

RESEARCH ARTICLE

Cloudiness delays projected impact of climate change on coral reefs

Pedro C. González-Espínosa^{1,2*}, Simon D. Donner^{1,2}

1 Department of Geography, University of British Columbia, Vancouver, BC, Canada, **2** Institute for the Oceans and Fisheries, University of British Columbia, Vancouver, BC, Canada

* pcgonzaleze@gmail.com



OPEN ACCESS

Citation: González-Espínosa PC, Donner SD (2023) Cloudiness delays projected impact of climate change on coral reefs. PLOS Clim 2(2): e0000090. <https://doi.org/10.1371/journal.pclm.0000090>

Editor: Lin Liu, First Institute of Oceanography, Ministry of Natural Resources, CHINA

Received: July 4, 2022

Accepted: December 1, 2022

Published: February 8, 2023

Peer Review History: PLOS recognizes the benefits of transparency in the peer review process; therefore, we enable the publication of all of the content of peer review and author responses alongside final, published articles. The editorial history of this article is available here: <https://doi.org/10.1371/journal.pclm.0000090>

Copyright: © 2023 González-Espínosa, Donner. This is an open access article distributed under the terms of the [Creative Commons Attribution License](#), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Data Availability Statement: The coral bleaching database is available at <https://zenodo.org/record/6780843>, the python and R codes, and CDO script is available in the repository <https://doi.org/10.5281/zenodo.6795835>. The NOAA Coral Reef

Abstract

The increasing frequency of mass coral bleaching and associated coral mortality threaten the future of warmwater coral reefs. Although thermal stress is widely recognized as the main driver of coral bleaching, exposure to light also plays a central role. Future projections of the impacts of climate change on coral reefs have to date focused on temperature change and not considered the role of clouds in attenuating the bleaching response of corals. In this study, we develop temperature- and light-based bleaching prediction algorithms using historical sea surface temperature, cloud cover fraction and downwelling shortwave radiation data together with a global-scale observational bleaching dataset observations. The model is applied to CMIP6 output from the GFDL-ESM4 Earth System Model under four different future scenarios to estimate the effect of incorporating cloudiness on future bleaching frequency, with and without thermal adaptation or acclimation by corals. The results show that in the low emission scenario SSP1-2.6 incorporating clouds into the model delays the bleaching frequency conditions by multiple decades in some regions, yet the majority (>70%) of coral reef cells still experience dangerously frequent bleaching conditions by the end of the century. In the moderate scenario SSP2-4.5, however, the increase in thermal stress is sufficient to overwhelm the mitigating effect of clouds by mid-century. Thermal adaptation or acclimation by corals could further shift the bleaching projections by up to 40 years, yet coral reefs would still experience dangerously frequent bleaching conditions by the end of century in SSP2-4.5. The findings show that multivariate models incorporating factors like light may improve the near-term outlook for coral reefs and help identify future climate refugia. Nonetheless, the long-term future of coral reefs remains questionable if the world stays on a moderate or higher emissions path.

1 Introduction

Climate change is a key risk for coral reefs [1,2]. Tropical corals are composed of coral polyps and microalgal symbionts living within the corals' tissue which provide up to 95% of their photosynthetic products to the coral [3]. This symbiotic relationship can be disrupted by increases in ocean temperatures of as little as 1–2°C above those usually experienced in summer, resulting in the phenomenon known as coral bleaching [2,4]. Climate change has led to more

Watch CoralTemp Version 3.1 Daily Global 5 km is publicly available at <https://www.star.nesdis.noaa.gov/pub/sod/mecb/crw/data/5km/v3.1/nc/v1.0/daily/sst/>. The Downward short-wave radiation at the surface (RSDS) and total cloud area (CLT) data from the Geophysical Fluid Dynamics Laboratory's ESM4 model (GFDL-ESM4) are publicly available at <https://esgf-node.llnl.gov/search/cmip6/> (source ID = GFDL-ESM4).

Funding: This work is supported by the Mexican Council for Science and Technology (CONACYT) doctoral scholarship (number 438530) to P.C.G.E. and by the Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery Grant to S.D.D. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing interests: The authors have declared that no competing interests exist.

frequent and more extreme mass coral bleaching events worldwide over the last four decades, and widespread loss of living corals [2,5,6]. Moreover, coral reefs have been projected to face dangerously frequent bleaching conditions by mid-century, even in a 1.5°C warming scenario [7,8].

The heterogeneity of coral responses to environmental stress represents a challenge for predicting mass coral bleaching events in real-time and for projecting the response of corals to climate warming [9,10]. In addition to thermal or heat stress, other stressors such as solar radiation, turbidity, salinity, air exposure, or pollution can effect the coral-algal relationship [11–13]. Although elevated temperature is often reported as the primary cause of mass coral bleaching, the interaction between temperature and other environmental variables modulates the bleaching response [14]. Light exposure in particular plays a central role for corals [15,16]. Light is critical to coral growth but excess exposure can inhibit or damage the photosynthetic processes of the microalgal symbionts [17–19]. High irradiance, when coupled with high temperatures, can disrupt the balance between light absorption and electron transport rates, promoting the production of reactive oxygen species (ROS) that can trigger photoinhibition, impair the photosynthetic apparatus of the microalgal symbionts [20] and, in turn, exacerbate thermal stress [15,16,21]. Moreover, the reductions in zooxanthellae pigment density and increased light absorption can cause a positive feedback which worsens the effects of elevated temperatures [22]. To minimize the potential photodamage due to excess light, corals and their symbionts have acclimation strategies including regulating the density of symbionts and/or the ratio of photosynthetic pigments [23], restructuring their skeletal morphologies [24], hosting different *Symbiodinium* species [25,26] or increasing antioxidant contents [27].

While light reaching the surface of the corals is modulated by properties of seawater itself, field observations indicate that clouds can reduce the amount of incoming solar radiation and limit the effects of thermal stress on corals [28–31]. A recent global analysis found that incorporating cloud cover can improve the accuracy of mass coral bleaching prediction [32]. While models are beginning to include evolutionary [33] and ecological processes [34,35] in projecting the future of coral reefs, the forcing variables in those models are generally still restricted to temperature. There has yet to be an analysis of the integrated effect of thermal stress, solar radiation and cloudiness on future bleaching conditions.

In this study, we test for the first time whether including cloudiness in coral bleaching projections models affects the projected frequency of mass coral bleaching conditions at regional and global scales under climate change. First, building on previous work [32], we use a historical mass bleaching dataset to develop a new bleaching prediction algorithm incorporating thermal stress and cloudiness that are designed for use with climate model output. Second, we contrast the projected frequency of mass coral bleaching through the year 2100 with and without the role of clouds under four future scenarios, using CMIP6 output from the GFDL-ESM4 Earth System Model. To test for robustness, the analysis is repeating using an algorithm incorporating incoming shortwave radiation rather than cloudiness. Finally, we assessed whether thermal adaptation or acclimation by corals and their symbionts could influence the role of clouds in future bleaching projections. The results indicate that incorporating light, in the form of either cloudiness or incoming shortwave radiation, can delay bleaching projections in low-to-moderate emissions scenarios and help identify future climate refugia.

2 Methods

2.1 Historical bleaching reports

The coral bleaching data used in this study were derived from version 2.0 [36] of a high-resolution global mass coral bleaching database [6] that includes reports through the year 2017. Each

report includes a categorized bleaching severity from levels 0 to 3 based on the protocol of ReefBase, where category 0 refers to no bleaching (<1% of observed living coral area is bleached), category 1 refers to mild bleaching (1–10% bleached), category 2 refers to moderate bleaching (11–50% bleached) and category 3 refers to severe bleaching (>50% bleached). To align with the available historical high-resolution climate data [see sections 2.2 & 2.3], we focused on all bleaching reports from 2001 through 2017 (n = 33,768) which reported the month or date of observation.

