

Temporary refugia for coral reefs in a warming world

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Climate-change impacts on coral reefs are expected to include temperature-induced spatially extensive bleaching events¹. Bleaching causes mortality when temperature stress persists but exposure to bleaching conditions is not expected to be spatially uniform at the regional or global scale². Here we show the first maps of global projections of bleaching conditions based on ensembles of IPCC AR5 (ref. 3) models forced with the new Representative Concentration Pathways⁴ (RCPs). For the three RCPs with larger CO₂ emissions (RCP 4.5, 6.0 and 8.5) the onset of annual bleaching conditions is associated with ~510 ppm CO₂ equivalent; the median year of all locations is 2040 for the fossil-fuel aggressive RCP 8.5. Spatial patterns in the onset of annual bleaching conditions are similar for each of the RCPs. For RCP 8.5, 26% of reef cells are projected to experience annual bleaching conditions more than 5 years later than the median. Some of these temporary refugia include the western Indian Ocean, Thailand, the southern Great Barrier Reef and central French Polynesia. A reduction in the growth of greenhouse-gas emissions corresponding to the difference between RCP 8.5 and 6.0 delays annual bleaching in ~23% of reef cells more than two decades, which might conceivably increase the potential for these reefs to cope with these changes.

In classic vulnerability models exposure and sensitivity determine potential impact, which in combination with adaptive capacity determines vulnerability⁵. From a planning perspective, knowledge of vulnerability can be informative in all fields, helping to prioritize investments and reduce risk⁶. Environmental management and conservation is no exception and practitioners are assessing the relative vulnerability of species, habitats and dependent industry to the high disturbance frequencies expected as the climate changes⁷.

Coral reefs are widely documented as being among the most sensitive of ecosystems to climate change¹. The sensitivity of coral communities on reefs certainly varies in space and time but detailed information on sensitivity is available only for the very small percentage of reefs where extensive research and long-term monitoring surveys have been conducted (for example, <8% of the Great Barrier Reef in Australia⁸). Robust information on adaptive capacity for corals has not been established yet. Adaptive capacity will vary among communities (with different compositions) and as in many systems is strongly dependent on exposure to stress^{9,10}. The only global analyses for reefs in the area of adaptation combine predicted adaptation rates with projections of exposure to various seawater warming rates^{11,12}. Information on spatial and temporal variability in exposure is hence among the most useful information managers and conservationists of coral reefs and other systems can gain access to.

Here, we project exposure to conditions conducive to coral bleaching for all reef locations using coupled ocean–atmosphere

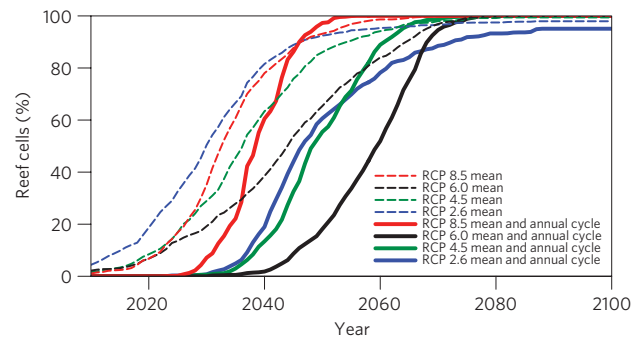


Figure 1 | Percentage of reef cells projected to experience bleaching per year. Projected years reef cells experience bleaching conditions annually for three RCP scenarios, using model ensembles that are un-adjusted (mean alone) and adjusted (for the annual cycle and mean).

general circulation models (GCMs). Thermal bleaching disrupts the symbiosis between corals and the microscopic algae called zooxanthellae that corals need to thrive. Warmer-than-usual sea surface temperatures (SSTs) result in overwhelmed photosystems in the zooxanthellae that produce oxygen radicals in high light. The zooxanthellae are then expelled, and the white skeleton becomes visible through transparent tissue¹³. Corals can regain their algae and recover but mass coral mortality can occur when stress persists¹⁴.

