Coral Reefs
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REPORT

Effects of modeled tropical sea surface temperature variability on coral reef bleaching predictions

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Abstract Future widespread coral bleaching and subsequent mortality has been projected using sea surface temperature (SST) data derived from global, coupled ocean–atmosphere general circulation models (GCMs). While these models possess fidelity in reproducing many aspects of climate, they vary in their ability to correctly capture such parameters as the tropical ocean seasonal cycle and El Niño Southern Oscillation (ENSO) variability. Such weaknesses most likely reduce the accuracy of predicting coral bleaching, but little attention has been paid to the important issue of understanding potential errors and biases, the interaction of these biases with trends, and their propagation in predictions. To analyze the relative importance of various types of model errors and biases in predicting coral bleaching, various intra- and inter-annual frequency bands of observed SSTs were replaced with those frequencies from 24 GCMs 20th century simulations included in the Intergovernmental Panel on Climate Change (IPCC) 4th assessment report. Subsequent thermal stress was calculated and predictions of bleaching were made. These predictions were compared with observations of coral bleaching in the period 1982–2007 to calculate accuracy using an objective measure of forecast quality, the Peirce skill score (PSS). Major findings are that: (1) predictions are most sensitive to the seasonal cycle and inter-annual variability in the ENSO 24–60 months frequency band and (2) because models tend to understate the seasonal cycle at reef locations, they systematically underestimate future bleaching. The methodology we describe can be used to improve the accuracy of bleaching predictions by characterizing the errors and uncertainties involved in the predictions.

Keywords Coral bleaching · Climate change · Coupled ocean–atmosphere general circulation models

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Introduction

Tropical corals live in conditions close to their upper thermal limit (Hoegh-Guldberg 1999). When this threshold is crossed, bleaching can occur. Bleaching is the whitening of reef-building corals due to a reduction in their symbiotic dinoflagellate zooxanthellae and/or loss of the pigments in the symbionts (Brown 1997). Bleaching can cause coral mortality, and reduce growth, coral cover, species diversity, and disease resistance (Hoegh-Guldberg 1999; Fitt et al. 2001). Although other causes for coral bleaching exist, bleaching due to anomalous high sea surface temperatures (SSTs) is of greatest concern.

Mass bleaching, the whitening of entire reef tracts or regions, such as occurred in 1998 and 2005, is attributed to anthropogenic climate change superimposed on natural variability (Donner et al. 2007). Climate change is projected to cause bleaching to occur annually on reefs all over the globe within 20–40 years (Hoegh-Guldberg 1999; Donner et al. 2005), and in the Caribbean, biannually or more frequent by 2020 in a business as usual scenario (Donner et al.

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2007). Threats to coral reefs are more complex than just bleaching. Ocean acidification (Kleypas et al. 1999; Silverman et al. 2007), another product of anthropogenic climate change, reduces calcification rates and threatens coral reef health. Local stressors, including pollution and fishing, damage reefs. All these threats interact with the resilience of reefs and their ability to recover from bleaching to shape the ecosystems future. Here, we limit this study on predicting mass bleaching and we aim to evaluate the importance of various intra- and inter-annual frequency bands on coral bleaching. We do this by analyzing data and models utilizing a band-pass time series analysis approach. This will elucidate errors in models and enable improvements in coral bleaching predictions.

Accurate coral bleaching forecasts can aid managers of marine protected areas to decide where to focus reef management efforts (Marshall and Schuttenberg 2006; McClanahan et al. 2007). Accurate forecasts are also necessary to assess what levels of greenhouse gases prevent dangerous, perhaps irreversible, climate change impacts for corals (Reaser et al. 2000; Smith et al. 2009) and what levels allow coral reef ecosystems to adapt to climate change, as required by the 2nd article of the United Nations Framework Convention on Climate Change (Oppenheimer and Petsonk 2005).

Predictions of bleaching frequency have been made using coupled ocean–atmosphere general circulation model (GCM) SSTs (Hoegh-Guldberg 1999; Sheppard 2003; Donner et al. 2005, 2007; Hoeke et al. 2011). GCMs produce projections of future climatic conditions based on greenhouse gas emission scenarios that represent different emission paths. These models have, besides their varying "accuracy" (or "skill") in simulating such parameters as the tropical ocean seasonal cycle and El Niño Southern Oscillation (ENSO) variability, other deficiencies. As we describe below, although forecasts abound, little effort has gone into quantitatively assessing and understanding the factors that influence predictive "skill".

Ultimately, the goal of this work is to objectively identify the major sources of error in the climate models that most impact the skill and quality of bleaching forecasts, so that the models will be improved. This is an extension of our prior work (van Hooidonk and Huber 2009a), in which the skill of bleaching predictive techniques was systematically analyzed for the first time. There are several predictions and hind-casts of coral bleaching in the literature. They range from simple fixed thermal thresholds (Hoegh-Guldberg 1999; Sheppard 2003; Sheppard and Rioja-Nieto 2005) and accumulative stress indexes (Gleeson and Strong 1995; Goreau and Hayes 1994; Donner et al. 2005; Donner 2009) to complex multivariate models (Maina et al. 2008). These predictions depict a range of possible futures, some of the methods and results are highlighted here.