2.2 Historical sea surface temperature and thermal stress

To describe historical coral thermal exposure, sea surface temperature (SST) data from 0.05° x 0.05° lat-long resolution CoralTemp V3.1 [37] was used to compute the Degree Heating Month (DHM) value corresponding to each coral bleaching report in the database. The DHM is a monthly-scale version of the Degree Heating Week index used in real-time bleaching prediction; the monthly rather than weekly index from [32] is employed in order to develop an algorithm that aligns with the available resolution of most archived climate model output [38–40]. Here, DHM is computed by summing the SST anomaly in excess of the maximum monthly mean (MMM), a maximum value from a climatology, over a 3-month rolling window [7,40,41] using the following formula:

$$DHM = \sum_{i=1}^3 \max[(SST_i - MMM_{Max}), 0]$$

The MMM_{Max} [42], represents the mean of the warmest monthly SST from each year during the period 1985–2004 calculated for each grid cell. The MMM_{Max} is a variation of the MMM threshold that is used in recent models [33,40] because it better characterizes the bleaching threshold in regions where the timing of the seasonal peak in SST varies from year to year.

2.3 Historical cloudiness and incoming radiation

To represent the amount of light energy that corals receive, 1° x 1° lat-long total cloud area (CLT) and incoming shortwave radiation at the surface data (represented by the variable downwelling shortwave radiation or RSDS) for the 2001–2017 period were retrieved from CERES project (CERES-EBAF Edition 4.0; [43,44]). Since corals acclimate to background light conditions, monthly anomalies for each variable (CLTa, RSDSa) were computed by subtracting monthly values from their respective 2001–2017 monthly climatologies [32]. This data can be used to test the hypothesis that exposure to excessive light (i.e. positive RSDSa or incoming shortwave radiation anomaly) for a given location and time of year due to anomalously low cloud cover (i.e. negative CLTa or total cloud area anomaly) correlates with higher bleaching severity, and vice versa. Using the RSDSa and the CLTa data provided two different methods for characterizing incoming light in a bleaching prediction algorithm. The effect of each variable was tested separately as a check on the robustness of the underlying hypothesis that incorporating light influences the accuracy of bleaching prediction.

2.4 Bleaching prediction model development

We used the historical bleaching observations together with the climate variables to develop three different bleaching prediction models by performing mixed-effect models with a random effect structure (lmerTest package in R [45]). In the first or control model, only thermal stress (DHM) was used as a fixed effect, with geographical position set as a random intercept to

control the spatial structure in the data. In the other two models, thermal stress (DHM) and either cloud anomaly (CLTa) or incoming shortwave radiation anomaly (RSDSa) were used as fixed effects, with geographical position again set as a random intercept.

The models also include an interactive term, as follows:

$$\text{Severity} = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_{12} X_{12}$$

Where:

severity = is the predicted value of the projected severity of bleaching

β_0 = is the severity intercept

$\beta_1 X_1$ = the regression coefficient (β_1) of the first independent variable (e.g., DHM)

$\beta_2 X_2$ = the regression coefficient of the second independent variable (e.g., CLTa, the total cloud cover anomaly)

$\beta_{12} X_{12}$ = the regression coefficient (β_{12}) of the interaction of both variables (e.g., DHM: CLTa)

Latitude was selected to represent geographical position, because sensitivity analyses performed with latitude, longitude, and both latitude and longitude as random intercepts produced similar results (Table A in [S1 Text](#)).

To assess the performance of the bleaching prediction models we computed the accuracy (the percentage of correctly classified instances out of all instances) but also the Cohen's Kappa (the difference between the observed overall accuracy of the model and the overall accuracy that can be obtained by chance) for which higher values represent better model performance ([46]).

2.5 Future projections

We applied the two multiple variable bleaching severity models (Section 2.4) to 1985–2100 output from the Geophysical Fluid Dynamics Laboratory's ESM4 model (GFDL-ESM4) for four of the socio-economic pathways (SSPs) employed by the climate modelling community. Analysis was conducted for all the $1^\circ \times 1^\circ$ lat-long model cells worldwide containing coral reefs, according to the Millennium Coral Reef Mapping Project [47]. The GFDL-ESM4 model was selected because it has moderate climate sensitivity (1.6°C for transient climate sensitivity and 2.6°C for equilibrium climate sensitivity) among ESMs and coupled ocean-atmosphere general circulation models (GCMs) from the Coupled Model Intercomparison Project 6 (CMIP6; [48]).

The workflow was as follows: independent variables (DHM, CLTa, RSDSa) required by the bleaching severity models (Section 2.4) were computed from GFDL-ESM4 output. Monthly values for the SST, total cloud area (CLT) and incoming shortwave radiation at the surface (RSDS) at $1^\circ \times 1^\circ$ lat-long grid resolution were retrieved from the <https://esgf-node.llnl.gov/search/cmip6> node for the four SSPs described above and from a historical all-forcing simulation. Historical (1985–2014) and projected (2015–2100) output data were concatenated to create a complete-time series. As is common in climate change impacts research, we corrected for biases in model output (Fig A in [S1 Text](#)) using the delta method [49]; raw output for SST, CLT and RSDS were adjusted by adding the model anomalies (simulated projected values–simulated historical climatology) to the observed climatologies for respective variables. The adjusted SST values were then used to compute a DHM time series, using the method described in Section 2.2, and the adjusted CLT and RSDS values were used to compute the total cloud area anomaly (CLTa) and the incoming shortwave radiation anomaly (RSDSa) time series, as described in Section 2.3.

For each grid cell containing coral reefs, we used the coefficients from the bleaching projection models (Section 2.4) to compute the projected bleaching severity based on the computed

DHM, CLTa or RSDSa time series (1985–2100). Given the documented uncertainty in model cloud projections [50], a sensitivity analysis was performed in which the bleaching severity calculations were repeated using projected DHMs but observed CLTa and RSDSa from the climatology rather than the projected values.

To assess the effects of incorporating cloudiness on future projections of coral bleaching frequency and severity, the results from the bleaching severity models are compared to that of the common DHM-only method used in past climate change projection studies. Past studies used a threshold of $DHM \geq 2^{\circ}\text{C}\cdot\text{month}$ to indicate the likelihood of occurrence of severe bleaching conditions [33,38–40]. Here, a threshold of $DHM \geq 2.5^{\circ}\text{C}\cdot\text{month}$ was employed, since the $DHM \geq 2^{\circ}\text{C}\cdot\text{month}$ threshold tends to overpredict the bleaching frequency when interacting with another variable (Fig B in [S1 Text](#)), i.e. even though cloudiness anomalies reduce bleaching severity, it depends on its magnitude and the interaction effect with DHM [32]. Following previous studies, we express results in terms of year that the probability of bleaching conditions in each grid cell exceeds 0.2 (bleaching occurring more than twice per decade) [33,39,40] and the year that bleaching conditions in each grid cell become an annual occurrence ($p = 1$) [van Hooindonk \[38\]](#). In those results, the year refers to the midpoint of a 10-year running analysis, e.g., for bleaching probability for the year 2020 is based on occurrences from the period 2015–2024.

To examine if thermal adaptation or acclimation by corals, their algal symbionts or human interventions [51–54] changes the effect of incorporating cloudiness on bleaching projections, a series of simple additional sensitivity analyses were conducted. The bleaching projections were recomputed three times, assuming a $+0.5^{\circ}\text{C}$, $+1.0^{\circ}\text{C}$ and $+1.5^{\circ}\text{C}$ adjustment in the threshold above which thermal stress accumulates (MM_{\max}), following estimates of maximum likely adaptation employed in previous projection studies [33,39]. For example, if the thermal threshold is estimated to be 29.5°C (for a certain moment), it is expected that some corals would bleach under these conditions, while some others would resist because their threshold is 0.5°C higher (30°C) due to natural physiological acclimation, assisted evolution or other mechanisms.

