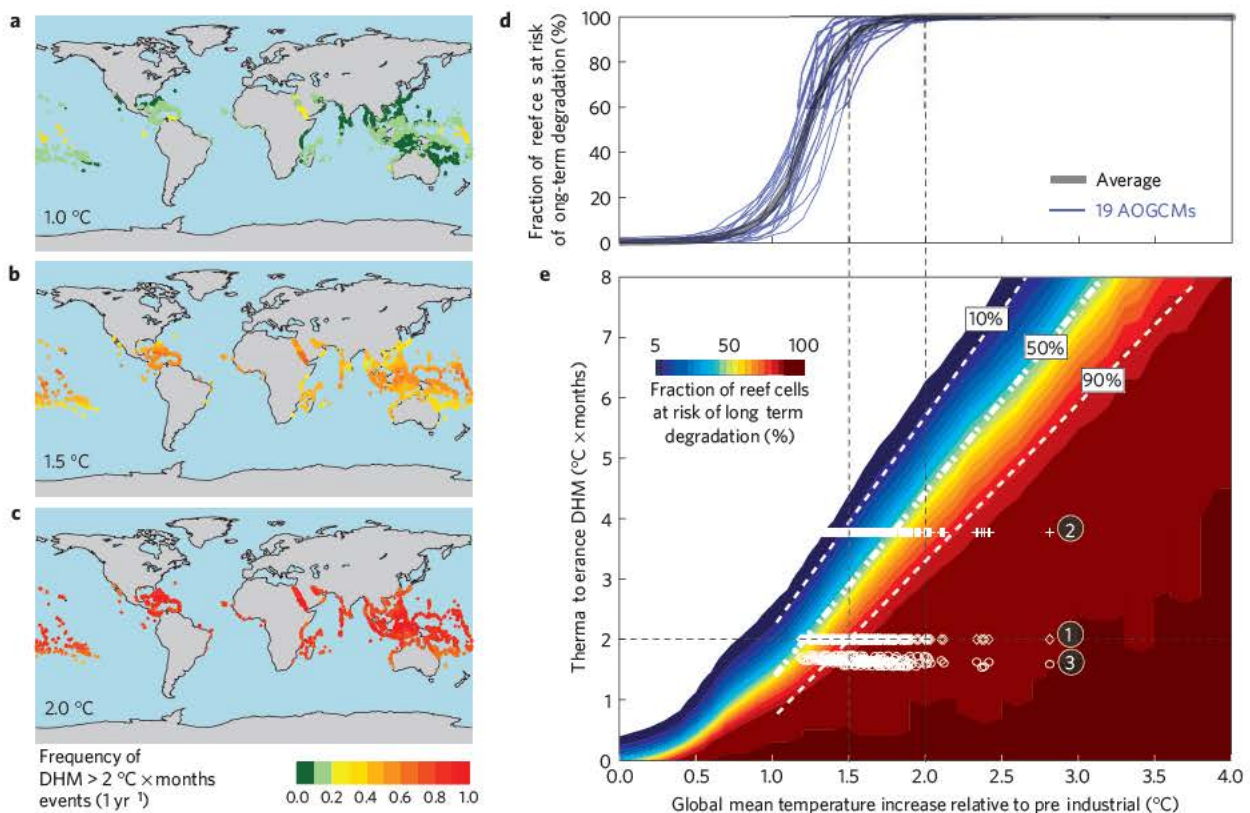


Figure 2 | Thermal stress at different levels of global warming. **a–c**, Frequency of DHM > 2°C x month events with 1.0°C (**a**), 1.5°C (**b**) and 2.0°C (**c**) of global mean warming. Colour scale indicates the average of the 19 AOGCM-specific frequencies calculated at each coral reef grid point. Green points represent frequencies below 0.2 yr⁻¹ and yellow to red points represent frequencies above that critical limit for long-term degradation. **d**, Corals at risk of long-term degradation for constant thermal threshold DHM = 2°C x month and individual AOGCMs. The average across 19 AOGCMs (thin blue lines) is shown as a thick grey line. **e**, Fraction of the world's coral reef cells (coloured areas) at risk of long-term damage due to frequent (>1 in 5 years) coral bleaching events, depending on global mean temperature (x axis) and assumed thermal threshold (y axis). A constant DHM = 2°C x month thermal threshold is indicated by the horizontal dashed line. Two hundred random ensemble members for the 2050 climate state conditions under RCP3-PD with constant thermal threshold (white diamonds, black circled 1), thermal adaptation (white plus symbols, black circled 2), and aragonite-dependent thresholds (white circles, black circled 3) are shown.

will probably not be able to counterbalance biological and physical erosion, which is necessary for the maintenance of the all-important carbonate structures of coral reefs²⁷.

The results of these additional experiments are reported in Supplementary Section S4. They show that delayed onsets of the considered effect of acidification (or possibly other agents reducing thermal sensitivity of corals) may not appear in the results because of the high number of reef cells that are already projected to be at risk of long-term degradation assuming present bleaching thresholds of 2°C x months.

It is important to note that the estimation of long-term degradation uniformly starts on the present bleaching threshold of 2°C x months independent of spatial variations of the aragonite saturation. Changes in bleaching thresholds are expressed in terms of the tropical average (30°S–30°N) aragonite saturation, thus implicitly assuming that corals are adapted to spatial deviations from this average.