Of the various threats reefs face as the climate changes, an increasing frequency and severity of coral bleaching events warrants focus owing to: the large scale of these phenomena, anticipated increases in the frequency and severity of these events¹, the level of understanding and strong causal links between SST and bleaching¹⁵, and the accessibility of historical and modelled SST data.

Coral reef futures have been predicted with GCMs before^{11,15,16} and in some previous cases, as well as here, the mean and annual cycle of the models have been adjusted to correct model biases^{17,18}. The projections presented here are unique in three ways. First, using climate model ensembles is the standard for climate prediction but ensembles have never been used to project bleaching conditions. Second, we use the new generation of models included in the Coupled Model Intercomparison Project Phase 5 (CMIP5; ref. 3) forced with the new RCPs (ref. 4). Third, our projections identify temporary refugia from temperature stress and locations where bleaching conditions occur sooner than the median year.

Spectral analysis of the GCMs used in our ensembles (Supplementary Table S1) reveals that for reef locations, the models in CMIP5 under-represent variability in the annual cycle but less so than was the case with the previous generation of models¹⁹. The mean—the baseline from which projections are produced—is also different from observations. Failing to correct the annual cycle

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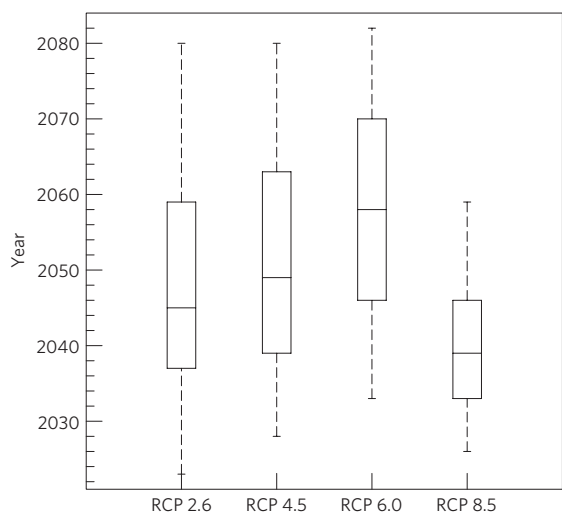


Figure 2 | Model spread for each of the RCPs. For each model the median (centre line), 25th and 75th (boxed) and 5th and 95th (dashed lines) percentiles are shown for the onset of annual bleaching conditions.

and mean reduces skill by under- or over- projecting bleaching conditions (Fig. 1).

The range of sensitivities in CMIP5 models²⁰ ranges from ~ 2 to ~ 4.5 °C warming per doubling of CO₂ concentration and these differences result in the various models producing a range of projections for the same RCP experiment (Fig. 2 and Supplementary Tables S2 and S3). There is good agreement between the sensitivities of the models and the projected first occurrence of annual bleaching conditions; models with the highest sensitivity reported, HadGEM2-ES and IPSL-CM5A-LR (ref. 20), show the earliest occurrences of annual bleaching. Besides different sensitivities, different models have different errors. Some of these biases might be time dependent, such as an error in the reproduction of the Pacific Decadal Oscillation. A common method for improving predictive skill is to form a multi-model ensemble, now the standard in climate prediction²¹. Here we have created an ensemble of bias-adjusted model results for the RCPs and derived the median for each location for two different bleaching scenarios: the year in which bleaching conditions start to occur annually and the year a decade starts in which bleaching conditions occur at least twice¹¹.

Many reefs may recover and sustain provision of various ecosystem goods and services when two events occur per decade. However, the return time between bleaching events enabling sufficient recovery for reefs to remain coral-dominated will vary among communities, and will drive the likelihood that coral communities can adapt. Further, rates of reef degradation will also be driven by the intensity and frequency of a large number of other stressors on reefs aside from thermal bleaching. For these reasons, our primary focus here is on the onset of annual bleaching conditions as a metric for the sustainability of coral reefs. As a time point, the onset of annual bleaching conditions is conservative because severe reef degradation is likely to occur before rather than after that projected date.