Finally, to explore the temporal and spatial change in cloudiness but also to visualize the magnitude of the change between scenarios we compared the total cloud trend (CLT_{trend}), for the period 2015–2100.

All data retrievals, processing and statistical tests were conducted using Python (version 3.7.4), R project (version 3.6.3), Climate Data Operators (CDO; version 1.9.8) and ArcGIS Pro (version 2.6).

3 Results

The mixed-effects regression analysis showed that models including both thermal stress (DHM) and one of the variables representing incoming light (CLTa or RSDSa) were stronger predictors of bleaching severity than the DHM-only control model ([Table 1](#)).

For the cloud model, the negative correlation between bleaching severity and CLTa (total cloud cover anomaly) indicates that at a given level of thermal stress, the severity of bleaching decreases with higher cloudiness ([Table 1](#)). As expected, the results for solar radiation model showed an opposite pattern, where both DHM and RSDSa (incoming solar radiation anomaly) were significantly positively correlated, which means that, for a given DHM value, the bleaching severity is higher with a higher incoming short-wave radiation anomaly (i.e., fewer clouds). Since both the cloud and incoming solar radiation models confirm the hypothesis that higher clouds (less light) modulate the response of corals to thermal stress, and the accuracy and Kappa of two models are similar, we focus the remainder of the results on the cloud model.

Table 1. Mixed-effects model coefficients for the models using DHM + Cloud (CLTa) or Solar radiation (RSDSa) metrics.

Model name	Variables	Relation	Coefficients	p-value	Accuracy	Kappa
DHM-only (control)	DHM	+	7.787e-01	< 2e-16	0.520	0.269
Cloud (DHM-CLTa)	DHM	+	7.796e-01	< 2e-16	0.803	0.710
	CLTa	-	-3.108e-03	6.28e-06		
	DHM:CLTa	+	2.662e-03	0.00341		
Solar radiation (DHM-RSDSa)	DHM	+	7.786e-01	< 2e-16	0.801	0.710
	RSDSa	+	2.480e-03	5.41e-09		
	DHM:RSDSa	-	-3.208e-04	0.57		

<https://doi.org/10.1371/journal.pclm.0000090.t001>

In the future projections, the cloud model showed a lower fraction of reef cells experiencing high frequency bleaching conditions in all four scenarios when compared against the DHM-only model (Fig 1). In both cases, the effect is greatest in the lower emissions scenarios and before or around mid-century; it is maintained through 2100 only in SSP1-2.6 (Fig 1A–1D; Table B in S1 Text). To test whether the results are sensitive to model projected changes in cloudiness, all analyses were repeated using the CLTa from the observed climatological period (2001–2014) instead of the projected values. The effect of employing observed CLTa on the projected bleaching conditions were minimal at the global scale in all scenarios (Fig C and Fig D in S1 Text for RSDSa).

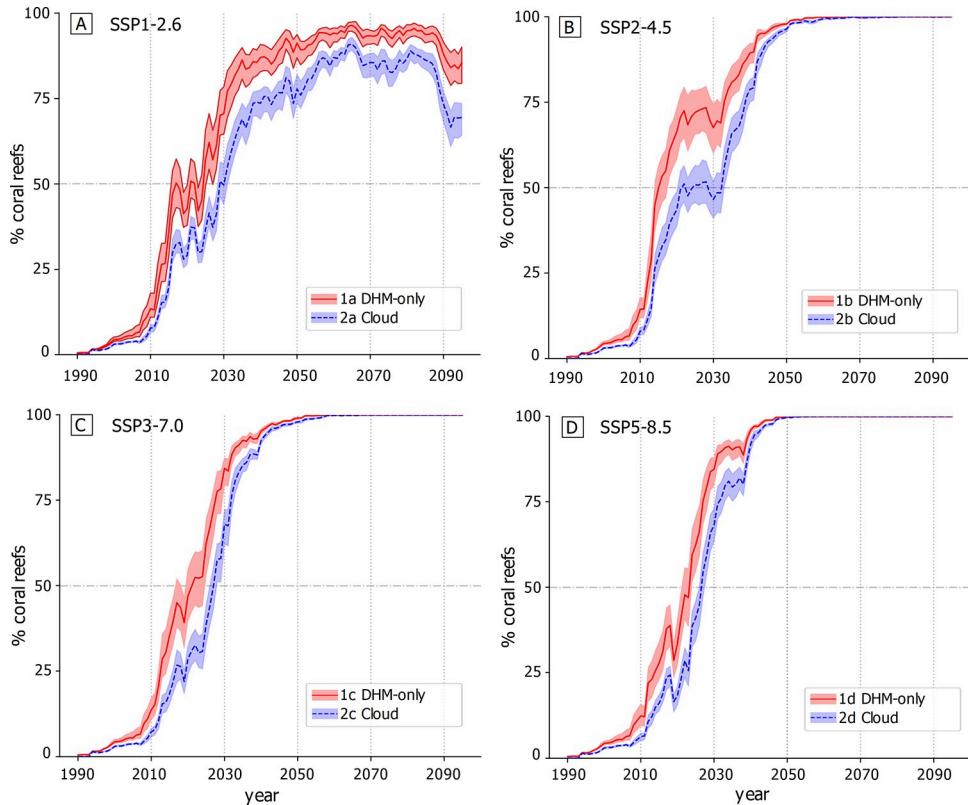


Fig 1. Comparison of percent of global reef cells predicted to experience high-frequency bleaching under four SSP scenarios by 2100, using the GFDL-ESM4 model with delta correction for all variables. High-frequency bleaching is defined as a reef cell that experiences bleaching conditions at least twice in the surrounding ten years. Shaded represent the 95% confidence interval window. The “cloud” model corresponds to the model that includes thermal stress and cloud anomaly metrics (DHM-CLTa).

