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Large-scale stress factors affecting coral reefs: open ocean sea surface temperature and surface seawater aragonite saturation over the next 400 years

K. J. Meissner · T. Lippmann · A. Sen Gupta

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Abstract One-third of the world's coral reefs have disappeared over the last 30 years, and a further third is under threat today from various stress factors. The main global stress factors on coral reefs have been identified as changes in sea surface temperature (SST) and changes in surface seawater aragonite saturation (Ω_{arag}). Here, we use a climate model of intermediate complexity, which includes an ocean general circulation model and a fully coupled carbon cycle, in conjunction with present-day observations of inter-annual SST variability to investigate three IPCC representative concentration pathways (RCP 3PD, RCP 4.5, and RCP 8.5), and their impact on the environmental stressors of coral reefs related to open ocean SST and open ocean Ω_{arag} over the next 400 years. Our simulations show that for the RCP 4.5 and 8.5 scenarios, the threshold of 3.3 for zonal and annual mean Ω_{arag} would be crossed in the first half of this century. By year 2030, 66–85% of the reef locations considered in this study would experience severe bleaching events at least once every 10 years. Regardless of the concentration pathway, virtually every reef considered in this study (>97%) would experience severe thermal stress by year 2050. In all our simulations, changes in surface seawater aragonite saturation lead changes in temperatures.

Keywords Climate models · IPCC representative concentration pathways · Aragonite saturation · Sea surface temperature · Coral reefs

Introduction

There are numerous stress factors that can detrimentally impact the health of coral reefs. These include changes in sea surface temperature (SST) and salinity (SSS), sea level and ocean currents, nutrient availability and/or sedimentation rates, and light levels or surface seawater aragonite saturation (Ω_{arag}). Fisheries, local land use, water chemistry, extreme weather, and predation by coral-eating starfish can also have important impacts on coral health. Changes to the frequency, scale, and rate of change of any of the above factors will impact corals and their associated ecosystems. Some of these factors can be modulated by large-scale, global factors (e.g., temperature and aragonite saturation) although local processes can also introduce large heterogeneities. Others are driven by local factors (e.g., coastal land-use change and fisheries). Furthermore, many of these factors have the potential to interact in non-linear ways. For example, corals can deteriorate in response to an individual stressor such as coral bleaching in response to increased temperature (e.g., Glynn 1988; Hoegh-Guldberg 1999, 2005; Hoegh-Guldberg et al. 2005). However, it has been found to be more detrimental to the health of corals when multiple stressors act simultaneously (Langdon and Atkinson 2005; Anthony et al. 2008, 2011). Depending on the species, genotype, geographic location, history, and environmental factors, corals show a wide range of abilities in their capacity of coping with stress factors and recovery (Coles et al. 1976; Hoegh-Guldberg 1999; Brown et al. 2002; Graham et al. 2011).

Between 1980 and 2000, 27% of the world's coral reefs disappeared as a result of both local and global drivers (Wilkinson 2000), and a further 35% are seriously threatened (Wilkinson 2008). Bruno and Selig (2007) analyze a coral cover database of 6001 surveys between 1968 and

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2004 and show that some remote areas with little or no local stress factors are declining as rapidly as areas facing local anthropogenic stresses. This suggests that global factors might have a strong impact on the decline of reef health.

As a direct consequence of anthropogenic CO₂ emissions, sea surface temperatures are rising over most parts of the planet (e.g., Deser et al. 2010) while the large-scale availability of carbonate ions [CO₃²⁻] in the ocean is decreasing (e.g., Royal Society 2005). Projections suggest that these changes will accelerate in the future (Meehl et al. 2007). While the large-scale temperature and [CO₃²⁻] only represent a background state on which is superimposed a high level of small-scale spatial variability, such background changes will affect the extreme values experienced at reef locations. It is therefore important to understand and predict the future rate of change in both of these key properties.