In the seminal work of Hoegh-Guldberg (1999), fixed local thresholds were established by analyzing literature reports on bleaching. These thresholds were used in combination with GCM output to predict future bleaching. The annual mean SST of GCMs in most models differs from observations; this bias prevents comparison between a measured climatology and predicted SSTs. Therefore, the mean was corrected in this and some other studies. Data were used from older models, the ECHAM3/LCG, ECHAM4/OPYC3a, and the CSIRO-DAR model. One midrange Intergovernmental Panel on Climate Change (IPCC) greenhouse gas emission scenario, IS92a, was used. In this scenario, effective CO_2 concentration increases at 1% per year after 1990. These older generation models are characterized by a coarse spatial resolution, some as low as $5.6° \times 5.6°$. At this resolution, one grid cell, or pixel, in the tropics is over 600 km wide. More importantly, the ECHAM3/LCG model does not reproduce ENSO variability sufficiently (Voss et al. 1998). Underestimating this variability reduces the number of projected El Niño events. Because El Niño events cause anomalously warm SSTs at reef locations, they can cause coral bleaching (Hoegh-Guldberg 1999; Gill et al. 2006). Thus, underrating ENSO variability could cause predictions of bleaching to shift to later dates. Still, this study predicts yearly bleaching on all studied locations by 2030.

In Donner et al. (2005), bleaching was projected for all global reef locations by calculating degree heating months (DHMs) from the UK Meteorological Office HadCM3 and National Center for Atmospheric Research (NCAR) PCM1 GCMs. This was done for two emission trajectories, the Special Report on Emissions Scenarios (SRES) B2 and A2 emissions scenarios. Based on an assumed global bleaching threshold of one DHM, biennial bleaching is projected for 95–98% of all reefs by 2050–2059 in the A2 scenario. More recently, Donner (2009) projected bleaching using DHMs calculated from two other models (Geophysical Fluid Dynamics Laboratory (GFDL) models CM2.0 and CM2.1) and five emission scenarios. These scenarios range from a commitment scenario, in which greenhouse gas concentrations are kept at year 2000 levels, to the fossil fuel–intensive A2 and A1F1 scenarios. In the A1B scenario, severe bleaching in all reefs globally is projected at least once per 5 years around 2035.

In three studies that project future reef health, the annual mean SST was corrected and the amplitude of the annual cycle scaled to that of observations (Sheppard 2003; Sheppard and Rioja-Nieto 2005; Hoeke et al. 2011). In Hoeke et al. (2011), the SSTs from the SRES A1B scenario of 17 GCMs were used as input data for a coral growth and mortality model predicting changes in coral cover in the Hawaiian archipelago for the period 2000–2099.

Uncertainties associated with SST variability in GCMs

It is well established that coupled GCMs have different transient and equilibrium sensitivities of temperature to increases in greenhouse gas concentrations, and consequently, different trends in mean values over the twentieth century and beyond (Meehl et al. 2007). They also differ in their abilities to correctly capture other aspects of SST over the observational era. There is, for example, considerable difference in the amplitude of the SST seasonal cycle (Covey et al. 2000; Wu et al. 2008), the representation of the inter-tropical convergence zone (Lin 2007a), and the El Niño and Southern Oscillation (ENSO) variability (Lin 2007b), amplitude, period, and spatial patterns (Guilyardi 2006; Guilyardi et al. 2009). These differences can in part be explained by an unresolved theoretical explanation of ENSO dynamics. The range of ENSO variabilities in models extends from regular bi-annual ENSO events to variability close to the observed 2–7 years periodicity (Guilyardi et al. 2009). Another bias, evident in many models, is the lack of phase locking. El Niño and La Niña anomalies are largest in the boreal winter, and often models show little or no links to the seasonal cycle, or show El Niño and La Niña anomalies in the wrong part of the annual cycle (Guilyardi et al. 2009). Current GCMs do not show agreement in the sign of change in ENSO variability (Vecchi and Wittenberg 2010) in observations of the 20th century or in predictions. Because ENSO events can cause tropical SST anomalies conductive to bleaching (Lough 2000; Gill et al. 2006; Eakin et al. 2009), differences in projections of ENSO can have considerable impacts on predictions of coral bleaching.

The mass coral bleaching of interest in this study arises from crossing an upper threshold temperature, and hence, accurate prediction of bleaching events is sensitive to changes in the annual mean and changes in extremes of temperature. In the unperturbed climate, the upper threshold must only rarely be crossed; natural thermal bleaching events must arise upon the superposition of a rare unusually strong low-frequency event (such as an El Niño event) on top of seasonal temperature maxima (summer). This phenomenon, where the combination of two signals results in a stronger signal than either one alone, is known as constructive interference. Thus, in the anthropogenically perturbed state, in which trends in mean temperature are well established, accurately predicting bleaching over the next century must involve accurate predictions of the constructive interference of the trend in the mean and any trends in the modes of seasonal and inter-annual to multi-decadal variability.

Consequently, the problem of predicting thermally induced coral reef bleaching can be decomposed into discrete components: first, having an accurate climatology and a thermal threshold above which bleaching is projected to occur; second, long-term (century) trends in annual mean temperatures averaged over the whole tropics; third, predicting the changes in tropical temperature seasonality on long-time scales (the long-term trend in seasonality); fourth, predicting the spatial pattern of these trends; and fifth, predicting the inter-annual, decadal, and finally multi-decadal variability around these trends.

A failure in any of these components and in their relative phasing leads to invalid forecasts. As an example, a model that correctly captures every aspect of climate, with only a seasonal cycle that has an amplitude smaller than observations, may predict bleaching many decades after it should occur, because the model never crosses the bleaching threshold. A model, with overly strong multi-decadal variability as the only deficiency, might forecast bleaching earlier in the century, followed by an incorrect period of no or little bleaching, followed by overly frequent bleaching.

These biases could potentially be accounted for, but bias removal requires an in-depth analysis of the different modes of variability and of trend evolution. This has never been attempted in studies that predict bleaching. To summarize, GCMs are being used to project future bleaching, but the influence of model error and biases on the skill and timing of predictions is unknown. What has been done is bias removal in terms of mean temperature at each location, and in three cases, (Sheppard 2003; Sheppard and Rioja-Nieto 2005; Hoeke et al. 2011) also a correction of the amplitude of the annual cycle has been made. The interaction of all the other modes of variability on bleaching prediction remains largely uncharted territory.