<https://doi.org/10.1371/journal.pclm.0000090.g001>

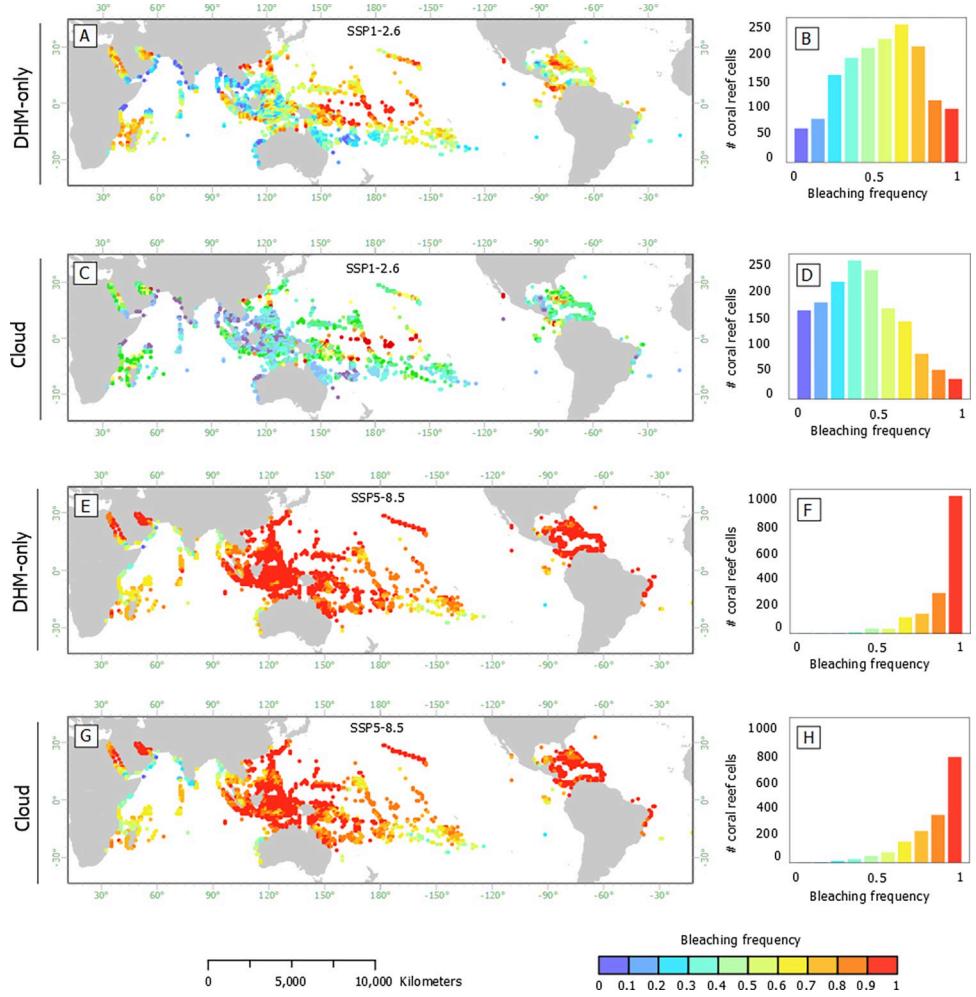


Fig 2. Geographical distribution of projected frequency of bleaching conditions for the year 2050 in scenarios SSP1-2.6 and SSP5-8.5 using the DHM-only (A,B,E,F) and the cloud model (C,D,G,H). The cloud model corresponds to the model that includes thermal stress and clouds anomaly metrics (DHM-CLTa). This figure uses a public domain map from the Natural Earth data website.

<https://doi.org/10.1371/journal.pclm.0000090.g002>

Incorporating cloudiness most substantially reduces the projected frequency of bleaching conditions for mid-century in parts of the Coral Triangle, South Pacific, Northern Hawaii, Caribbean, Red Sea and East Africa in SSP1-2.6 scenario (Fig 2A–2C). On the other hand, the choice of prediction method has little impact on regional patterns in projected frequency of bleaching conditions under the high emission scenario SSP5-8.5 (Fig 2E, 2F and 2H). In the SSP5-8.5 scenario, the bleaching condition frequencies are on average lower in 2050 using the cloud model, however bleaching conditions still occurs annually (frequency = 1) across most of the Caribbean, Coral Triangle, Red Sea, Persian Gulf, western equatorial Pacific, Coral Sea, southern Gulf of California, eastern tropical Pacific and eastern Brazilian reefs (Fig 2E–2G).

Simulated thermal adaptation or acclimation considerably restricts the occurrence of the high frequency bleaching conditions in all four scenarios (Fig 3). In the low emissions scenario SSP1-2.6, the hypothetical adjustment of $+0.5^{\circ}\text{C}$ in addition to the cloudiness protection is sufficient for $<50\%$ of coral reefs to face high-frequency bleaching conditions this century (Fig 3A). In the moderate SSP2-4.5 emission scenario, the onset of high-frequency bleaching conditions for most reefs is delayed for a decade or more by an adjustment of $+0.5^{\circ}\text{C}$, but 100% of

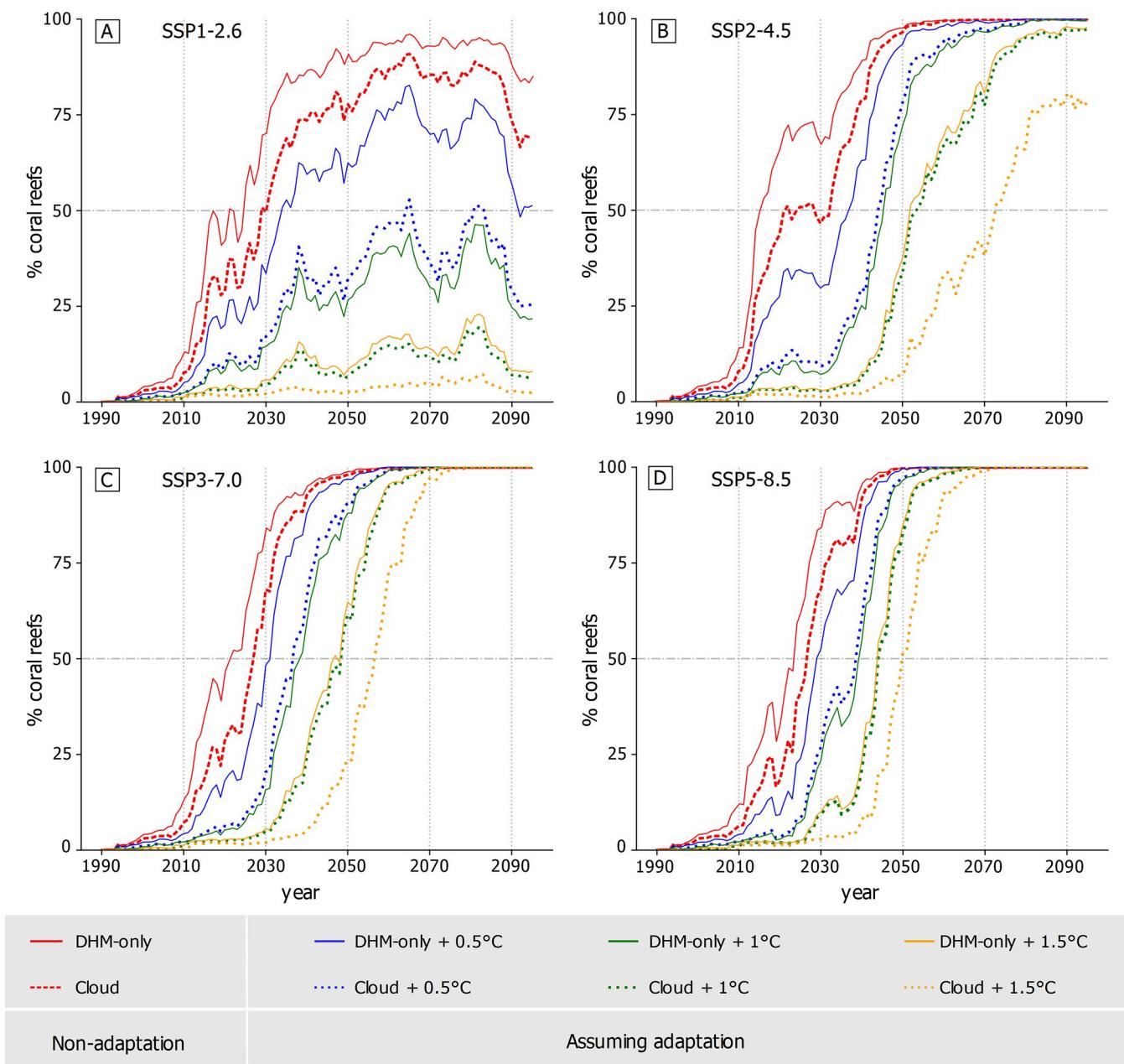


Fig 3. Percent of global reef cells predicted to experience high frequency bleaching conditions (more than twice in ten years, or $p>0.2$) assuming the presence of thermal adaptation, acclimation or human interventions that raise the bleaching threshold. The cloud model corresponds to the model that includes thermal stress and clouds anomaly metrics (DHM-CLTa). A) SSP1-2.6, B) SSP2-4.5, C) SSP3-4.5, D) SSP5-8.5.