There are several studies that use ocean models to investigate future changes in open ocean seawater aragonite saturation. Kleypas et al. (1999b) use the Hamburg Ocean Carbon Cycle global model (HAMOCC) to investigate future Ω_{arag} distributions until 2100. HAMOCC includes a full carbon cycle that reacts to increasing atmospheric concentrations, while the ocean dynamics are fixed at present-day conditions over the transient simulation. According to their study, surface seawater aragonite saturation will decrease by 30% in the tropics by the middle of this century, leading to a decrease in biogenic aragonite precipitation by 14–30%. Guinotte et al. (2003) analyze future changes in open ocean Ω_{arag} at locations where coral reefs exist today. They use the NCAR Community Climate System Model CCSM (Boville and Gent 1998) to compute SSTs over the Pacific Basin following the conservative IPCC SRES B2 scenario (Nakicenovic and Swart 2000). As this model does not include a carbon cycle, saturation state is calculated assuming a strictly thermodynamic relationship between the ocean surface and atmospheric pCO₂. Their results indicate that essentially all reef locations in the Pacific Ocean are likely to become marginal for coral reefs with respect to open ocean seawater aragonite saturation state by 2069. Donner et al. (2005) assess the frequency of future bleaching events under the IPCC SRES A2 and B2 scenarios with the Hadley Centre's HadCM3 and the National Center for Atmospheric Research's PCM models. While their simulations could not predict changes in seawater aragonite saturation, they found that bleaching could become an annual or biannual event for the majority of global coral reefs in the next 30–50 years. Hoegh-Guldberg et al. (2007) use the UVic Earth System Climate Model (UVic ESCM) forced with the IPCC SRES A2 emissions pathway (Nakicenovic and

Swart 2000) to analyze future changes of open ocean Ω_{arag} and their impact on reef accretion. They conclude that some regions (such as the Great Barrier Reef) attain low levels of open ocean Ω_{arag} more rapidly than others (e.g., Central Pacific). Projections by Hoegh-Guldberg (2004) suggest that mass mortality events of the scale of the 1997 El Niño will become annual events later this century. Hoegh-Guldberg (2005) used a simulation of the ECHAM4/OPYC3 model to identify when the bleaching threshold will be passed for corals in Moorea, French Polynesia.

Here, we explore three of the new IPCC representative concentration pathways (RCP) scenarios (RCP 3PD, RCP 4.5, and RCP 8.5) with the UVic ESCM (Weaver et al. 2001) to analyze the change in both open ocean SST and Ω_{arag} at the locations of present-day coral reefs over the next 400 years. By considering observed inter-annual variability in conjunction with SST projections, we are able to estimate future bleaching events by examining degree heating weeks (a metric widely used in observations).

Methods

Model description

The UVic Earth System Climate Model (UVic ESCM) consists of an ocean general circulation model (Modular Ocean Model, Version 2; Pacanowski 1995) coupled to a vertically integrated two-dimensional energy-moisture balance model of the atmosphere, a dynamic-thermodynamic sea ice model based on Semtner (1976), Hibler (1979), and Hunke and Dukowicz (1997), a land surface scheme, a dynamic global vegetation model (Meissner et al. 2003), and a sediment model (Archer 1996). The model is described in Weaver et al. (2001). It is driven by seasonal variations in solar insolation at the top of the atmosphere and seasonally varying wind stress and wind fields (Kalnay et al. 1996). The coupled model has a resolution of 3.6° in longitude and 1.8° in latitude and conserves energy, water, and carbon to machine precision without the use of flux adjustment. The UVic ESCM also includes a fully coupled carbon cycle taking into account the terrestrial carbon fluxes and reservoirs (Meissner et al. 2003; Matthews et al. 2005) as well as the inorganic (Ewen et al. 2004) and organic (Schmittner et al. 2008) carbon cycle in the ocean. The UVic ESCM is computationally very efficient and has been developed to address scientific questions related to climate variability on time scales of hundreds of years to millennia. The systematic comparison of the coupled model with observations shows good agreement (Weaver et al. 2001; Meissner et al. 2003; Eby et al. 2009). In the past, the UVic ESCM has been used to

address a broad range of scientific questions related to future climate change and palaeoclimates.

Inter-annual variability

The tropical regions inhabited by coral reefs are subject to high levels of inter-annual variability associated primarily with the El Niño Southern Oscillation (ENSO). Large-scale mass bleaching events are particularly associated with strong El Niño events. This leads to a dilemma in trying to estimate future change to reef systems. First, there are both spatial and temporal biases in the simulation of ENSO in state-of-the-art climate models (e.g., Van Oldenborgh et al. 2005; Leloup et al. 2008; Guilyardi et al. 2009). Furthermore, there is little consistency with regard to how ENSO will change in the future, with both increased and decreased amplitudes and frequency projected by climate models (Guilyardi et al. 2009; Collins et al. 2010).