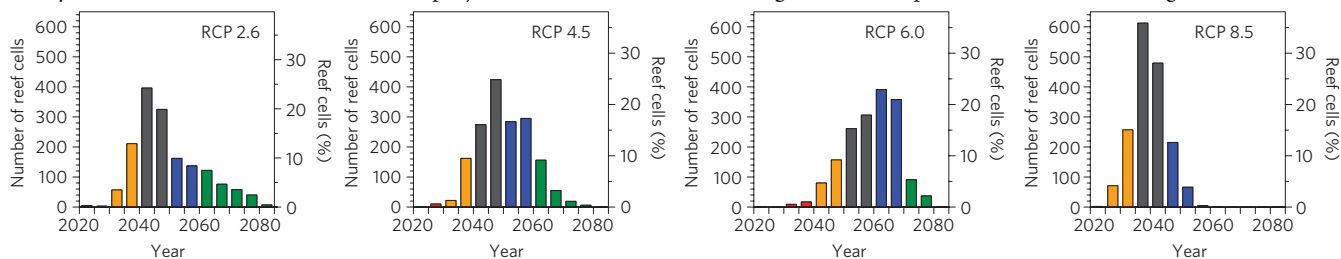


Figure 3 | Histogram of projected years when bleaching conditions start to occur annually. The distribution of reef cells ($n = 1,707$) across year ranges for projected annual bleaching conditions. Colours correspond to the colour scale in Fig. 4.

RCP 2.6 is a scenario with strong reductions in greenhouse-gas emissions; RCP 4.5 and 6.0 are experiments driven by emissions scenarios that result in CO₂ stabilization⁴. RCP 8.5, in contrast, more closely portrays the status quo; a high emissions baseline is used in combination with aggressive emissions growth and no emissions stabilization. It should be noted that RCP 2.6 has higher total radiative forcing than RCP 6.0 until 2030 and that RCP 4.5 has higher forcing than RCP 6.0 until 2065. This means that given the same sensitivity of a model, at least until 2030 higher temperatures are expected in RCP 2.6 than in RCP 6.0, and at least until 2065 temperatures will be higher in RCP 4.5 than in RCP 6.0. The median year of all reef locations in which bleaching conditions start to occur annually varies more than a decade between these RCPs; 2046 for RCP 2.6, 2047 for RCP 4.5, 2057 for RCP 6.0, and 2040 for RCP 8.5. The range in years for projected annual bleaching conditions varies greatly between RCPs. In RCP 4.5 and 6.0 (52 and 50 years, respectively) the range is nearly 1.5 times that of RCP 8.5 (33 years, Fig. 3). There is little spatial variability in the differences in the standard deviations across experiments, indicating that the spatial patterns found are robust (Supplementary Fig. S4).

The narrowed range in projected years for annual bleaching conditions in RCP 8.5 means that there are fewer temporary refugia; locations projected to experience annual bleaching conditions 5–15 years later than average (26.0% of reef cells versus 29.1% (RCP 6.0) and 23.7% (RCP 4.5)). For RCP 8.5, only one reef location experiences annual bleaching conditions 15 or more years later than the median in comparison with 4.5% and 1.6% in RCP 4.5 and 6.0, respectively (Fig. 4); this location is in the Austral Islands (French Polynesia). Locations projected to bleach annually later are refugia from temperature stress but these are very temporary in nature; all locations experience annual bleaching conditions by 2075 for RCP 4.5, by 2078 for RCP 6.0 and by 2056 for RCP 8.5. However, our projections indicate that for RCP 6.0—a scenario with lower greenhouse-gas emissions than RCP 8.5—97% of reef locations would experience annual bleaching conditions later than 2040; the median year such conditions occur at reef locations in RCP 8.5. For 394 locations (of 1,707, $1^\circ \times 1^\circ$) this amounts to at least two more decades in which some reefs might conceivably be able to improve their adaptive capacity. In RCP 2.6, 84 locations do not experience annual bleaching conditions in the period 2006–2100. This highlights and quantifies the potential benefits for reefs of reducing emissions in terms of reduced exposure to stressful temperatures.