The goal of this study is to evaluate the importance of various modes of variability on predicting coral bleaching. We evaluate modes ranging from the 3 months harmonic to events with a 5 years periodicity. GCM SSTs were available only as monthly data, and the observed SSTs were from a data set for the period 1982 to present. These data sets provide an upper (5 years) and lower limit (3 months) for the frequencies analyzed. Variability with periodicities shorter than 3 months is probably of limited importance for predicting bleaching due to the autoregressive nature of tropical SSTs. Decadal and lower frequency modes of variability cannot be analyzed in this study due to the length of the observed SST time series.

To assess the importance of various modes, the skill of bleaching predictions for 24 GCMs in the IPCC 4th assessment report was quantified. First, certain frequency bands of observed SSTs, such as the annual cycle, were replaced with those bands from GCMs, and then, thermal stress was calculated and subsequent predictive quality assessed. Here, it is assumed that all reported bleaching occurred due to thermal stress, and that, corals do not adapt to temperature stress by shuffling of their symbionts or any other mechanism. This assumption is made knowing that there is debate on if and if so how much shuffling of symbionts occurs in the wild (Berkelmans and van Oppen 2006; Hoegh-Guldberg et al. 2002; Hoegh-Guldberg 2005; Goulet 2006). Coral mortality following a bleaching event varies with species (Loya et al. 2001) and locations (Brown 1997). Together with other factors such as connectivity between reefs (Hughes et al. 2003) and irradiance (Anthony et al. 2007), complex interactions can arise affecting recovery and resilience. The observational data set of coral bleaching used here does not include consistent data on coral mortality. Because of this limitation, we make no statements on subsequent coral mortality and do not include any speculative adaptive capability of the corals.

With better observations of coral reefs, recording bleaching and non-bleaching, and more knowledge on expected rates of adaption, these assumptions and simplifications would not have been necessary. These assumptions are shared weaknesses of most current bleaching predictions.

We show that bleaching forecasts are sensitive to every frequency band, from 3 months to multi-annual. Especially, the annual cycle and ENSO frequency band are vital to getting correct predictions. Lastly, implications for projecting future bleaching events are drawn, and recommendations for predicting bleaching with GCMs are given.

Methods

This study requires having accurate observed SST distributions, SST distributions from coupled general circulation models from 20th century simulations for comparison, modeled SSTs for the coming century for analysis of future impacts, and a database of bleaching observations in order to establish bleaching thresholds and test predictive skill.

Observed SSTs

Observational SST data for the period 1982–2007 were obtained from NOAA Optimal Interpolated SST version 2 data (Reynolds et al. 2002) provided by the NOAA/OAR/ESRL PSD, Boulder, Colorado, USA, from their web site at http://www.esrl.noaa.gov/psd/data/gridded/data.noaa.oisst.v2.html. These SST data are computed weekly at $1^\circ \times 1^\circ$ resolution combining in situ and satellite data. Missing values, such as near-coast pixels, were filled in by nearest-neighbor values derived by solving Poisson's equation via relaxation.

Modeled SSTs from GCMs

SST temperature data were retrieved for the 20C3M and SRES A1B scenarios for each available GCM from the World Climate Research Programme's (WCRP's) Coupled Model Intercomparison Project phase 3 (CMIP3) multi-model data set at http://www.esg.llnl.gov. In the 20C3M scenario, greenhouse gasses increase as observed through the 20th century. This 20th century experiment enables the comparison of observations with modeled SST, and thus characterization of the skill of the GCMs. The individual models do not perfectly resemble observations of SST, but moderate skill has been demonstrated (Lin 2007b; Reifen and Toumi 2009) and they have previously been used in projections for large marine ecosystems (Wang et al. 2010).

The SRES A1B scenario represents a future world of very rapid economic growth, low population growth, and rapid introduction of new and more efficient technology with balanced fossil/non-fossil energy sources. It is a scenario with CO_2 emissions in the middle to high range compared to the other scenarios. For a description of all emissions in this scenario, see Nakićenović and Swart (2000). It has been used to project coral reef futures (Donner et al. 2007; Donner 2009; Baskett et al. 2010; Hoeke et al. 2011). All models were re-gridded to a $1^\circ \times 1^\circ$ resolution using bilinear interpolation. Missing values were filled in by nearest-neighbor values derived from solving Poisson's equation via relaxation. If multiple runs were available for a model, the different members of the ensemble were averaged. For practical reasons, the monthly data were converted to weekly data by selecting for each date in the observed weekly time series the closest value from the GCM data. Thus, each GCM value was repeated for ~ 4 times, and no weekly variability was added.

Creating hybrid observed and GCM SST time series

To estimate the influence of errors in each of the GCMs frequency bands separately, we use hybrids of GCM and observed SST time series. In this way, it was possible to only retain the frequency band of interest from the GCM and use all other frequencies from observations. A hybrid was created by selecting a certain frequency range of the GCMs, such as the annual frequency band. Then this frequency band was subtracted from the observations and the two were combined to create a hybrid time series. This hybrid only differs in the selected frequency band from observations.

To select the frequency band in question, a band-pass filter was used. Band-pass filters remove all data except for a specified frequency band. Here, a Lanczos filter was used with cut-offs at 2 and 4, 5 and 7, 8 and 10, 11 and 13, 16 and 20, and finally 24 and 60 months (Duchon 1979). The 24–60 months frequency is an exception. This band includes El Niño variability, and while some GCMs might accurately simulate El Niño variability and amplitude, the timing of major ENSO events is not aligned with observed events. When the timing of ENSO events is incorrect, mass bleaching episodes will be projected to occur in different years then observed, and thus drastically decrease skill of projections. To circumvent this issue, a different method was employed for the 24–60 months bandwidth. First, the desired 24–60 months band was selected. Then, the variance of this signal was calculated for the GCMs and observations at each location. The ratio between the two variances was multiplied with the 24–60 months signal from the observations. This product of band pass–filtered signal and ratio of variances was then used to replace the 24–60 months bandwidth in the original observations. The resulting hybrid time series for each GCM contain all the characteristics of the observations, and only the 24–60 months variance of each GCM.