As such, in order to examine the effect of combined mean state changes and natural variability on coral habitat, we use the observed natural variability as a proxy for natural variability in the future (i.e., we assume that the frequency and amplitude of ENSO remains unchanged). Due to the lack of dynamical processes in the atmospheric component of the UVic ESCM, the model does not reproduce inter-annual variability. We therefore add the weekly observed (and detrended) natural variability for the last 30 years to the mean state changes projected by the UVic ESCM to make an estimate of how thermal stress (as measured by the degree heating week (DHW) metric) might change in the future. Weekly SST measurements from the NOAA Optimum Interpolation (OI) Sea Surface Temperature (SST) V2 are used to estimate the natural variability. This method avoids model biases inherent in climate model representations of natural variability (Van Oldenborgh et al. 2005; Leloup et al. 2008; Guilyardi et al. 2009; Collins et al. 2010).

Emission scenarios

All our transient simulations stem from the same equilibrium simulation that has been integrated under preindustrial boundary conditions for over 10,000 years. We then force the model according to the RCP forcing pathways (Moss et al. 2010) that will be used as part of the fifth IPCC assessment report. The pathways specify atmospheric CO₂ concentrations, the radiative forcing from all non-CO₂ greenhouse gases, fractions of the land surface devoted to crop and pasture land, and the direct effect of sulfate aerosols as an alteration of the surface albedo for the next 400 years (Avis et al. 2011). Three pathways have been simulated, RCP 3PD (IMAGE), RCP 4.5 (MiniCAM), and RCP 8.5 (MESSAGE). The names are based on their

respective peak radiative forcing and the integrated assessment group responsible for each. Scenario RCP 3PD (IMAGE) is a long-term strategy that stabilizes greenhouse gas (GHG) emissions at a low level while land use and population increase in a similar way to the IPCC SRES B2 scenario. This is the lowest emission scenario considered. Global population reaches 10 billion by 2100 and “international institutions decline in importance, with a shift toward local and regional decision-making structures and institutions” (Nakicenovic and Swart 2000). Radiative forcing peaks at mid-century at 3.1 W m⁻² before declining to 2.6 W m⁻² by 2100 as outlined by van Vuuren et al. (2007). Scenario RCP 4.5 (MiniCAM) experiences a peak radiative forcing of 4.5 W m⁻² by 2100 from which point GHG emissions are maintained in order to stabilize total radiative forcing into the long-term future—a low-to-medium emissions stabilization scenario. Population peaks in 2070 at 9 billion and is described as being very exogenous in terms of population, gross domestic product growth, and energy efficiency (Clarke et al. 2007). Finally, scenario RCP 8.5 (MESSAGE) is a high-emission scenario based on the SRES A2 scenario as described by Nakicenovic and Swart (2000) and detailed in Riahi et al. (2007). This scenario imposes increasing GHG emissions during this century, reaching a radiative forcing of 8.5 W m⁻² at year 2100. The scenario represents a very heterogeneous world, with a high population growth of 12 billion by 2100, reflecting the most recent consensus of demographic projections (Riahi et al. 2007). Delayed fertility transition, economic growth, and technological development are primarily regionally oriented, fragmented, and slow (Nakicenovic and Swart 2000; Riahi et al. 2007). Figure 1 shows time series of atmospheric carbon dioxide concentrations corresponding to each of the RCP scenarios

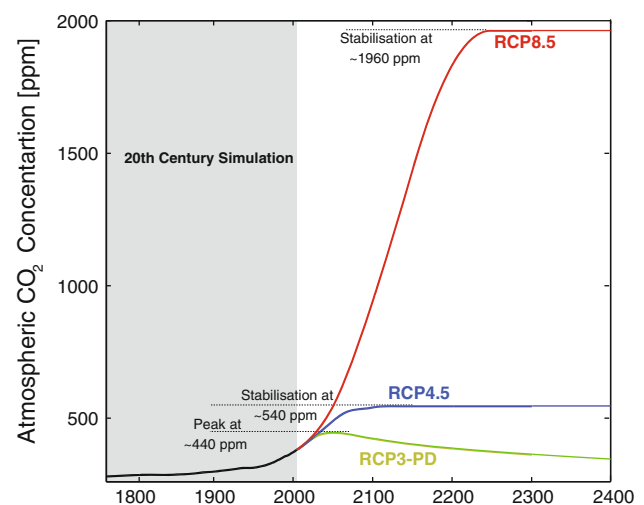


Fig. 1 Time series of atmospheric CO₂ concentrations in ppm for RCP 3PD, RCP 4.5, and RCP 8.5

considered in this study; all three transient simulations were integrated until year 2400.