<https://doi.org/10.1371/journal.pclm.0000090.g003>

reef cells would still experience bleaching conditions twice per decade before the end of the century, around 2080 (Fig 3B). If an adjustment of $+1^{\circ}\text{C}$ to $+1.5^{\circ}\text{C}$ occurs, the delay in the onset of high-frequency bleaching conditions would be up to 40 years in SSP3-4.5 (Fig 3B). In contrast, in the higher emissions scenarios, SSP3-7.0 and SSP5-8.5, high-frequency bleaching conditions is only delayed by two to three decades even with the high adjustment assumption ($+1.5^{\circ}\text{C}$), and all reefs cells still experience high-frequency bleaching conditions by the end of the century (Fig 3C and 3D).

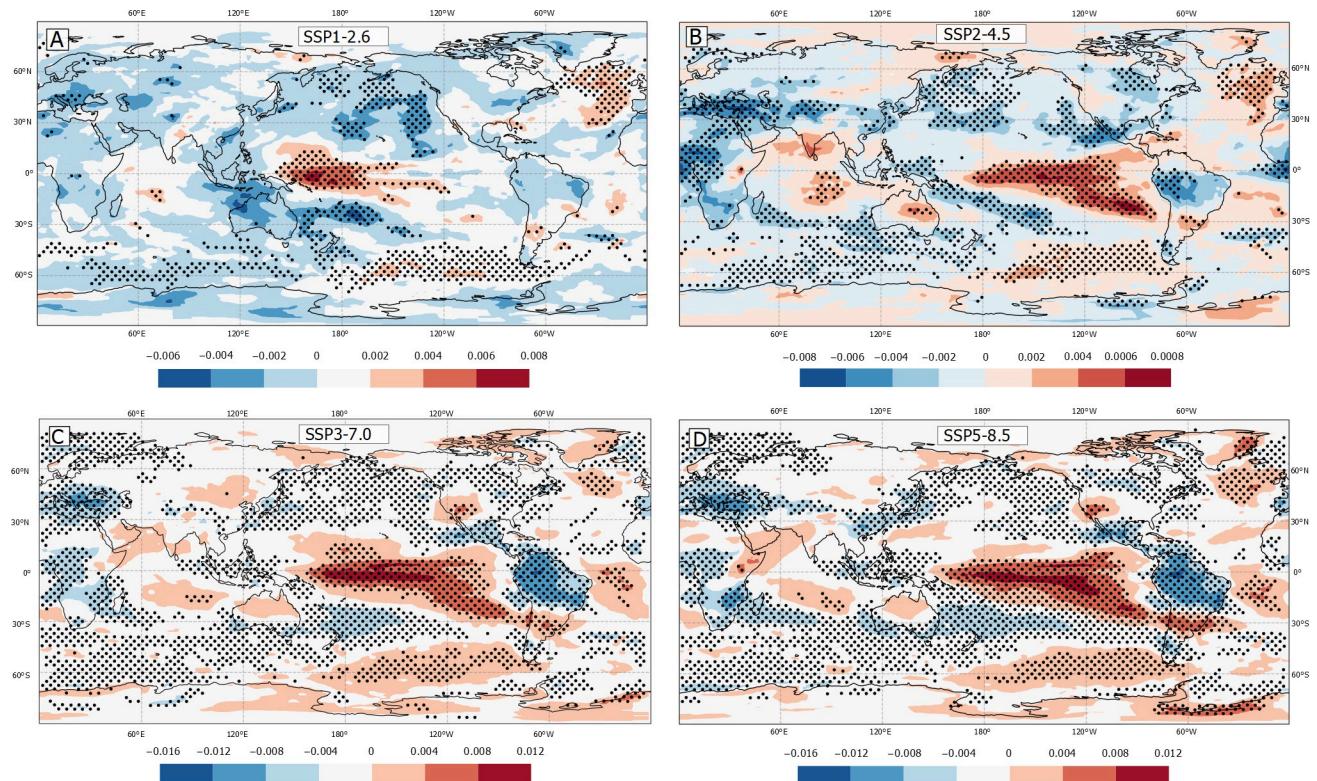


Fig 4. Cloud trends (CLT_{trend}) for the period 2015–2100 (units: % cloudiness/yr). The dots indicate sites with significance level of p -value < 0.05 . This figure uses a public domain map from the Natural Earth data website. A) SSP1-2.6, B) SSP2-4.5, C) SSP3-4.5, D) SSP5-8.5.

<https://doi.org/10.1371/journal.pclm.0000090.g004>

Finally, the total cloud trend (CLT_{trend}) shows the spatial patterns in simulated “total cloud area” (CLT). It illustrates typical projected global cloud pattern changes due to internal climate variability and their potential influence on future bleaching projections (Fig 4A–4D). Areas of positive CLT_{trend} indicate regions where including clouds in the bleaching prediction algorithm could most influence future bleaching projections. This pattern is similar to the SSP1-2.6 and SSP5-8.5 scenarios and supports the present-day “cloudy refugia” index map described in previous research [32]. However, it is also evident that the spatial pattern in the trend shifts from being positive (SSP1-2.6) to very positive with higher values across the equatorial Pacific (SSP5-8.5) reducing, thus, the possible protection of clouds in high emission scenarios.

4 Discussion and conclusions

Ocean warming has been clearly documented as the key driver of the observed increase in mass coral bleaching events over the last four decades [2,5,6]. However, geographical patterns in mass coral bleaching are increasingly being linked to multiple environmental variables including, but not restricted, to temperature [9,55–57]. Global coral bleaching projections, including those driving summary statements in the recent Intergovernmental Panel on Climate Change reports [58,59], have nevertheless relied on model-based estimates of bleaching-level thermal stress [7,8,38,39,60]. Although there have been recent advances in projecting coral ecological and evolutionary responses to climate change [33–35], the location of potential future climate refuges [61], such large-scale projections are still largely reliant on temperature as the independent variable. Those hindcast or smaller scale projection studies which included multiple environmental variables have generally excluded light.

Here, we find that incorporating cloud cover into global projections can delay the onset of high frequency bleaching conditions, based on the documented effect that clouds have had on mitigating against thermal stress. For example, in the most optimistic scenario analyzed in this study, SSP1-2.6, clouds could delay the onset of high-frequency bleaching by multiple decades, although the majority of the world's reefs still experience dangerously frequent bleaching conditions by the end of the century (~90% of reef cells with the DHM-only model vs. ~70% with the cloud model). However, the results from higher emissions scenarios point to a limit to the mitigating effect of clouds, as the capacity for DHM to increase exceeds that of clouds (i.e. the model incorporates cloud cover, which has a maximum value of 100%). Even in the moderate scenario SSP2-4.5, more than 95% of reef cells would experience high frequency bleaching conditions by 2050 (Fig 1).

Bleaching conditions are projected to become dangerously frequent across time and space in the absence of adaptation, physiological acclimation, shifts in coral community structure or human interventions like active restoration or assisted evolution [58,62]. More advanced models have found that incorporating evolutionary processes [33,40,63] or population dynamics [34,35] improves the forecast for the world's coral reefs. The coarse adaptation sensitivity test applied here finds that the mitigating effect of clouds increases assuming some positive adjustment of the thermal threshold for corals, but that this mitigating effect of clouds is still limited in moderate or high emissions scenarios. For example, in the moderate emission scenario SSP2-4.5, the cloud effect combined with a +1.5° C increase in the bleaching thresholds still leads to ~75% of reef cells experiencing bleaching conditions at least once every five years by the end of the century (Fig 3B). Although this research does not incorporate ecological or evolutionary processes, the difference in the projected bleaching frequencies between simulations, including cloud effects and both cloud effects and adaptation or acclimation, highlight the importance of considering additional driving variables in climate change impact projections. Moreover, results from studies like this could help to reinforce the accomplishment of the objective of curbing greenhouse gas emissions to tackle climate change.