To illustrate the effect of the annual cycle on future mass bleaching, the GFDL CM2.1 model SRES A1B scenario run was chosen. The annual cycle of this model was replaced with the annual cycle of each of the other 23 models and that of observations. For the annual cycle from observations, OISST V2 data for the years 1982–2007 were used. All 25 SST time series were mean corrected to the mean of the original model. An overview of the data sources used per experiment is given in Table 1.

Degree heating weeks

To calculate degree heating weeks (DHWs; Gleeson and Strong 1995), the positive anomalies above the climatological maximum expected summertime temperature (MMM) for the previous 12 weekly values were summed up. In this study, the MMM is defined as the warmest monthly temperature from the observed climatology, derived from data for years 1971–2000 (Reynolds et al. 2002). For a more detailed methods description, see van Hooidonk and Huber (2009a). The most important difference from the NOAA method (http://www.osdpd.noaa.gov/PSB/EPS/method.html) is that, here, DHWs start to accumulate as soon as the temperature exceeds the maximum expected summertime temperature. In the NOAA method, DHWs start to accumulate when the temperature reaches at least 1°C above the expected summertime temperature. Compared to the NOAA Coral Reef Watch method, this overestimates DHW values. The method, where only anomalies 1°C above the MMM are used, produces fewer years with DHWs above zero and reduces the skill (see van Hooidonk and Huber 2009a). By keeping the method similar to our previous work, we can reuse the previously reported skill of predictions made with the observations of SST in this study.

Quantifying quality of predictions

The quality of forecasts can be quantified using objective skill scores such as the Peirce skill score (PSS). PSS has been successfully used in quantifying the skill of coral bleaching predictions based on observations of SST (van Hooidonk and Huber 2009a). It uses the frequencies of correct predictions (hits), bleaching events that were not predicted (misses), false alarms, and correct predictions of non-occurrence to calculate a score. This score ranges from −1 to 1, a perfect predictive technique scores 1, random guessing will score 0 (Jolliffe and Stephenson 2003). To get the frequencies of each of these possibilities, predicted bleaching episodes have to be compared to observations of bleaching. An optimal DHW threshold was established for each reef location by comparing historical observed DHW values with observations of bleaching (see van Hooidonk and Huber 2009a). Then, each incidence, where the hybrid time series' maximum yearly DHW value exceeded the

Table 1 Data used in the experiments, observations are from the optimal interpolated sea surface temperature data set (OISST), and the GCMs are the SSTs from the 20th century runs of the coupled ocean–atmosphere general circulation models

Experiment	Data from GCMs	Annual cycle from
3 months (Fig. 4)	2–4 months variability	Observations
6 months (Fig. 4)	5–7 months variability	Observations
9 months (Fig. 4)	8–10 months variability	Observations
12 months (Fig. 4)	11–13 months variability	Annual cycle from each of the GCMs as it is included in the 11–13 months variability
16–20 months (Fig. 4)	16–20 months variability	Observations
24–60 months (Fig. 4)	24–60 months variance	Observations
Annual cycle (Fig. 6)	GFDL CM2.1 model SRES A1B scenario	From each of the GCMs, and for one treatment from observations

optimal DHW threshold at that location, was counted as a predicted bleaching event. These predicted events were compared to observations of bleaching from the period 1982–2007, obtained from http://www.reefbase.org, to calculate the quality of the predictions.

The observational database of coral bleaching is comprised of contributions by individuals. Although a standard form is available, no standardized procedure or global coordinated effort exists to date. Non-bleached reefs are underreported, and bleaching episodes in remote areas might have been missed (van Hooidonk and Huber 2009b). Here, it is assumed that when no records of bleaching exist, no bleaching happened.

Results

SST time series

Spectral analysis comparing observed and modeled tropical SST time series shows that models generally show less variability than observations. The GCMs underestimate the annual and semi-annual frequencies and show a spurious quad-annual variability (Fig. 1a). Time series of SSTs can be considered an autoregressive process, where at a given time, the SST is strongly dependent on the SST of the previous time step. Therefore, SST time series can be considered as “red noise”, and a Markov power spectrum can be used to determine the significance of selected periodicities (Dyer 1971). Averaged overall reef locations, the annual and semi-annual peaks are significant deviations from the 5 to 95% confidence interval of the Markov spectrum. As an example, the result of one of the filtering treatments is shown in Fig. 1b. When only the 11–13 months frequencies of the GCMs were retained, the frequency response is similar to the observations at all frequencies except around the annual cycle.

The filtering treatments resulted in different synthetic time series of SSTs at each location. To provide a concrete example of the effect of filtering, two hybrid time series and observational data are plotted (Fig. 2) for a location in the Caribbean (12.5°N 69°W). This figure contrasts two GCMs with different annual cycles. The filtered SST time series with the 12 months frequency band variability added from the GCMs show that the NCAR PCM1 GCM (Fig. 2a) has a larger amplitude of the seasonal cycle compared to observations, and the IAP FGOALS 1.0G GCM has a seasonal cycle smaller than the observations at this location (Fig. 2b).