Threshold identification

Coral reef communities currently exist within relatively narrow bounds of temperature, light availability, and seawater aragonite saturation (Hoegh-Guldberg 2005). When coral reef communities experience abnormally warm temperatures, the thermal stress affects the photosynthetic reactions of the symbiotic dinoflagellates causing dysfunction and bleaching to occur (Glynn 1988; Hoegh-Guldberg 1999; Hoegh-Guldberg et al. 2005). There is no uniform and globally constant maximum temperature at which corals will undergo bleaching, but it is likely that all shallow-water zooxanthellate corals will eventually succumb to bleaching if warm season SSTs increase by 1–3°C above preindustrial values (Veron et al. 2009). Following the marginality cluster identified by Kleypas et al. (1999a), Guinotte et al. (2003) define three ranges of temperature to assess the marginality of coral reefs: “high-temperature regions” are defined where maximum monthly mean temperatures exceed 31.1°C, “transitional regions” where maximum monthly mean temperatures are between 30 and 31.1°C, and “high-normal regions” where the range is between 19 and 30°C. It should be noted, however, that severe past bleaching events have been recorded in regions where maximum monthly SSTs were significantly colder than 31.1°C. Mass bleaching events can now be effectively identified using satellite SST observations. Bleaching is predicted to start occurring when a threshold of 1°C above the typical regional warm season maxima is exceeded for more than 4 weeks (Goreau and Hayes 1994; Toscano et al. 2000; Hoegh-Guldberg 2011). Bleaching becomes progressively worse for higher temperatures or longer periods over which the threshold temperature is exceeded. Several studies use “degree heating weeks” (DHW), the product of exposure intensity (degrees C above threshold) and duration (in weeks), to predict bleaching events (NOAA Hotspot Program; Hoegh-Guldberg 1999; Strong et al. 2000). This metric was initially developed by the satellite monitoring and prediction component of NOAAs Coral Reef Watch program (Liu et al. 2003). It uses a running 12-week sum of sea surface temperature anomalies above the climatological maximum, where only weeks when SST anomalies exceed the climatological maximum by a certain threshold are counted. As such, corals are considered to be under stress when temperatures are considerably above their typical annual maxima with stress accumulating over time. While it is usual to calculate this metric using a spatially constant threshold (normally 1°C), Boylan and Kleypas (2008) demonstrated that a spatially varying threshold (twice the standard deviation of warm season

SST anomalies) is better able to predict bleaching events: reefs living in regions with a low background variability in SST being more sensitive to high temperature events than reefs that evolved in an environment with higher SST variability. Both metrics are examined here. Comparison of these metrics with observed bleaching events suggests that mild bleaching will start to occur when the 12-week-accumulated DHW exceeds 4°C-weeks and become severe above 8°C-weeks. In addition to the DHW metric, “degree heating months” (DHM) have also been used in the past, mainly by modeling studies that only have access to monthly SST output (e.g., Donner et al. 2005; Tevena et al. 2011).