Consideration of additional driving variables, like incoming light and clouds, is particularly critical for identifying potential climate change refugia. These projections agree with past work [32] finding that the central and south Pacific, including parts of French Polynesia, and the central equatorial Pacific, including the Republic of Kiribati's Gilbert Islands, the Phoenix Islands and Line Islands, are regions where coral reefs have the highest likelihood of some cloud protection during future thermal stress. Although these regions are still at risk, and have experienced extensive bleaching events, field evidence does confirm that cloudiness may have reduced coral response to past thermal stress events [28,31]. Coral bleaching is often associated with extreme ENSO conditions, the enhanced convective activity in these parts of the Pacific, associated with anomalously warm SSTs, also drive cumulus cloud development [64]. An additional consideration, not included in this study, is that light reaching the coral surface can also be influenced by turbidity which increases light attenuation in the water column [65]. A study based on present-day turbidity concluded that parts of the Coral Triangle, Northern Great Barrier Reef, or some Indian Ocean reefs in Kenya and Tanzania may receive protection from thermal stress [66]. Notably, the potential refugia identified in these models incorporating light differ from those identified in studies only employing thermal stress [39,61].

This analysis provides the first assessment on how the interaction of thermal stress and solar radiation could influence the response of coral reefs at regional and global scales to climate change. Although output from only one ESM was employed to test the hypothesis that including cloudiness would alter future bleaching projections, the similarity between the results using observed vs. model projected cloudiness suggests that the simulated influence of clouds on bleaching projections would be broadly similar with other models. In reality, at the

local level, the effect of clouds on bleaching likelihood will depend on factors like cloud height, cloud composition, and light attenuation in the water column, which vary at finer spatial resolution than models can simulate. The negative feedback whereby high SST can enhance convection and low-level cloudiness, which then reduces downward short-wave radiation, may protect some low latitude reefs, as has been observed in Kiribati [28]. Further analyses incorporating cloud types, temperatures, height, and radiative properties for different regions would unveil fine-tuned responses of corals due to thermal stress and cloudiness. Performing an analysis using fine-scale variability of cloud type and other properties could be done as a case study in a location with high resolution bleaching severity data (e.g., the Mesoamerican Barrier Reef System or the Great Barrier Reef). Notwithstanding, while a limitation of this research is that cloud properties (like mentioned above) were not considered our findings broadly show that clouds may spare some coral reefs from dangerously frequent bleaching conditions in the near term. Even with the mitigating effect of clouds, this study finds that coral reefs remain under existential threat in the long-term without sharp reductions in greenhouse gas emissions.

Supporting information

S1 Text.

(PDF)

Acknowledgments

The authors thank Alex Tso and Alejandra Virgen-Urcelay for their assistance in developing the coral bleaching database. We also specifically thank Mark Eakin and Denise Devotta of NOAA Coral Reef Watch for contributing data for the 2014–2016 global coral bleaching event to the database, and William Skirving of NOAA Coral Reef Watch for assistance with the CoralTemp data. We thank John Dunne and Peter Kalmus for helpful insights in developing the research. We also thank Andrés Cisneros-Montemayor and Xinru Li for their comments and suggestions.

Author Contributions

Conceptualization: Pedro C. González-Espínosa, Simon D. Donner.

Data curation: Pedro C. González-Espínosa.

Formal analysis: Pedro C. González-Espínosa.

Methodology: Pedro C. González-Espínosa.

Supervision: Simon D. Donner.

Writing – original draft: Pedro C. González-Espínosa, Simon D. Donner.

Writing – review & editing: Simon D. Donner.

References

1. Hoegh-Guldberg O, Kennedy EV, Beyer HL, McClenen C, Possingham HP. Securing a long-term future for coral reefs. *Trends Ecol Evol* [Internet]. 2018; 33(12):936–44. Available from: <https://doi.org/10.1016/j.tree.2018.09.006> PMID: 30385077
2. Hughes TP, Kerry JT, Álvarez-Noriega M, Álvarez-Romero JG, Anderson KD, Baird AH, et al. Global warming and recurrent mass bleaching of corals. *Nature* [Internet]. 2017; 543(7645):373–7. Available from: <https://doi.org/10.1038/nature21707> PMID: 28300113

3. Yellowlees D, Rees TAV, Leggat W. Metabolic interactions between algal symbionts and invertebrate hosts. *Plant Cell Environ* [Internet]. 2008; 31(5):679–94. Available from: <https://doi.org/10.1111/j.1365-3040.2008.01802.x> PMID: 18315536
4. Glynn PW, D'Croz L. Experimental evidence for high temperature stress as the cause of El Niño-coincident coral mortality. *Coral Reefs* [Internet]. 1990; 8(4):181–91. Available from: <http://dx.doi.org/10.1007/bf00265009>.
5. Heron SF, Maynard JA, van Hooidonk R, Eakin CM. Warming trends and bleaching stress of the world's coral reefs 1985–2012. *Sci Rep* [Internet]. 2016; 6(1). Available from: <https://doi.org/10.1038/srep38402> PMID: 27922080
6. Donner SD, Rickbeil GJM, Heron SF. A new, high-resolution global mass coral bleaching database. *PLoS One* [Internet]. 2017; 12(4):e0175490. Available from: <https://doi.org/10.1371/journal.pone.0175490> PMID: 28445534
7. Frieler K, Meinshausen M, Golly A, Mengel M, Lebek K, Donner SD, et al. Limiting global warming to 2°C is unlikely to save most coral reefs. *Nat Clim Chang* [Internet]. 2013; 3(2):165–70. Available from: <http://dx.doi.org/10.1038/nclimate1674>.
8. Schleussner C-F, Lissner TK, Fischer EM, Wohland J, Perrette M, Golly A, et al. Differential climate impacts for policy-relevant limits to global warming: the case of 1.5°C and 2°C. *Earth Syst Dyn* [Internet]. 2016; 7(2):327–51. Available from: <http://dx.doi.org/10.5194/esd-7-327-2016>.
9. McClanahan TR, Darling ES, Maina JM, Muthiga NA, D'agata S, Jupiter SD, et al. Temperature patterns and mechanisms influencing coral bleaching during the 2016 El Niño. *Nat Clim Chang* [Internet]. 2019; 9(11):845–51. Available from: <http://dx.doi.org/10.1038/s41558-019-0576-8>.
10. Sully S, Burkepile DE, Donovan MK, Hodgson G, van Woesik R. A global analysis of coral bleaching over the past two decades. *Nat Commun* [Internet]. 2019; 10(1):1264. Available from: <https://doi.org/10.1038/s41467-019-09238-2> PMID: 30894534
11. González-Espínosa PC, Donner SD. Predicting cold-water bleaching in corals: role of temperature, and potential integration of light exposure. *Mar Ecol Prog Ser* [Internet]. 2020; 642:133–46. Available from: <http://dx.doi.org/10.3354/meps13336>.
12. Ban SS, Graham NAJ, Connolly SR. Evidence for multiple stressor interactions and effects on coral reefs. *Glob Chang Biol* [Internet]. 2014; 20(3):681–97. Available from: <https://doi.org/10.1111/gcb.12453> PMID: 24166756
13. Roth MS. The engine of the reef: photobiology of the coral–algal symbiosis. *Front Microbiol* [Internet]. 2014; 5:422. Available from: <https://doi.org/10.3389/fmicb.2014.00422> PMID: 25202301
14. Suggett DJ, Smith DJ. Coral bleaching patterns are the outcome of complex biological and environmental networking. *Glob Chang Biol* [Internet]. 2020; 26(1):68–79. Available from: <https://doi.org/10.1111/gcb.14871> PMID: 31618499
15. Fitt W, Brown B, Warner M, Dunne R. Coral bleaching: interpretation of thermal tolerance limits and thermal thresholds in tropical corals. *Coral Reefs* [Internet]. 2001; 20(1):51–65. Available from: <http://dx.doi.org/10.1007/s003380100146>.
16. Lesser MP. Experimental biology of coral reef ecosystems. *J Exp Mar Bio Ecol* [Internet]. 2004; 300(1–2):217–52. Available from: <http://dx.doi.org/10.1016/j.jembe.2003.12.027>.
17. DiPerna S, Hoogenboom M, Noonan S, Fabricius K. Effects of variability in daily light integrals on the photophysiology of the corals *Pachyseris speciosa* and *Acropora millepora*. *PLoS One* [Internet]. 2018; 13(9):e0203882. Available from: <https://doi.org/10.1371/journal.pone.0203882> PMID: 30240397
18. Iluz D, Dubinsky Z. Coral photobiology: new light on old views. *Zoology (Jena)* [Internet]. 2015; 118(2):71–8. Available from: <https://doi.org/10.1016/j.zool.2014.08.003> PMID: 25467066
19. Takahashi S, Nakamura T, Sakamizu M, van Woesik R, Yamasaki H. Repair machinery of symbiotic photosynthesis as the primary target of heat stress for reef-building corals. *Plant Cell Physiol* [Internet]. 2004; 45(2):251–5. Available from: <https://doi.org/10.1093/pcp/pch028> PMID: 14988497
20. Weis VM. Cellular mechanisms of Cnidarian bleaching: stress causes the collapse of symbiosis. *J Exp Biol* [Internet]. 2008; 211(Pt 19):3059–66. Available from: <https://doi.org/10.1242/jeb.009597> PMID: 18805804
21. Smith DJ, Suggett DJ, Baker NR. Is photoinhibition of zooxanthellae photosynthesis the primary cause of thermal bleaching in corals? *Glob Chang Biol* [Internet]. 2005; 11(1):1–11. Available from: <http://dx.doi.org/10.1111/j.1529-8817.2003.00895.x>.
22. Enríquez S, Méndez ER, -Prieto RI. Multiple scattering on coral skeletons enhances light absorption by symbiotic algae. *Limnol Oceanogr* [Internet]. 2005; 50(4):1025–32. Available from: <http://dx.doi.org/10.4319/lo.2005.50.4.1025>.
23. Stambler N, Dubinsky Z. (2004). Stress effects on metabolism and photosynthesis of hermatypic corals. In: *Coral Health and Disease*. Berlin, Heidelberg: Springer Berlin Heidelberg; 2004. p. 195–215.