Degree heating weeks

After correcting the annual mean SST of GCMs, GCMs with a larger amplitude in annual cycle than observed SSTs will show higher annual maximum SSTs and this results in higher calculated DHWs (Fig. 3a). GCMs that exhibit a lower amplitude of annual cycle, compared to observations, can produce lower DHWs (Fig. 3b). To clarify,

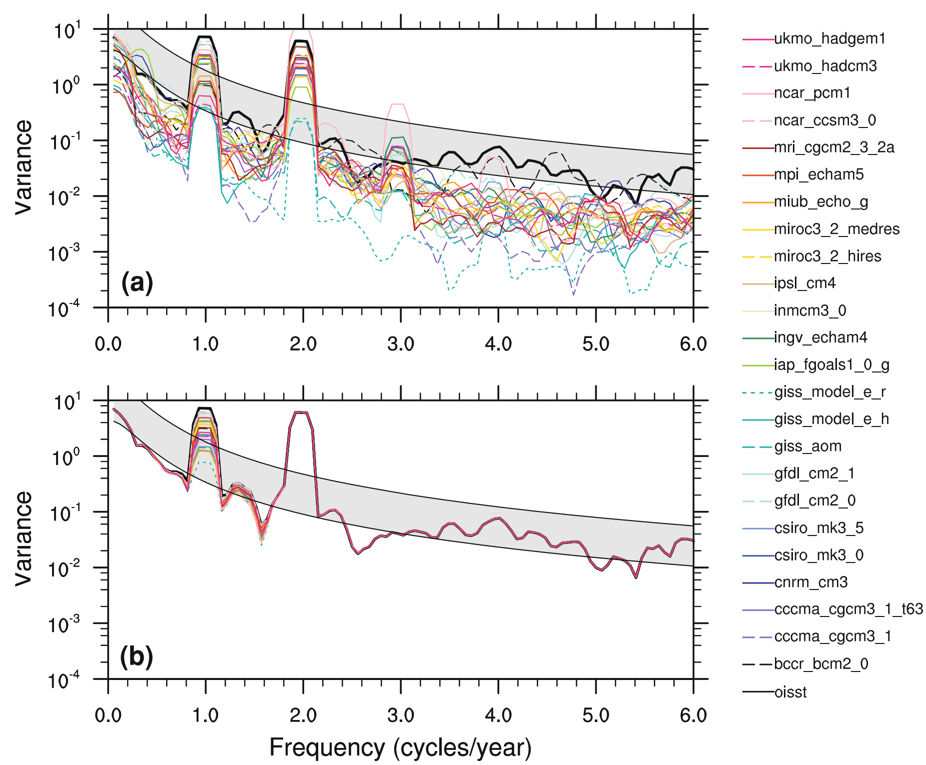

Fig. 1 Frequency spectra of unaltered GCMs and for observations of SST (**a**) and spectra of observations of SST where the frequencies around the annual cycle (11–13 months) were replaced by those frequencies from GCMs (**b**). SST data are averaged over all locations with reefs, and only the period 1983–1999 was used. On the *x*-axis, the frequency is plotted in cycles per year, to the *left* on the axis, lower frequencies are plotted, and frequencies increase to the *right*. The area between the 5 and 95% confidence bounds of the Markov “Red Noise” spectrum of the observations is *shaded gray*

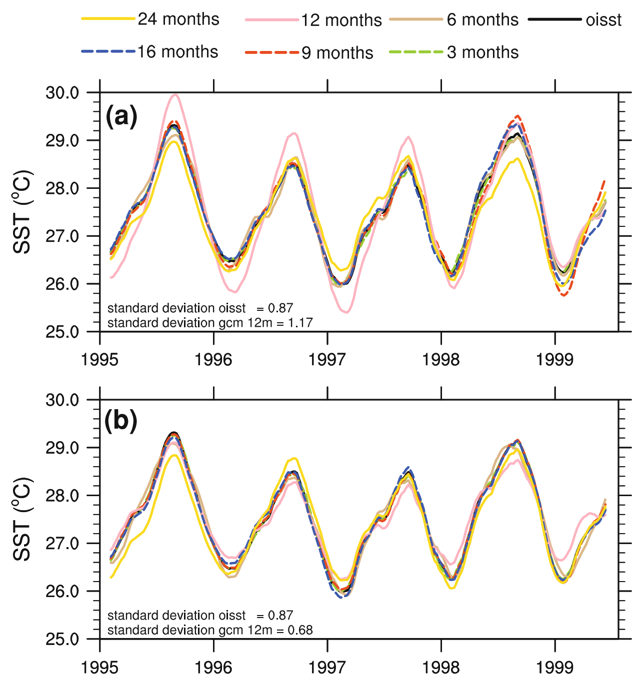

Fig. 2 SSTs from OISST and the five treatments of the NCAR PCM1 (**a**) and IAP FGOALS 1.0 g (**b**) GCMs at 12.5°N 69°W. Data are smoothed with a running average of 12 weeks for clarity

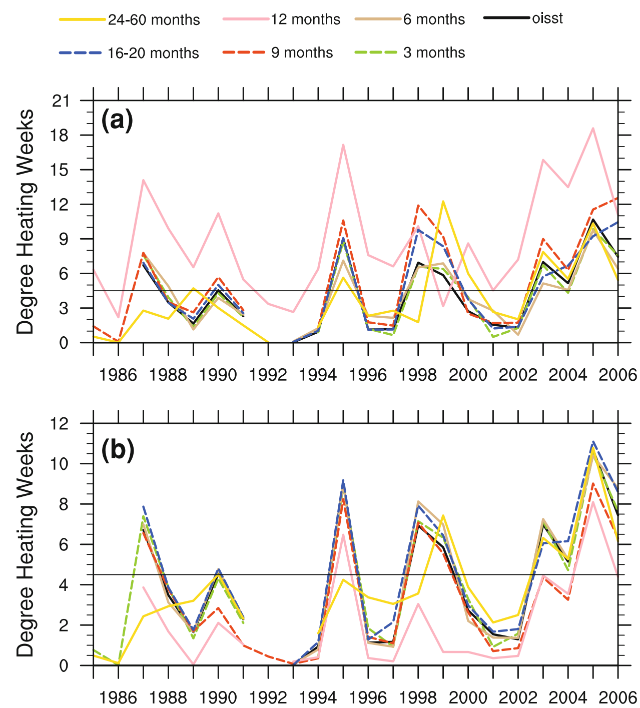

Fig. 3 DHWs from OISST and the six treatments of the NCAR PCM1 (**a**) and GISS AOM (**b**) GCMs for a location in the Caribbean (12.5°N 69°W). The *thin horizontal line* at DHW = 4.5 is the optimal DHW threshold at this location based on historical observed DHWs compared to observations of bleaching at this location