Reef recovery from mass coral bleaching and mortality events varies widely but is usually very limited within the first five years^{7,32}. Therefore, we assume that 0.2 yr⁻¹ is the maximum tolerable frequency¹⁰ of recurrent severe thermal stress events (which is otherwise considered to be highly conservative in light of the fact that most recovery takes 10–30 years⁷). If the frequency surpasses 0.2 yr⁻¹, lasting damage are assumed to occur, henceforth referred to as long-term degradation. We calculate AOGCM-specific fractions of years with DHM values > 2°C x months within

different global mean temperature bins over all available scenario runs and for each individual coral reef grid cell (see Fig. 1 and Supplementary Section S2). Alternatively, long-term degradation might be assumed as soon as the temporal distance between two DHM > 2°C x months events for a single reef cell is less than 5 years. Both approaches provide similar results, as shown in Supplementary Fig. S3.

Frequency of bleaching at different global warming levels

The left panels of Fig. 2 show the frequency of exceeding DHM = 2°C x month for individual grid cells and in three different global mean temperature bins averaged over all AOGCMs. The frequency of exceeding the bleaching threshold tends to be higher at lower latitudes. This might explain some of the heterogeneity of coral losses found previously²⁰. At 1.5°C global warming, the average projected bleaching frequency is higher than 0.2 yr⁻¹ at all reef cells.

The fraction of reef cells, separated by AOGCM, that experience thermal stress at a frequency that might lead to long-term degradation shows an almost stepwise behaviour with increasing global mean temperatures (see Fig. 2d). The thick grey line represents the AOGCM average over the individual fractions. This ex-post average can be opposed to an ex-ante average where all AOGCM simulations are treated as if they were ensemble members of a single AOGCM and the fraction of affected reef cells was based on that ensemble. Arguments for the ex-post averaging are given in Supplementary Section S5.

Table 1 | The fraction of reef cells at risk of long-term degradation for global mean warming relative to pre-industrial levels (top rows).