Locations where bleaching conditions are projected to occur annually sooner or later (five or more years) both represent potential conservation priorities. Locations projected to experience annual bleaching conditions sooner may require urgent action to reduce the anthropogenic stress that can hamper recovery following episodic disturbances such as bleaching events¹⁶. Locations likely to bleach later may have the best chance of persisting. Our projections suggest such investments can be made at both types of location concurrent with efforts to reduce emissions. The spatial patterns when bleaching conditions occur annually are highly similar between experiments (Fig. 4). For all experiments, some reefs in the following locations experience annual bleaching conditions 5–15,

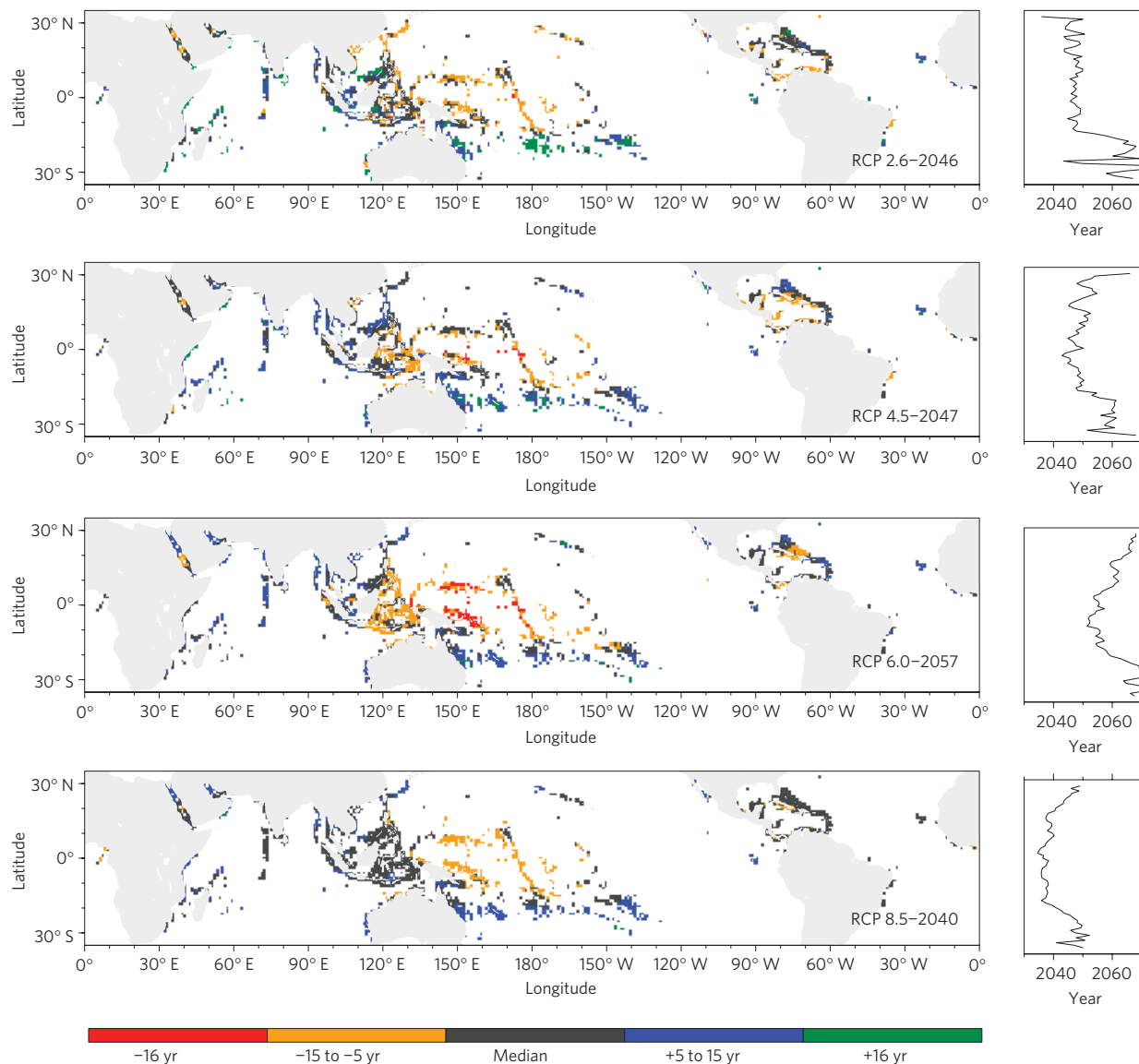


Figure 4 | Global projections of the year annual bleaching conditions start for all reef locations. On the left, maps for all RCPs showing years that reef locations start to experience bleaching conditions annually (colour scale); median values are shown next to the RCP labels. Zonal means are shown on the right.

or 16 or more years later than the median (blue and green in Fig. 4): the Southern part of the Great Barrier Reef, the western Indian Ocean, Persian Gulf, Red Sea, Thailand, New Caledonia and French Polynesia. Other locations—consistent between experiments—experience annual bleaching conditions 5–15, or 16 or more years earlier than the median (orange and red in Fig. 4). These include the western Pacific warm pool, northwestern Australia, west Papua New Guinea and the central Pacific islands of and around Tokelau.