consider the DHWs calculated from the filtered observed SSTs combined with the annual frequency band of the NCAR PCM1 GCM. Because the NCAR PCM1 model has a larger amplitude in seasonal cycle at reef locations, the threshold above which DHWs start to accumulate is crossed more often and more DHWs accumulate (Fig. 3a).

Quality of forecasts in PSS

To quantify the importance of the differences between modeled and observed thermal stress, an objective assessment of predictive skill was made for all the treatments of the GCMs. For all reef locations globally, the average PSS of predictions based on observations of SST is 0.83 (van Hooidonk and Huber 2009a). This is the theoretical maximum value that this methodology can yield for our purposes, i.e., a model that accurately captures every observed detail of SST variability over the 1982–2007 period can be expected to get a maximum PSS of 0.83. Since model predictions obviously differ in many ways from observations, we expect PSS to be reduced. For the treatments where frequency bands around 3, 9, and 16–20 months of the GCMs were used, a small decrease in PSS score can be seen, and the spread between the different GCMs is small relative to the other treatments. This is a small effect, because the dominant modes in SST time series at reef locations are the annual cycle, ENSO, and possibly other low-frequency modes. The largest reduction of skill is found when the annual cycle of the GCMs was included. The average PSS of all models then drops to 0.45. In other words, the single biggest factor in improving coral reef bleaching predictions from models is accurate reproduction of the seasonal cycle. For the 12 months treatment, some of the models that do well are as follows: MIROC 3.2 hires, GFDL CM 2.1 and 2.0, IPSL CM 4, and MPI ECHAM 5.

A large reduction in skill can also be seen for the 24–60 months treatment (Fig. 4). These results reflect how important ENSO is as a driver of coral bleaching (Lough 2000; Gill et al. 2006). The observed reduction in skill is due to a bias in ENSO amplitude and cannot be attributed to incorrect timing of ENSO events. Since the method applied guaranteed that the timing of ENSO events was correct (i.e., the same as observations), only their amplitude was model predicted. The spread in skill between the models is largest in this treatment. Some of the models that retain large skill with this treatment are as follows: IPSL CM 4, GFDL CM 2.0 MIROC 3.2 medres, CNRM CM 3, and INMC 3.0. For the GCMs with smaller variance in this frequency band than observations (ratio between variance of GCM and observations <1), PSS drops of linearly with decreasing ratio ($R^2 = 0.80$). When the variance in the ENSO bandwidth is similar or greater in the GCMs, the hit rate does continue to increase, but the false alarm rate increases as well.

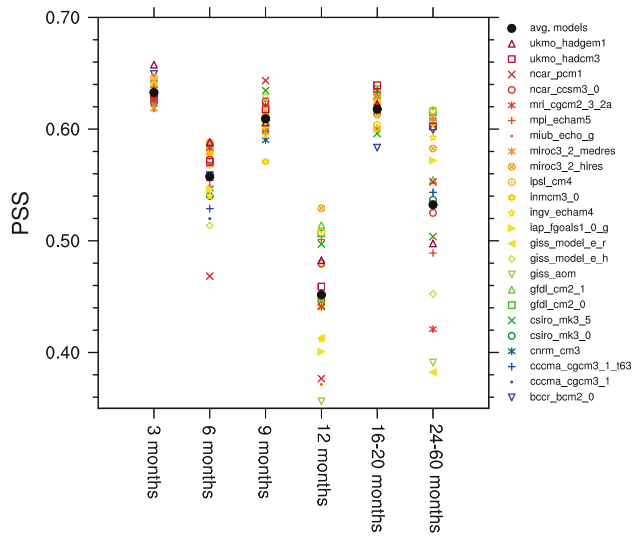

Fig. 4 Peirce skill score (PSS) calculated from modified GCMs for all reported bleached locations globally. Data are shown for observed SSTs, where frequencies around 3, 6, 9, 12, and 16–20 months were replaced with the same quantity from the GCMs, and for one case, where the variance of the observations in the 24–60 months frequency band was replaced with the same quantity of the GCMs (see Table 1)

Impact of differences in GCMs on projected bleaching

In this section, we explore how the identified sensitivities to annual cycle and ENSO amplitude impact future bleaching predictions. To illustrate the consequences of not correcting the annual cycle to match observations, bleaching predictions were made using the SRES A1B scenario of the GFDL CM 2.1 model, in which the annual cycle was replaced with: (1) the annual cycle of each of the GCMs separately and (2) with the annual cycle from OISST V2 data based on the period from 1982 to 2007. The GFDL CM 2.1 model is considered to have one of the better representations of the tropics (Gleckler et al. 2008). As a measure to compare these different treatments, the first predicted occurrence of bleaching twice per decade was chosen. This cut-off has been used before as a possible unrecoverable point for coral reefs (Donner et al. 2007). The point of this exercise is not to determine the absolute date at which reefs reach an unrecoverable point, but to illustrate the effect of just the seasonal cycle on such a prediction. The results show that most models predict the first occurrence of bleaching twice per decade on 50% of all reef locations to occur between 2025 and 2055 (Fig. 5a). In other words, the differences in annual cycle of GCMs introduce an uncertainty of 30 years until bleaching begins to occur every 5 years. This difference of 30 years is of similar scale as other uncertainties, such as caused by selecting different emission scenarios, or uncertainties related to possible adaptive capacity of corals to warming (Coles and Brown 2003; Rowan 2004).