Although there has been considerable research examining how changes in SST impact coral reefs, surface seawater aragonite saturation (Ω_{arag}) levels are also an important factor for the well-being of corals (Kleypas et al. 1999a; Guinotte et al. 2003). Calcifying organisms produce CaCO_3 mainly in the form of calcite, Mg-calcite or aragonite. While aragonite is chemically identical to calcite, it differs in crystal structure and both aragonite and Mg-calcite are more soluble than calcite (Andersson et al. 2008). Present-day corals produce aragonite, whereas crustose coralline algae produce Mg-calcite; the calcification rate of corals is controlled by the aragonite saturation state of seawater (Ω_{arag}), which is related to the availability of carbonate ions $[\text{CO}_3^{2-}]$. Increasing atmospheric CO_2 results in a decrease in the availability of carbonate ions for calcification and therefore a decrease in Ω_{arag} (see Erez et al. (2011) for a thorough overview). Although Atkinson and Cuet (2008) argue that there is still considerable uncertainty as to what extent ocean acidification will affect present-day coral reefs, experimental and field evidence suggest that calcification depends strongly on local seawater pCO_2 . Silverman et al. (2007) investigated the community calcification of an entire coral reef in the Red Sea and found that calcification increases with temperature and seawater aragonite saturation state. The measured calcification rates correlated well with precipitation rates of inorganic aragonite predicted by empirical equations. In situ measurements from the Molokai reef flat in Hawaii suggest that threshold pCO_2 values (values for which calcification equals dissolution) vary widely between individual substrates (Yates and Halley 2006); the authors found a range in thresholds between 476 and 1,003 μatm for pCO_2 , and between 113 and 184 $\mu\text{mol kg}^{-1}$ for CO_3^{2-} . Many mesocosm studies show direct impact on coral reef calcification from lowering Ω_{arag} (Gattuso et al. 1998; Kleypas et al. 1999b; Langdon et al. 2000; Leclercq et al. 2002; Marubini et al. 2003). Schneider and Erez (2006) show that the net calcification rate of *Acropora eurystroma* becomes negative in laboratory experiments when Ω_{arag} drops below 2.8. Kleypas et al. (1999a) compile

statistically derived environmental averages and extremes among present-day reefs. They find an average open ocean surface seawater aragonite saturation of 3.83 with minimum and maximum values of 3.28 and 4.06, respectively. No reefs considered in this study existed in environments with Ω_{arag} values below 3. Kleypas et al. (1999a) also suggest that the reduced seawater aragonite saturation at higher latitudes might be one of the limiting factors (in addition to temperature and light penetration) for coral habitat. Guinotte et al. (2003) define four classes for annual mean open ocean seawater aragonite saturations with values over 4 being “optimal”, values in the range of 3.5–4 being “adequate”, values of 3–3.5 being “marginal,” and values below 3 being “extremely low”. Here, we follow Kleypas et al. (1999a) and define their minimum average value of 3.3 as a threshold for open ocean Ω_{arag} .

Results

Figure 2 shows latitude–time diagrams of the annually and zonally averaged sea surface aragonite saturation as well as annually and zonally averaged SST anomalies (relative to preindustrial) for the three emission scenarios. RCP scenario 3PD is the only scenario that shows some degree of recovery for both aragonite saturation state and SST anomalies within the next 400 years. Under this RCP, the maximum SST change lags the aragonite minimum by ~ 40 years. The turning point for seawater aragonite saturation corresponds closely to the time when atmospheric CO_2 concentrations begin to drop (Fig. 1). Zonal mean SST anomalies do not exceed 1.9°C , and zonal mean

aragonite saturation stays above 3 between 30°N and 30°S where most corals are found. For RCP scenario 4.5, no recovery in terms of SST or Ω_{arag} can be seen during the simulation period. By year 2050, the zonal mean Ω_{arag} falls below 3.3 at all latitudes, and after year 2100, SST anomalies exceed 2°C between 20°S and 60°N . Finally, under RCP 8.5 forcing the zonal mean Ω_{arag} is below 3.3 at all latitudes at year 2040 and below 1.5 by 2180. By year 2070, zonal mean SST anomalies exceed 2°C between 50°S and 60°N . Under the high-emission pathway, high-latitude waters become under saturated with respect to aragonite before the end of the century.

For all three scenarios, open ocean seawater aragonite saturations respond more quickly to changes in atmospheric CO_2 than sea surface temperatures. This discrepancy in response time is due to the fact that surface seawater aragonite saturation almost instantly equilibrates with atmospheric CO_2 , whereas the high heat capacity of water leads to a significant lag between changes in atmospheric CO_2 (and therefore radiative forcing) and ocean temperatures. Figure 2 illustrates this effect for both increases in atmospheric CO_2 (all three scenarios; e.g., RCP 4.5, year 2100, seawater aragonite saturation is already in equilibrium while SSTs are still increasing with time) and decreases in CO_2 (e.g., RCP 3PD, year 2080, SSTs are still rising while atmospheric CO_2 concentrations are decreasing and seawater aragonite saturation is recovering.).

While Fig. 2 shows the temporal evolution of zonal mean SST and seawater aragonite saturation, it cannot give information on region-specific impacts. Figure 3 displays snapshots of the simulated ocean for years 2030, 2050, and 2100 for the two extreme scenarios RCP 3PD and RCP 8.5.