Threshold	Global mean surface temperatures relative to pre-industrial (°C)				
	1.0 °C	1.25 °C	1.5 °C	1.75 °C	2.0 °C
DHM = 1	88% (74–98%)	99% (91–100%)	100% (100–100%)	100% (100–100%)	100% (100–100%)
DHM = 2	16% (3–29%)	55% (17–84%)	89% (63–100%)	98% (89–100%)	100% (98–100%)
DHM = 3	3% (0–7%)	11% (0–27%)	43% (7–88%)	79% (54–97%)	94% (74–100%)
	Fraction at risk (percentage of coral reef cells)				
	10%	30%	50%	70%	90%
DHM = 1	0.6 °C (0.4–0.7 °C)	0.7 °C (0.6–0.8 °C)	0.8 °C (0.7–0.9 °C)	0.9 °C (0.8–1.0 °C)	1.0 °C (0.9–1.2 °C)
DHM = 2	0.9 °C (0.7–1.2 °C)	1.1 °C (1.0–1.3 °C)	1.2 °C (1.1–1.4 °C)	1.3 °C (1.2–1.5 °C)	1.5 °C (1.3–1.8 °C)
DHM = 3	1.3 °C (1.1–1.5 °C)	1.4 °C (1.3–1.6 °C)	1.5 °C (1.4–1.7 °C)	1.7 °C (1.4–1.9 °C)	1.9 °C (1.5–2.3 °C)

Shown is the average, as well as the full range across diagnosed AOGCMs for three different thermal thresholds, with DHM = 2 being the default in this study. Corresponding global mean temperatures are provided for specific levels of reef cell degradation (bottom rows).

The results indicate that there would be long-term degradation of coral reef ecosystems in all present coral reef cells without a change in thermal tolerance ($\text{DHM} > 2^\circ\text{C} \times \text{months}$) at 2°C global mean temperature rise, an upper limit agreed to in international climate policy negotiations³³ (Fig. 2d). This result is robust across different AOGCMs, with the lowest value being that 98% of coral reefs are subject to long-term degradation (Table 1). Even at 1.5°C global mean warming, an alternative international temperature goal to be reviewed for international policy 2015 (ref. 33), our results suggest that around 89% (63–100%) of coral reef ecosystems would face long-term degradation assuming no change in thermal tolerance (Fig. 2d). At the present rate of warming ($\sim 0.2^\circ\text{C}/\text{decade}$), a 1°C warming above pre-industrial levels is going to be surpassed in the coming one or two decades, which might already put 16% (3–29%) of reef locations at risk.

We find a quasilinear relationship between the required thermal tolerance (DHM) and global mean temperature change (ΔT) for any given fraction of reef cells (x) at risk of degradation (see Fig. 2e). Thus, the required bleaching threshold is given by $\text{DHM}(\Delta T, x) = y_{0,x} + m_x \Delta T$ with the coefficients $y_{0,x}$ and m_x provided in Table 2. These coefficients were derived for our ex-post average results across 19 AOGCMs for global warming levels in excess of 1°C relative to pre-industrial levels. Above 1°C of global warming, a thermal adaptation of 3.5, 3.1 and 2.6 DHM per degree of global warming would be necessary to offset the increased thermal stress such that no more than 10%, 50% or 90% of coral reef locations face the risk of long-term degradation, respectively.

The results broadly agree with those of a previous study¹⁰ on the basis of a comparison of projections for single SRES scenarios (Supplementary Fig. S6) and ref. 34. We specifically test whether the inclusion of spatially coarser AOGCMs (coarser than 1.5° longitudinal ocean resolution) might have biased the results of this study (Supplementary Table S1). The global mean temperature that corresponds to 50% of coral reefs being at risk of disappearance given a $\text{DHM} > 2^\circ\text{C} \times \text{months}$ thermal tolerance is 1.23°C relative to pre-industrial levels on average across all 19 diagnosed AOGCMs. For the 9 lower- or 10 higher-resolution models, this average does not change noticeably, that is, 1.22°C and 1.24°C , respectively, indicating no evidence for such a bias.

Frequency of bleaching under different RCP scenarios

To put the different levels of global warming into perspective and to explore possible effects of thermal adaptation and ocean acidification on bleaching thresholds, we project global mean warming levels and CO_2 concentrations probabilistically for the harmonized emissions of the Representative Concentration Pathways (RCPs)

Table 2 | Regression results for the necessary thermal tolerance of corals (DHM) depending on the global mean warming (ΔT) relative to pre-industrial levels and the fraction of reef cells that will be at risk of long-term degradation (x).