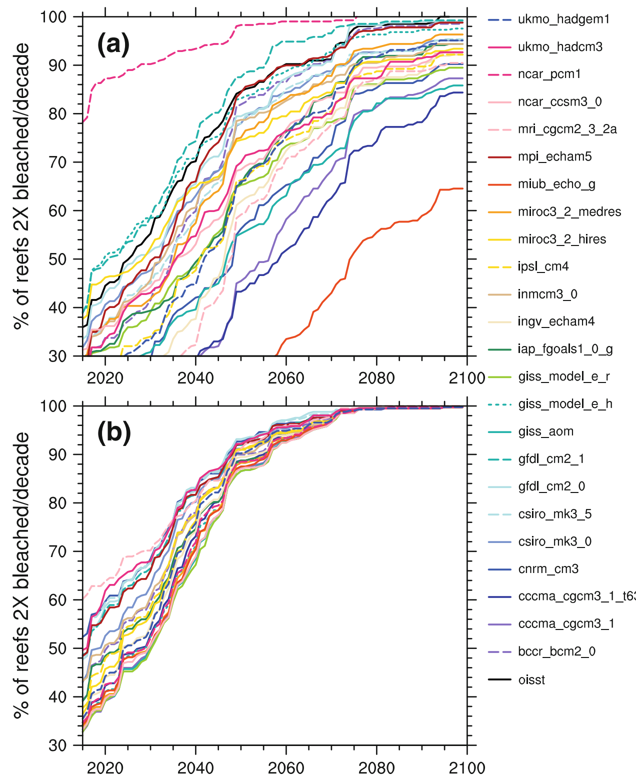

Fig. 5 **a** Percentage of reef cells predicted to experience at least two bleaching episodes in the preceding decade. Data are from the SRES A1B scenario GFDL CM2.1 model with the annual cycle replaced with the annual cycles of the other GCMs and observations (OISST). **b** Percentage of reef cells predicted to experience at least two bleaching episodes in the preceding decade. Data are from the SRES A1B scenario GFDL CM2.1 model with the 24–60 months variance replaced with this variance of the other GCMs

As shown in Fig. 1a, GCMs exhibit lower variance around the annual cycle. This reduced variance in seasonality will reduce future projected thermal stress. When the annual cycle of GCMs is used, most predictions show a smaller fraction of reefs bleached at any given time in the next century than a prediction made with the observed annual cycle (Fig. 6).

To analyze the impact of the differences in ENSO variance on projected future bleaching, a method similar to that used in the analysis of the annual cycle was used. The variance of the 24–60 months bandwidth of the GFDL CM 2.1 SRES A1B model was replaced with the variance of this bandwidth of the other GCMs and future bleaching was projected. The effect is smaller than the effect of the annual cycle (Fig. 5b).

Discussion

As expected, replacing the annual cycle from observations with the annual cycle from GCMs degrades the skill of the

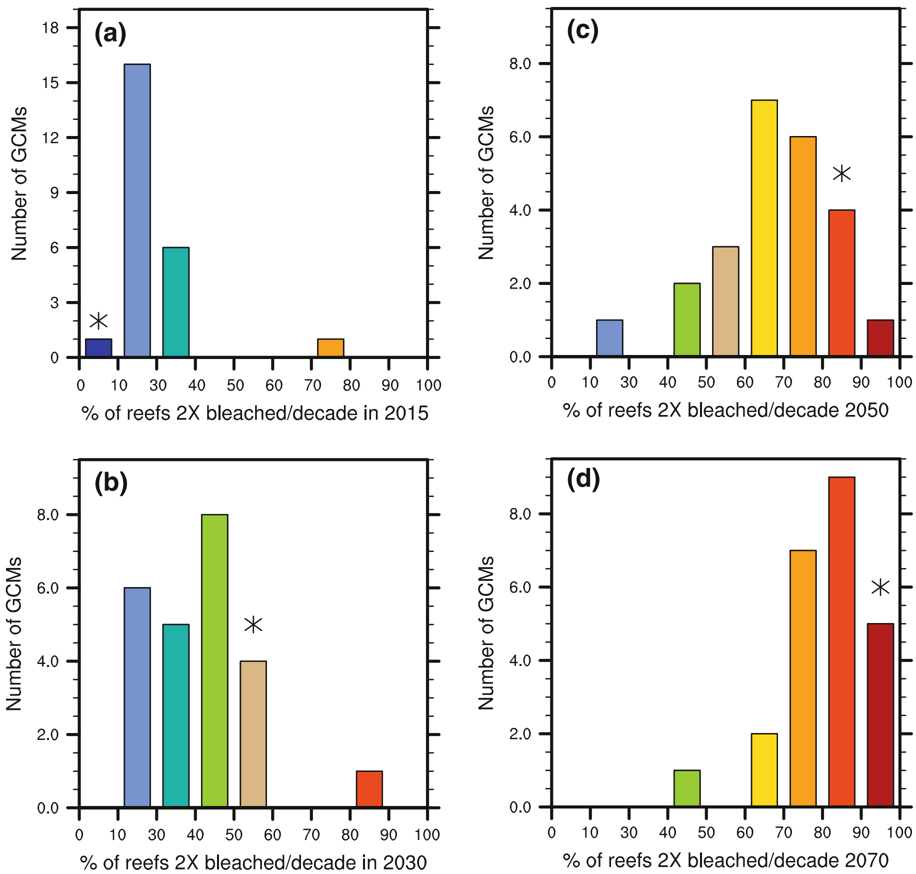

Fig. 6 Histogram of the percentage of reef cells predicted to experience at least two bleaching episodes in that decade. Results are plotted for the periods **a** 2005–2015, **b** 2020–2030, **c** 2040–2050, and **d** 2060–2070. Data are from the SRES A1B scenario GFDL CM2.1 model with the annual cycle replaced with the annual cycles of the other GCMs. The percentage of reefs bleached twice in that decade when the annual cycle is replaced with observations is marked (*asterisk*)