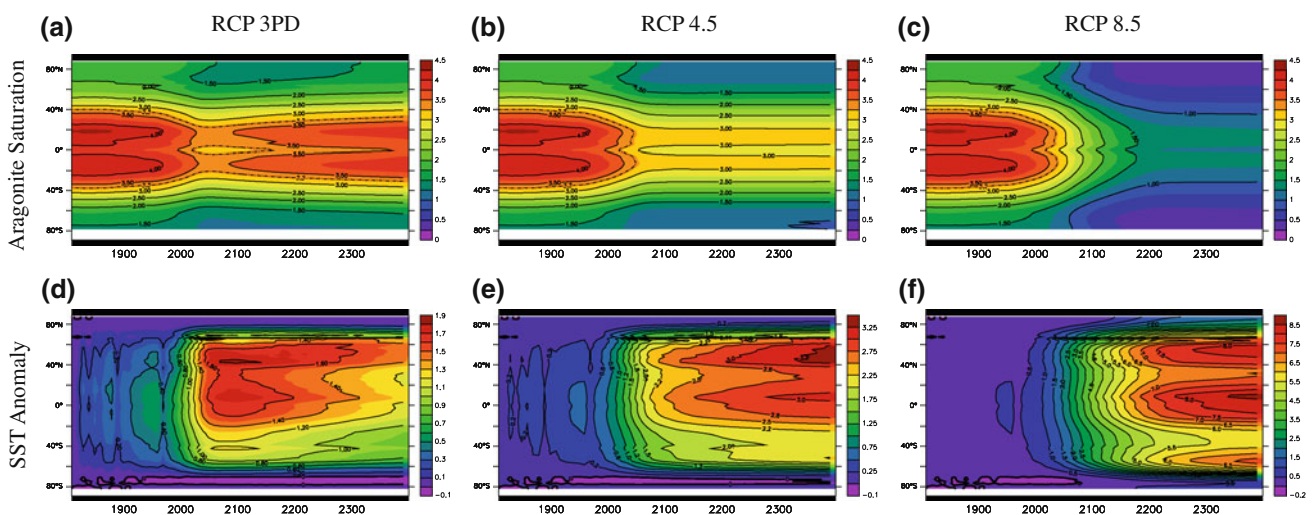


Fig. 2 Hovmöller diagrams of annual and zonal mean surface seawater aragonite saturation (first row) and annual and zonal mean sea surface temperature (second row). Simulations RCP 3PD, 4.5, and

8.5 are shown in the first, second, and third column, respectively. A dash-dotted line indicates the 3.3 isoline for surface seawater aragonite saturation

We compute the probability that severe stress ($DHW > 8$) will occur for each of these time slices; based on a threshold of twice the standard deviation of yearly SST (from the climatologically warmest month at each location, Boylan and Kleypas (2008)). A value of 10 represents a 10% probability that a severe bleaching event will occur during that year, or, in other words, a 10-year recurrence time between severe events. For both scenarios, the western Pacific is impacted first with the highest probabilities of severe stress occurring at year 2030 in Micronesia, the Northern Mariana Islands and around Papua New Guinea. A second region of high probability is situated at Kiribati and surrounding reefs. By year 2050, a clear difference can be seen between the two scenarios, while for RCP 8.5 virtually every coral reef (except those situated in major upwelling zones) will typically experience biannual severe bleaching events according to our analysis, probabilities of 50% or higher are mostly found in the western Pacific and eastern Indian Ocean for RCP 3PD. By year 2100, severe bleaching events are an annual occurrence in the RCP 8.5 simulation. The recovery time from severe bleaching events depends on the taxa and local conditions; a minimum of 5 years (equivalent to 20% in our plots) was used by Tevena et al. (2011) based on Halford et al. (2004)

and Golbuu et al. (2007). In Fig. 4, we use a minimum recovery time of 10 years (equivalent to a probability of 10% in our figures) to allow recruitment of larvae from other source reefs (Halford et al. 2004).