Fraction of reef cells at risk of disappearance, x (%)	Intercept, $y_{0,x}$ (DHM)	Increase of thermal tolerance per degree of warming/slope, m_x (DHM/°C)
10	−1.3207	3.5052
50	−1.7194	3.0711
90	−1.9216	2.6074

developed for the Fifth Assessment of the Intergovernmental Panel on Climate Change (IPCC; see Supplementary Section S8). A Markov chain Monte Carlo method was used to constrain parameters of our reduced complexity climate model with historical observations, and we emulated nine carbon cycle models that were part of the C⁴MIP intercomparison to capture uncertainties related to the carbon cycle³⁵.

Figure 2e shows samples of the 2050 projections for the strong mitigation RCP3-PD scenario in the global mean temperature–bleaching threshold plane. In our standard case (white diamonds), we assume that the thermal tolerance of corals will not change over the coming decades to any real extent. For the lowest emission scenario, RCP3-PD, the projected global mean temperature increase by 2050 ranges from 1.0 to 1.5°C relative to the 1980–1999 period, or 1.5 – 2.0°C relative to the pre-industrial period. Half of the individual realizations of our historically constrained global mean temperature projections for RCP3-PD for the year 2050 find long-term damage to $>95\%$ of coral reefs, assuming no change in thermal tolerance (Supplementary Section S7). The projected degradation is widespread despite the fact that RCP3-PD presents the strongest mitigation scenario investigated at present for the IPCC AR5. For higher RCP scenarios, without a change in thermal tolerance, it is only a question of the time before most of the world's coral reefs face long-term degradation: by the end of this century, 100% of reef cells experience thermal stress ($\text{DHM} > 2^\circ\text{C} \times \text{months}$) at sufficiently high frequency ($>0.2\text{ yr}^{-1}$)—even under the lowest projected temperature increase (Supplementary Fig. S4 and Table S2)—to suggest long-term degradation from frequent coral bleaching events. In the thermal adaptation case,