Zonal means for projected years in which annual bleaching conditions start show a latitudinal gradient with higher latitude reefs experiencing bleaching conditions later. This signal is stronger in RCP 4.5 and 6.0 than in 8.5; it is absent in RCP 2.6. This zonal pattern can be explained in part by the patterns of SST trends seen in the models; the equatorial Pacific warms more than higher latitudes. High warming rates in the equatorial region could be caused by weakening trade winds flattening the thermocline and reducing upwelling in the region²². The spatial patterns for the projections of our second bleaching scenario are similar to those of the annual bleaching scenario (Supplementary Fig. S3). The median year in which bleaching conditions are projected to occur twice per decade

is 20+ years sooner for each scenario than is the case for annual bleaching conditions; 2019 in RCP 2.6 and 2018 in the RCP 4.5, 6.0 and 8.5 scenarios (Supplementary Fig. S3).

For RCP 4.5 and 6.0 the median year in which bleaching conditions start to occur annually is associated with a CO₂ concentration of 510 ppm CO₂ equivalent. Future warming at that concentration is to be expected owing to the long residence time of CO₂ in the atmosphere. Therefore, a safe target concentration for reefs must be lower, and a concentration of 450 ppm CO₂ has been proposed previously²³, and a lower target than that is supported by the findings here. Even in the pathway with most pronounced emission reductions (RCP 2.6), where CO₂ equivalent concentrations peak at 455 ppm (Supplementary Fig. S1), 95% of reef locations experience annual bleaching conditions by the end of the century. Present emission growth rates are increasing, as in RCP 8.5, which most closely represents a pathway without significant emissions reductions. Under this scenario, 480 ppm will be reached before 2040 (ref. 24), whereas RCP 6.0 does not reach this concentration until 2051. Actions to reduce emissions to even this modest level have yet to be implemented.