24. McCloskey LR, Muscatine L. Production and respiration in the Red Sea coral *Stylophora pistillata* as a function of depth. *Proc R Soc Lond* [Internet]. 1984; 222(1227):215–30. Available from: <http://dx.doi.org/10.1098/rspb.1984.0060>.
25. Baker AC. Flexibility and specificity in coral-algal symbiosis: Diversity, ecology, and biogeography of *Symbiodinium*. *Annu Rev Ecol Evol Syst* [Internet]. 2003; 34(1):661–89. Available from: <http://dx.doi.org/10.1146/annurev.ecolsys.34.011802.132417>.
26. Iglesias-Prieto R, Beltrán VH, LaJeunesse TC, Reyes-Bonilla H, Thomé PE. Different algal symbionts explain the vertical distribution of dominant reef corals in the eastern Pacific. *Proc Biol Sci* [Internet]. 2004; 271(1549):1757–63. Available from: <https://doi.org/10.1098/rspb.2004.2757> PMID: 15306298
27. Hill R, Larkum AWD, Prásil O, Kramer DM, Szabó M, Kumar V, et al. Light-induced dissociation of antenna complexes in the symbionts of scleractinian corals correlates with sensitivity to coral bleaching. *Coral Reefs* [Internet]. 2012; 31(4):963–75. Available from: <http://dx.doi.org/10.1007/s00338-012-0914-z>.
28. Donner SD, Carilli J. Resilience of Central Pacific reefs subject to frequent heat stress and human disturbance. *Sci Rep* [Internet]. 2019; 9(1):3484. Available from: <https://doi.org/10.1038/s41598-019-40150-3> PMID: 30837608
29. Jones G, Curran M, Swan H, Deschaseaux E. Dimethylsulfide and coral bleaching: Links to solar radiation, low level cloud and the regulation of seawater temperatures and climate in the great barrier reef. *Am J Clim Change* [Internet]. 2017; 06(02):328–59. Available from: <http://dx.doi.org/10.4236/ajcc.2017.62017>.
30. Leahy SM, Kingsford MJ, Steinberg CR. Do clouds save the great barrier reef? satellite imagery elucidates the cloud-SST relationship at the local scale. *PLoS One* [Internet]. 2013; 8(7):e70400. Available from: <https://doi.org/10.1371/journal.pone.0070400> PMID: 23894649
31. Mumby PJ, Chisholm JRM, Edwards AL, Andreouet S, Jaubert J. Cloudy weather may have saved Society Island reef corals during the 1998 ENSO event. *Mar Ecol Prog Ser* [Internet]. 2001; 222:209–16. Available from: <http://dx.doi.org/10.3354/meps222209>.
32. Gonzalez-Espinosa PC, Donner SD. Cloudiness reduces the bleaching response of coral reefs exposed to heat stress. *Glob Chang Biol* [Internet]. 2021; 27(15):3474–86. Available from: <https://doi.org/10.1111/gcb.15676> PMID: 33964101
33. Logan CA, Dunne JP, Ryan JS, Baskett ML, Donner SD. Quantifying global potential for coral evolutionary response to climate change. *Nat Clim Chang* [Internet]. 2021; 11(6):537–42. Available from: <http://dx.doi.org/10.1038/s41558-021-01037-2>.
34. McManus LC, Vasconcelos VV, Levin SA, Thompson DM, Kleypas JA, Castruccio FS, et al. Extreme temperature events will drive coral decline in the Coral Triangle. *Glob Chang Biol* [Internet]. 2019; 26(4):2120–33. Available from: <https://doi.org/10.1111/gcb.14972> PMID: 31883173
35. McManus LC, Forrest DL, Tekwa EW, Schindler DE, Colton MA, Webster MM, et al. Evolution and connectivity influence the persistence and recovery of coral reefs under climate change in the Caribbean, Southwest Pacific, and Coral Triangle. *Glob Chang Biol* [Internet]. 2021; 27(18):4307–21. Available from: <https://doi.org/10.1111/gcb.15725> PMID: 34106494
36. Urcelay A, Donner S. High resolution global mass coral bleaching dataset Version 2.0. Zenodo; 2022.
37. Skirving W, Marsh B, De La Cour J, Liu G, Harris A, Maturi E, et al. CoralTemp and the Coral Reef Watch Coral Bleaching Heat Stress product suite version 3.1. *Remote Sens (Basel)* [Internet]. 2020; 12(23):3856. Available from: <http://dx.doi.org/10.3390/rs12233856>.
38. van Hooidonk R, Maynard JA, Planes S. Temporary refugia for coral reefs in a warming world. *Nat Clim Chang* [Internet]. 2013; 3(5):508–11. Available from: <http://dx.doi.org/10.1038/nclimate1829>.
39. Donner SD. Coping with commitment: projected thermal stress on coral reefs under different future scenarios. *PLoS One* [Internet]. 2009; 4(6):e5712. Available from: <https://doi.org/10.1371/journal.pone.0005712> PMID: 19492060
40. Logan CA, Dunne JP, Eakin CM, Donner SD. Incorporating adaptive responses into future projections of coral bleaching. *Glob Chang Biol* [Internet]. 2014; 20(1):125–39. Available from: <https://doi.org/10.1111/gcb.12390> PMID: 24038982
41. Donner SD, Skirving WJ, Little CM, Oppenheimer M, Hoegh-Guldberg O. Global assessment of coral bleaching and required rates of adaptation under climate change. *Glob Chang Biol* [Internet]. 2005; 11(12):2251–65. Available from: <https://doi.org/10.1111/j.1365-2486.2005.01073.x> PMID: 34991281
42. Donner SD. An evaluation of the effect of recent temperature variability on the prediction of coral bleaching events. *Ecol Appl* [Internet]. 2011; 21(5):1718–30. Available from: <https://doi.org/10.1890/10-0107.1> PMID: 21830713
43. Loeb NG, Doelling DR, Wang H, Su W, Nguyen C, Corbett JG, et al. Clouds and the Earth's Radiant Energy System (CERES) Energy Balanced and Filled (EBAF) top-of-atmosphere (TOA) Edition-4.0

data product. *J Clim* [Internet]. 2018 [cited 2022 Jul 4]; 31(2):895–918. Available from: <https://journals.ametsoc.org/view/journals/clip/31/2/jcli-d-17-0208.1.xml>.