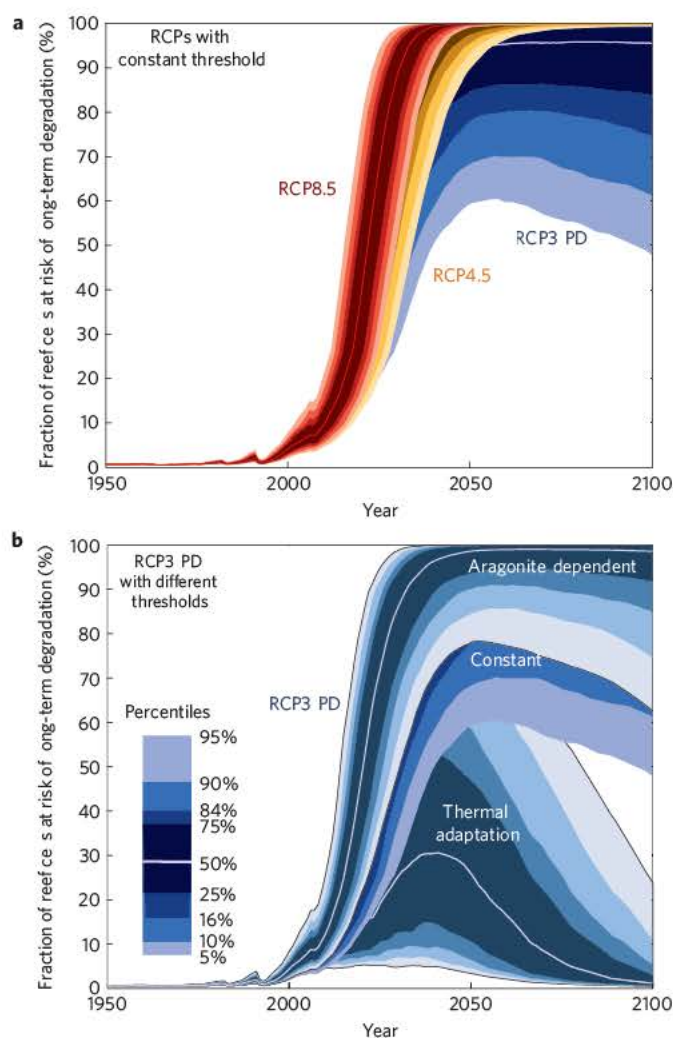


Figure 3 | Projected probabilistic fraction of the world's coral reefs subject to long-term degradation under the RCPs. a, Default projection, assuming a constant thermal threshold $\text{DHM} = 2^\circ\text{C} \times \text{months}$ and a five-year return period as leading to the demise of coral reefs. The colour steps mark the percentiles that are indicated at the colour bar in **b**. **b**, Under the scenario RCP3-PD, thermal adaptation (lower grey shaded areas), and aragonite-dependency (upper saturated blue shaded areas), decreases and increases the projected fraction of coral reef subject to long-term damage when compared with the default constant thermal threshold, respectively (see Table 1). See expanded Supplementary Fig. S5.

the bleaching threshold reaches $4^\circ\text{C} \times \text{months}$ by 2050 (white crosses). The fraction of coral reef cells that might be subject to long-term degradation can also be projected for other years and RCP scenarios (see Fig. 3).

The thermal adaptation scenario results reveal that two-thirds of the world's coral reefs would avoid long-term degradation under RCP3-PD (Fig. 3b and Supplementary Table S2). Declining temperatures would make 99% (95% to 99%, 68% uncertainty range) of the coral reef cells suitable for the survival of corals again by the end of the twenty-first century. The thermal adaptation scenario is likely to be optimistic given the combination of other stressors on coral reefs and the present downward trajectory of coral cover (for example, ref. 4). There is little experimental or observational evidence for the rapid evolution of thermal tolerance in reef-building corals, which tend to have long generation times (5–100 years) although corals might profit from generation times of the symbionts that are orders of magnitude shorter. The last

mechanism is problematic, however, as the thermal tolerance of reef-building corals is not solely determined by the symbiont and requires host evolution as well. Previous palaeontological studies highlighting the resilience of corals even under high CO_2 concentrations and warming tend to explore conditions at long-term equilibrium, over timescales of thousands of years, not decadal or centennial timescales^{19,20}, with more pronounced ocean acidification in the latter owing to the lag time in geological processes such as weathering. In addition, thermal adaptation capacities are likely to differ strongly between coral species, coral growth forms and habitats. The aggregate thermal tolerance for coral communities may increase as total coral cover and diversity declines, because selective coral mortality during bleaching events may lead to survival of only bleaching-resistant or resilient growth forms and species, or of corals in specific thermal refuges. The narrowing of coral gene pools as a result of these processes is likely to decrease the resilience of corals to other impacts such as disease and competition from other benthic species.

In cases of both constant or aragonite-dependent thermal thresholds, the period that corals would have to bridge in unfavourable environments will be on the timescale of centuries, certainly beyond 2100 (see Fig. 3). New stable ecosystems, dominated by macro-algae or other biota, could further hinder any recovery³⁶. We did not investigate the multiple synergistic effects of changing environmental conditions on coral reef systems, such as pollution, fishing pressure or other climate-related variables such as cloudiness and coastal runoff.