The open ocean seawater aragonite saturation is shown for the same scenarios and same time snapshots in Fig. 4. The black isoline indicates the open ocean seawater aragonite saturation threshold of 3.3. RCP 3PD maintains large parts of the tropical ocean above this threshold out to 2100 and beyond (not shown) while the global oceans in RCP 8.5 drop below 3 everywhere within this century. Red dots show reefs that according to our simulation are both thermally (probability of severe bleaching event higher than 10%) and chemically stressed (annual mean open ocean seawater aragonite saturation below 3.3) while orange dots show corals that are thermally stressed only. Reefs in light blue are chemically stressed while dark blue dots indicate reefs that are not subject to major open ocean temperature or seawater aragonite saturation stress. In our RCP 8.5 simulation, all corals are thermally stressed by year 2050, while only seven reef locations (out of 503) stay in healthy open ocean conditions by the end of the century in our RCP 3PD simulation (including reefs in New Caledonia, the Coral Sea, Pitcairn Islands and Bermuda).

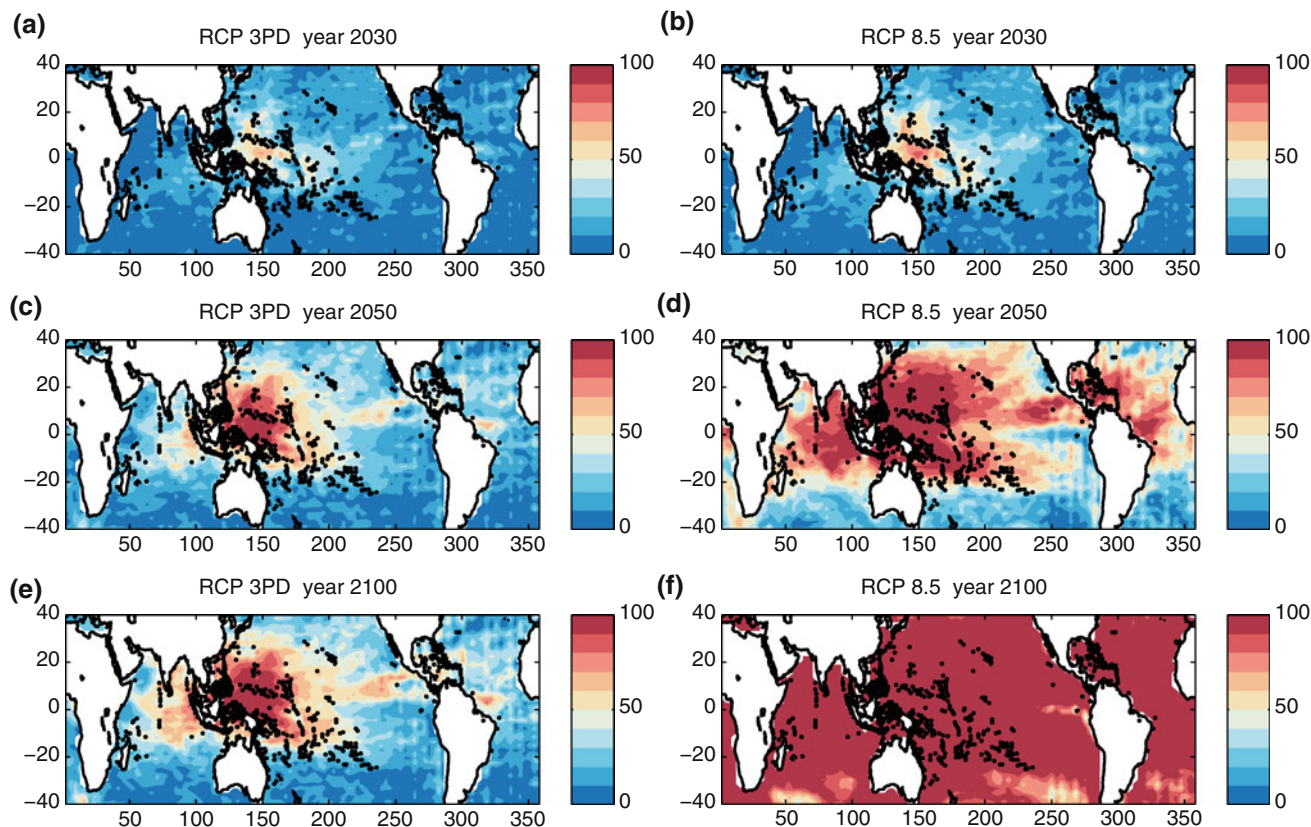


Fig. 3 Probability of a severe bleaching event ($DHW > 8$) occurring during a given year. *Left column* shows the RCP 3PD simulation (year 2030 (a), year 2050 (c), and year 2100 (e)); *right column* shows the RCP 8.5 simulation (year 2030 (b), year 2050 (d), and year 2100 (f))