predictions considerably. The skill expressed in PSS declined to 0.45 averaged over all models compared to 0.83 for predictions made with observations of SST. Also replacing the annual cycle, results in some models predicting bleaching 30 years earlier than other models. Lower variance and lower amplitude of the annual cycle at tropical reef locations (Fig. 1a) can lead to underestimates of thermal stress on reefs (Fig. 3b). When the annual cycle of the GFDL CM2.1 model was replaced by the annual cycles of other GCMs and observations, most treatments predicted levels of bleaching lower than when the annual cycle of observations was used (Fig. 6).

In some previous studies where future bleaching has been projected using GCMs, the amplitude or the variance in the annual cycle has not been corrected (Hoegh-Guldberg et al. 2002; Donner et al. 2005, 2007; Donner 2009). This raises the possibility that those predictions of coral demise might have been too optimistic. While it is impossible to know precisely how seasonal cycles in the tropical oceans will change in the future, the systematic underprediction of seasonality in the current generation of GCMs is probably a robust bias and causes the average GCM to predict widespread bleaching 2–3 decades later (Fig. 5a).

Many models show ENSO variability that differs from observations. ENSO periodicity in models ranges from regular bi-annual to the observed 2–7 years periodicity, the amplitude and spatial patterns of the anomalies are different, and future variability increases in some models and decreases in others (Guilyardi et al. 2009). It is unlikely that these biases cancel each other out perfectly in a multi-model ensemble and some systematic biases will remain. Most models show smaller variance in this band than observations (Fig. 1a). Similar to the effects of the annual cycle, modeled amplitude of ENSO lower than the observed amplitude leads to underprediction of bleaching and vice versa (Fig. 5b). The influence of just the variance of the 24–60 months frequency band on predicted bleaching of all reefs introduced an uncertainty on the timescale of two decades averaged over all reef locations (Fig. 5b). As some regions show larger SST anomalies during an El Niño event than others, and the skill of the models in representing ENSO is spatially heterogeneous as well, this reported uncertainty is likely an underestimation for some regions. Regional predictions such as made in Hoeke et al. (2011) could be sensitive to systematic biases of ENSO in models.

Besides uncertainties relating to future greenhouse gas emissions, uncertainties in coral bleaching thresholds, and uncertainties related to possible adaptive, acclimatization, and recovery capacity by corals (Coles and Brown 2003; Donner et al. 2005; Baker et al. 2008; Berkelmans and van Oppen 2006), there is an uncertainty associated with the choice of GCM. In the suite of A1B scenario models, the linear trend in SST averaged over all reef locations ranges from 1.5 (NCAR PCM 1) to 3.4°C (MIROC 3 2 HIRES) increase per century. A study comparing surface temperatures from GCMs with the observational HadCRUT3 data set found no evidence to suggest that a model that performed well in the past should do so in the future as well (Reifen and Toumi 2009). It also showed that surface temperatures were most accurately described by an ensemble of models. Selecting a small group of models that performed best in the past did not produce the most accurate representation of future surface temperatures; the best results were obtained with larger ensembles. Other studies support choosing larger ensembles as well (Weigel et al. 2010). This is in part because model biases are time dependent (Li et al. 2010). This has clear implications for future predictions of coral bleaching. To maximize skill, not just one model should be picked but an ensemble of all available models should be used, with equal weights assigned to each model (Weigel et al. 2010), as is done in Hoeke et al. (2011). But, given that the existing models consistently underestimate the seasonal cycle, even ensembles will have a persistent bias to predict widespread bleaching to occur too late.

A number of assumptions were made in this study; some were necessitated by the character of the observational database of coral bleaching. Better observations could lead to different thresholds above which bleaching is projected to occur, and thus influence the results of this study when focusing on the timing of predicted bleaching. However, it would not influence the main conclusion that the annual cycle has the biggest influence on the skill of bleaching predictions. Another limitation of current studies that project future reef health using GCMs is that currently, only monthly GCM values are publicly available. This applies also to this study; in the future cases (Figs. 5 and 6), no weekly variability was present, and in the hybrid 20th century cases, weekly variability came from the observed SSTs. Predictions made with monthly data will show a reduced skill. While not included in this study, spatial resolution could influence skill as well, and a similar methodology could be employed to test this. This is, especially, salient considering the forthcoming next generation of GCMs in the fifth IPCC assessment report. In the next generation models, more processes that influence climate will be incorporated, representations of chemistry will be improved, and vertical and horizontal resolution will be increased (see for example http://www.cesm.ucar.edu/models/cesm1.0/notable_improvements.html).

In conclusion, of all frequencies probed, the annual cycle has the strongest influence on the predictive skill. Therefore, when predicting bleaching with GCMs to obtain maximum skill, not only should an ensemble of GCMs be used but also the GCMs should be corrected in their mean, and most importantly, GCMs should be corrected in their annual cycle and their 24–60 months variability. A possible suggestion to overcome the deficiencies of the GCMs is to use all the information in the historical observed SSTs and only replace the trend with that of an ensemble of GCMs.

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