Conclusion

Despite the inclusion of optimistic scenarios concerning rates of evolutionary adaptation, our results confirm that coral reef ecosystems face considerable challenges under even an ambitious mitigation scenario that constrains global warming to 1.5°C above pre-industrial temperatures. Our projections suggest that most coral reefs will experience extensive degradation over the next few decades given the present behaviour of corals to thermal stress^{10,37}. To protect at least 50% of the coral reef cells, global mean temperature change would have to be limited to 1.2°C (1.1 – 1.4°C), especially given the lack of evidence that corals can evolve significantly on decadal timescales and under continually escalating thermal stress. There is little doubt from our analysis that coral reefs will no longer be prominent within coastal ecosystems if global average temperatures exceed 2°C above the pre-industrial period. Effective conservation of coral reefs in the face of changing climate and ocean chemistry is likely to depend on our understanding how these other variables affect coral reef resilience. There is little precedent for the rate and magnitude of warming in the recent geological history of corals, including the transition into the warm Eemian period³⁸. Further *in situ* observations and laboratory studies will help refine our understanding about the aggregated likely effects of acidification and warming for individual coral reef ecosystems. Despite these uncertainties, the window of opportunity to save large fractions of coral reefs seems small and rapidly closing.

Methods

Calculation of DHM. As is the case for the DHW used for real-time prediction of coral bleaching events^{8,9}, the DHM sums the excess warming above the MMM_{max} of the climatological 1980–1999 base period in a rolling 4-month window¹⁰ (see Supplementary Section S2). To quantify the global extent of bleaching events we use a $0.5^\circ \times 0.5^\circ$ map indicating 2160 geospatial locations of coral reefs worldwide from Reefbase (see www.reefbase.org) as adapted by ref. 10. DHM at each of these grid points were calculated after employing a simple linear downscaling of SST data to obtain temperature projections at the coral reef cells' locations. The downscaling/interpolation is based on the four closest AOGCM grid points to every coral reef cell, taking into account the AOGCM-specific land–sea masks and resolutions (see Supplementary Section S1). The difference from an approach that merges satellite and AOGCM data at individual locations was found to be minor for the SRES scenarios (see Supplementary Fig. S5).

The employed bleaching thresholds of $1^{\circ}\text{C} \times \text{month}$ (mild bleaching event comparable to $\text{DHW} > 4^{\circ}\text{C} \times \text{week}$) and $2^{\circ}\text{C} \times \text{month}$ (severe bleaching event comparable to $\text{DHW} > 8^{\circ}\text{C} \times \text{week}$) were derived from observed bleaching events on the community level¹¹. They do not distinguish between species that might show distinct thresholds²⁰.

Calculation of aragonite-dependent thermal thresholds. This translation of CO_2 concentrations to surface aragonite saturation is enabled by the fact that tropical surface aragonite saturation levels are, on a timescale of years to decades, in equilibrium with atmospheric CO_2 concentrations. Thus, we were able to closely emulate zonal ocean chemistry simulations³⁹ using a linear rational function (Supplementary Fig. S1). In our Monte Carlo approach, we draw doublets from the joint distribution of global mean temperature and CO_2 concentrations of our probabilistic RCP projections, translate the CO_2 concentrations to aragonite levels and apply the simplified aragonite-dependent thermal threshold.