44. Kato S, Rose FG, Rutan DA, Thorsen TJ, Loeb NG, Doelling DR, et al. Surface irradiances of Edition 4.0 Clouds and the Earth's Radiant Energy System (CERES) Energy Balanced and Filled (EBAF) data product. *J Clim* [Internet]. 2018 [cited 2022 Jul 4]; 31(11):4501–27. Available from: <https://journals.ametsoc.org/view/journals/clip/31/11/jcli-d-17-0523.1.xml>.

45. Kuznetsova A, Brockhoff PB, Christensen RHB. LmerTest package: Tests in linear mixed effects models. *J Stat Softw* [Internet]. 2017; 82(13). Available from: <http://dx.doi.org/10.18637/jss.v082.i13>.

46. Cohen J. A coefficient of agreement for nominal scales. *Educ Psychol Meas* [Internet]. 1960; 20(1):37–46. Available from: <http://dx.doi.org/10.1177/001316446002000104>.

47. Ocean data viewer [Internet]. UneP-wcmc.org. [cited 2022 Jul 4]. Available from: <http://data.unep-wcmc.org/datasets/1>.

48. Meehl GA, Senior CA, Eyring V, Flato G, Lamarque J-F, Stouffer RJ, et al. Context for interpreting equilibrium climate sensitivity and transient climate response from the CMIP6 Earth system models. *Sci Adv* [Internet]. 2020; 6(26):eaba1981. Available from: <https://doi.org/10.1126/sciadv.aba1981> PMID: 32637602

49. Navarro-Racines C, Tarapues J, Thornton P, Jarvis A, Ramirez-Villegas J. High-resolution and bias-corrected CMIP5 projections for climate change impact assessments. *Sci Data* [Internet]. 2020; 7(1):7. Available from: <https://doi.org/10.1038/s41597-019-0343-8> PMID: 31959765

50. Cesana G, Storelvmo T. Improving climate projections by understanding how cloud phase affects radiation. *J Geophys Res* [Internet]. 2017; 122(8):4594–9. Available from: <http://dx.doi.org/10.1002/2017jd026927>.

51. Berkelmans R, van Oppen MJH. The role of zooxanthellae in the thermal tolerance of corals: a “nugget of hope” for coral reefs in an era of climate change. *Proc Biol Sci* [Internet]. 2006; 273(1599):2305–12. Available from: <https://doi.org/10.1098/rspb.2006.3567> PMID: 16928632

52. Buerger P, Alvarez-Roa C, Coppin CW, Pearce SL, Chakravarti LJ, Oakeshott JG, et al. Heat-evolved microalgal symbionts increase coral bleaching tolerance. *Sci Adv* [Internet]. 2020; 6(20):eaba2498. Available from: <https://doi.org/10.1126/sciadv.aba2498> PMID: 32426508

53. Császár NBM, Ralph PJ, Frankham R, Berkelmans R, van Oppen MJH. Estimating the potential for adaptation of corals to climate warming. *PLoS One* [Internet]. 2010; 5(3):e9751. Available from: <https://doi.org/10.1371/journal.pone.0009751> PMID: 20305781

54. Howells EJ, Beltran VH, Larsen NW, Bay LK, Willis BL, van Oppen MJH. Coral thermal tolerance shaped by local adaptation of photosymbionts. *Nat Clim Chang* [Internet]. 2012; 2(2):116–20. Available from: <http://dx.doi.org/10.1038/nclimate1330>.

55. Maina J, Venus V, McClanahan TR, Ateweberhan M. Modelling susceptibility of coral reefs to environmental stress using remote sensing data and GIS models. *Ecol Model* [Internet]. 2008; 212(3–4):180–99. Available from: <http://dx.doi.org/10.1016/j.ecolmodel.2007.10.033>.

56. McClanahan TR, Maina JM, Darling ES, Guillaume MMM, Muthiga NA, D’agata S, et al. Large geographic variability in the resistance of corals to thermal stress. *Glob Ecol Biogeogr* [Internet]. 2020; 29(12):2229–47. Available from: <http://dx.doi.org/10.1111/geb.13191>.

57. McClanahan TR, Azali MK. Environmental variability and threshold model’s predictions for coral reefs. *Front Mar Sci* [Internet]. 2021; 8. Available from: <http://dx.doi.org/10.3389/fmars.2021.778121>.

58. Cooley S, Schoeman D, Bopp L, Boyd P, Donner S, Ghebrehiwet DY, et al. Oceans and Coastal Ecosystems and Their Services. In: *Change Climate 2022: Impacts, adaptation and vulnerability*. Contribution of the WGII to the 6th assessment report of the intergovernmental panel on climate change. Cambridge University Press. Available from: https://www.ipcc.ch/report/ar6/wg2/downloads/report/IPCC_AR6_WGII_Chapter03.pdf.

59. Hoegh-Guldberg O, Jacob D, Taylor M, Bind M, Brown S, Camilloni I et al. Impacts of 1.5°C global warming on natural and human systems. In: *Global Warming of 1.5°C: An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty*. IPCC. 2018.

60. Hoegh-Guldberg O. Climate change, coral bleaching and the future of the world’s coral reefs. *Mar Freshw Res* [Internet]. 1999; Available from: <http://dx.doi.org/10.1071/mf99078>.

61. Dixon AM, Forster PM, Heron SF, Stoner AMK, Beger M. Future loss of local-scale thermal refugia in coral reef ecosystems. *PLOS Clim* [Internet]. 2022; 1(2):e0000004. Available from: <http://dx.doi.org/10.1371/journal.pclm.0000004>.

62. National Academies of Sciences, Engineering, and Medicine, Division on Earth and Life Studies, Board on Life Sciences, Ocean Studies Board, Committee on Interventions to Increase the Resilience of Coral

Reefs. A research review of interventions to increase the persistence and resilience of coral reefs. Washington, D.C., DC: National Academies Press; 2019.

- 63. Teneva L, Karnauskas M, Logan CA, Bianucci L, Currie JC, Kleypas JA. Predicting coral bleaching hot-spots: the role of regional variability in thermal stress and potential adaptation rates. *Coral Reefs* [Internet]. 2012; 31(1):1–12. Available from: <http://dx.doi.org/10.1007/s00338-011-0812-9>.
- 64. Park S, Leovy CB. Marine low-cloud anomalies associated with ENSO. *J Clim* [Internet]. 2004; 17(17):3448–69. Available from: <http://www.jstor.org/stable/26251880>.
- 65. Cacciapaglia C, van Woesik R. Climate-change refugia: shading reef corals by turbidity. *Glob Chang Biol* [Internet]. 2016; 22(3):1145–54. Available from: <https://doi.org/10.1111/gcb.13166> PMID: 26695523
- 66. Sully S, van Woesik R. Turbid reefs moderate coral bleaching under climate-related temperature stress. *Glob Chang Biol* [Internet]. 2020; 26(3):1367–73. Available from: <https://doi.org/10.1111/gcb.14948> PMID: 31912964