The required action on emissions could be and is even likely to be many years away. With each passing year with no pronounced action a pathway such as RCP 2.6 becomes more and more unlikely. We show though what the value of these actions would be for the persistence of reefs as coral-dominated, highly diverse habitats supporting fish communities and dependent human populations and industries. It is also shown here though that there is significant spatial variability in the year reef locations experience bleaching conditions twice per decade or annually. Projections that combine the threats posed to reefs by increases in sea temperature and ocean acidification will further resolve where temporary refugia may exist. This first step though with ensembles of Intergovernmental Panel on Climate Change (IPCC) CMIP5 model output that have been adjusted for biases represents the most up-to-date understanding of spatial variability in the effects of rising temperatures on coral reefs on a global scale.

Methods

Monthly SST temperature data were retrieved for each available GCM (Supplementary Table S1 for list) from the World Climate Research Programme's CMIP5 data set³ for the relative concentration pathway experiments (RCP 2.6, $n = 15$; RCP 4.5, $n = 11$; RCP 6.0, $n = 10$; RCP 8.5, $n = 16$; from <http://pcmdi9.llnl.gov/esgf-web-fe/>). The new RCPs are comparable to the previously used SRES scenarios, but with considerable refinements, such as a strong reduction in aerosol emissions. For a detailed description of the RCPs and how they differ, see ref. 25. Although the spatial resolution in the new generation of GCMs has increased, the present resolution still does not represent small-scale processes that influence local reef conditions such as upwelling or heating on reef flats. Dynamical and statistical downscaling approaches could resolve these issues but are either computationally expensive or introduce additional assumptions and therefore are not applicable to global assessments such as those presented here. Statistical downscaling where satellite data are used to project temperatures at reef environments is possible¹¹ but even those techniques are limited by the spatial and temporal resolutions of the satellite data. Moreover, these statistical approaches train the downscaling model with observed data, data that can be dominated by short-term variability (such as diurnal or intraseasonal). The long-term variability is most important for projections of climate-change impacts²⁶.

To match the start of each model with the observed climatology, the models' mean temperatures were adjusted using observational data from the NOAA Optimal Interpolated SST V2 (ref. 27) obtained from NOAA/OAR/ESRL PSD, (<http://www.esrl.noaa.gov/psd/>). Model bias was removed at each location by subtracting the 2006–2011 mean of each model and adding the mean of the OISST 1982–2005 climatology to the entire time series. To improve projections of thermal stress, the annual cycles were replaced with those from the observed climatology¹⁹. Missing values such as near-coast pixels were filled in using an interpolation routine that solves Poisson's equation using relaxation. This function uses the non-missing data as boundaries and interpolates in the zonal direction.

From the 1982 to 2005 climatology the warmest month was selected at each location as the maximum monthly mean (MMM). Degree heating weeks (DHWs) start to accumulate when projected temperatures exceed the MMM, not the $MMM + 1^\circ\text{C}$ as in ref. 28. The positive anomalies for three months were added to get degree heating months (DHMs) and then converted to DHWs by multiplying by 4.34. DHM to DHW conversion is necessary to compare model DHWs with a previously established optimal global bleaching threshold of six DHWs (ref. 29). For each cell ($1^\circ \times 1^\circ$) we project the year in which it has ten (annual) and two projected bleaching conditions (>6 DHWs) in a decade. Projections are shown for reef locations alone, using the Merged reefbase/UNEP-WCMC and Millennium Coral Reef Mapping Project reefs database (<http://imars.usf.edu/MC/index.html>). Projections were made for each separate model and for each RCP experiment the median of all models was derived for each location. For each RCP experiment, maps for each of two bleaching scenarios ($2\times$ and $10\times$ per decade) were produced using the NCAR Command Language (NCL version 6.0.0) developed by NCAR/CISL/VETS.

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Author contributions

R.v.H. and J.A.M. designed the study. Climate data were collated and analysed by R.v.H. All authors contributed to writing the manuscript.

Additional information

Supplementary information is available in the [online version of the paper](#). Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to R.v.H.

Competing financial interests

The authors declare no competing financial interests.