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References

1. Wilkinson, C. *Status of Coral Reefs of The World: 2004* (Global Coral Reef Monitoring Network, 2004).
2. Hoegh-Guldberg, O. *et al.* Coral reefs under rapid climate change and ocean acidification. *Science* **318**, 1737–1742 (2007).
3. Shamberger, K. E. F. *et al.* Calcification and organic production on a Hawaiian coral reef. *Mar. Chem.* **127**, 64–75 (2011).
4. Bruno, J. F. & Selig, E. R. Regional decline of coral cover in the Indo-Pacific: Timing, extent, and subregional comparisons. *PLoS ONE* **2**, e711 (2007).
5. Hoegh-Guldberg, O. & Smith, G. J. The effect of sudden changes in temperature, light and salinity on the population–density and export of zooxanthellae from the reef corals *Stylophora pistillata* Esper and *Seriatopora hystrix* Dana. *J. Exp. Mar. Biol. Ecol.* **129**, 279–303 (1989).
6. Eakin, C. M. *et al.* Caribbean corals in crisis: Record thermal stress, bleaching, and mortality in 2005. *PLoS ONE* **5**, e13969 (2010).
7. Baker, A., Glynn, P. W. & Riegl, B. Climate change and coral reef bleaching: An ecological assessment of long-term impacts, recovery trends and future outlook. *Estuar. Coast. Shelf Sci.* **80**, 435–471 (2008).
8. Liu, G., Skirving, W. J. & Strong, A. E. Remote sensing of sea surface temperatures during 2002 barrier reef coral bleaching. *Eos Trans.* **84**, 137–144 (2003).
9. Liu, G., Strong, A. E., Skirving, W. J. & Arzayus, L. F. *10th Int. Coral Reef Symp.* 1783–1793 (International Coral Reef Symposium (ICRS) Proceedings, 2004).
10. Donner, S. D. Coping with commitment: Projected thermal stress on coral reefs under different future scenarios. *Plos ONE* **4**, e5712 (2009).
11. Donner, S. D., Skirving, W. J., Little, C. M., Oppenheimer, M. & Hoegh-Guldberg, O. Global assessment of coral bleaching and required rates of adaptation under climate change. *Glob. Change Biol.* **11**, 2251–2265 (2005).
12. Mitchell, J., Johns, T., Eagles, M., Ingram, W. & Davis, R. Towards the construction of climate change scenarios. *Climatic Change* **41**, 547–581 (1999).
13. Simpson, M. C. *et al.* *An Overview of Modelling Climate Change Impacts in the Caribbean Region with Contribution from the Pacific Islands* (United Nations Development Programme, 2009).
14. Hoeke, R. K., Jokiel, P. L., Buddemeier, R. W. & Brainard, R. E. Projected changes to growth and mortality of Hawaiian corals over the next 100 years. *PLoS ONE* **6**, e18038 (2011).
15. Donner, S. D., Knutson, T. R. & Oppenheimer, M. Model-based assessment of the role of human-induced climate change in the 2005 Caribbean coral bleaching event. *Proc. Natl Acad. Sci. USA* **104**, 5483 (2007).
16. Barshis, D. J. *et al.* Protein expression and genetic structure of the coral *Porites lobata* in an environmentally extreme Samoan back reef: Does host genotype limit phenotypic plasticity? *Mol. Ecol.* **19**, 1705–1720 (2010).
17. McClanahan, T. R. *et al.* in *Ecological Studies* Vol. 205 (ed. Caldwell, M. M.) 121–138 (Springer, 2009).
18. Yee, S. H., Santavy, D. L. & Barron, M. G. Comparing environmental influences on coral bleaching across and within species using clustered binomial regression. *Ecol. Model.* **218**, 162–174 (2008).
19. Hoegh-Guldberg, O., Ortiz, J. C. & Dove, S. The future of coral reefs. *Science* **334**, 1494–1495 (2011).
20. Pandolfi, J. M., Connolly, S. R., Marshall, D. J. & Cohen, A. L. Projecting coral reef futures under global warming and ocean acidification. *Science* **333**, 418–422 (2011).
21. Pandolfi, J. M., Connolly, S. R., Marshall, D. J. & Cohen, A. L. Response to ‘the future of coral reefs’. *Science* **334** (2011).
22. Weis, V. M. The susceptibility and resilience of corals to thermal stress: Adaptation, acclimatization or both? *Mol. Ecol.* **19**, 1515–1517 (2010).
23. Kleypas, J. A. & Langdon, C. *et al.* in *Coral Reefs and Climate Change: Science and Management* Vol. 61 (ed. Phinney, J. T.) 73–110 (AGU Monograph Series, Coastal and Estuarine Studies, Geophys. Union, 2006).
24. Langdon, C. & Atkinson, M. J. Effect of elevated pCO_2 on photosynthesis and calcification of corals and interactions with seasonal change in temperature/irradiance and nutrient enrichment. *J. Geophys. Res.* **110**, C09S07 (2005).
25. Schneider, K. & Erez, J. The effect of carbonate chemistry on calcification and photosynthesis in the hermatypic coral *Acropora eurytoma*. *Limnol. Oceanogr.* **51**, 1284–1293 (2006).
26. Ohde, S. & van Woesik, R. Carbon dioxide flux and metabolic processes of coral reefs, Okinawa. *Bull. Mar. Sci.* **65**, 559–576 (1999).
27. Silverman, J., Lazar, B., Cao, L., Caldeira, K. & Erez, J. Coral reefs may start dissolving when atmospheric CO_2 doubles. *Geophys. Res. Lett.* **36**, L05606 (2009).
28. Silverman, J., Lazar, B. & Erez, J. Effect of aragonite saturation, temperature, and nutrients on the community calcification rate of a coral reef. *J. Geophys. Res.* **112**, C05004 (2007).
29. Cohen, A. L., McCorkle, D. C., de Putron, S. J., Gaetani, G. A. & Rose, K. A. Morphological and compositional changes in the skeletons of new coral recruits reared in acidified seawater: Insights into the biomineralization response to ocean acidification. *Geochem. Geophys. Geosyst.* **10** (2009).
30. Anthony, K. R. N., Kline, D. I., Diaz-Pulido, G., Dove, S. & Hoegh-Guldberg, O. Ocean acidification causes bleaching and productivity loss in coral reef builders. *Proc. Natl Acad. Sci. USA* **105**, 17442–17446 (2008).
31. Wooldridge, S. A. A new conceptual model for the warm-water breakdown of the coral–algae endosymbiosis. *Mar. Freshwat. Res.* **60**, 483–496 (2009).
32. Hoegh-Guldberg, O. & Jones, R. J. Photoinhibition and photoprotection in symbiotic dinoflagellates from reef-building corals. *Mar. Ecol. Prog. Ser.* **183**, 73–86 (1999).
33. UNFCCC *The Cancun Agreements: Outcome of the Work of the Ad Hoc Working Group on Long-term Cooperative Action Under the Convention FCCC/CP/2010/7/Add.1.* (UNFCCC, 2010); available via <http://go.nature.com/vKU9wU>.
34. Buddemeier, R. W., Lane, D. R. & Martinich, J. A. Modeling regional coral reef responses to global warming and changes in ocean chemistry: Caribbean case study. *Climatic Change* **109**, 375–397 (2011).
35. Meinshausen, M. *et al.* Greenhouse-gas emission targets for limiting global warming to 2°C . *Nature* **458**, 1158 (2009).
36. Mumby, P. J., Hastings, A. & Edwards, H. J. Thresholds and the resilience of Caribbean coral reefs. *Nature* **450** (2007).
37. Hoegh-Guldberg, O. Climate change, coral bleaching and the future of the world’s coral reefs. *Mar. Freshwat. Res.* **50**, 839–866 (1999).
38. Jansen, E. & Overpeck, J. in *IPCC Climate Change 2007: The Physical Science Basis* (eds Solomon, S. *et al.*) 433–498 (Cambridge Univ. Press, 2007).
39. Caldeira, K. & Wickett, M. E. Ocean model predictions of chemistry changes from carbon dioxide emissions to the atmosphere and ocean. *J. Geophys. Res.* **110**, C09S04 (2005).

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Author contributions

A.G., K.F. and M. Meinshausen contributed equally to this paper. K.F. and M. Meinshausen designed the study. A.G., K.L. and M. Mengel analysed data with contributions by K.F. and M. Meinshausen. M. Meinshausen, K.F., S.D. and O.H.-G. wrote the paper.

Additional information

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Competing financial interests

The authors declare no competing financial interests.