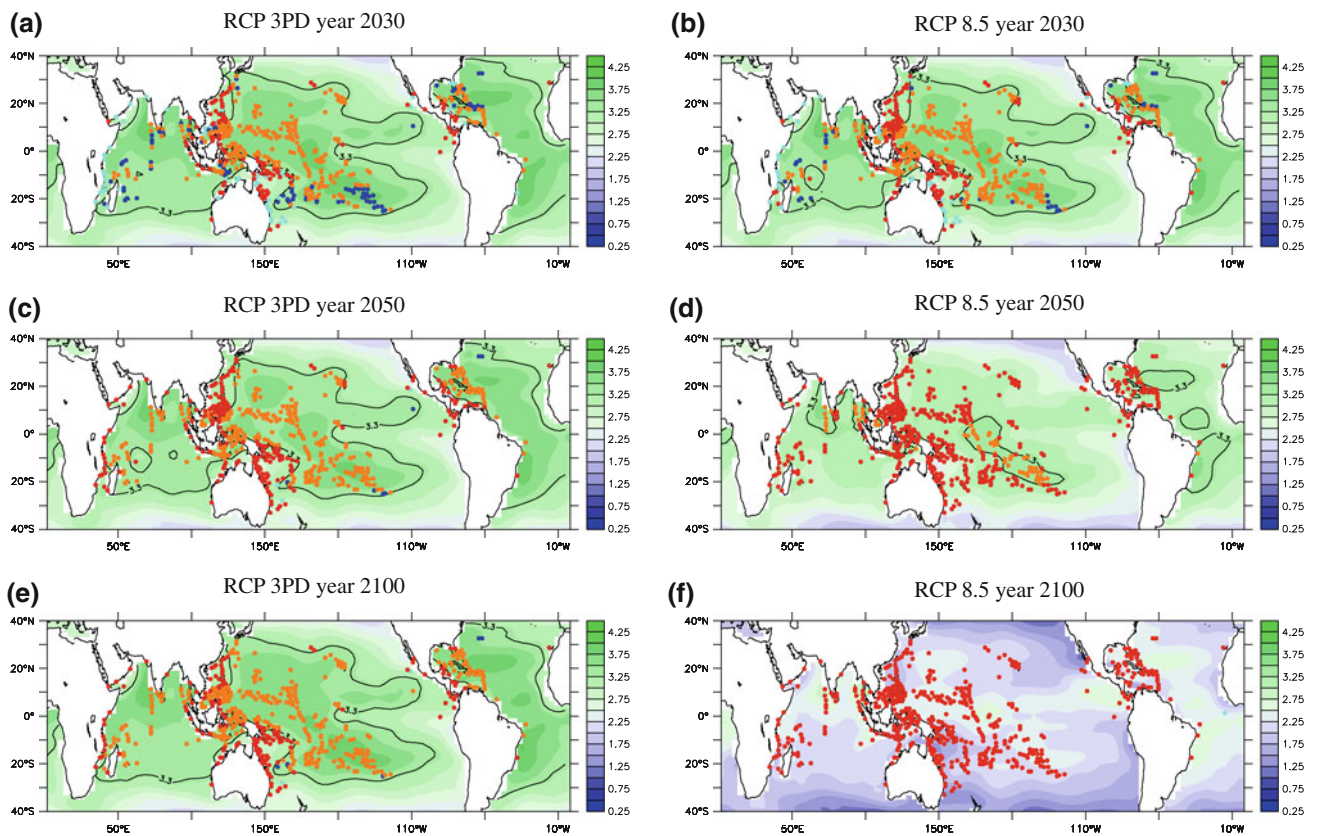


Fig. 4 Open ocean surface seawater aragonite saturation. *Left column* shows the RCP 3PD simulation (year 2030 **(a)**, year 2050 **(c)**, and year 2100 **(e)**); *right column* the RCP 8.5 simulation (year 2030 **(b)**, year 2050 **(d)**, and year 2100 **(f)**). Reefs in blue have a less-than-10% probability of experiencing a severe bleaching event (DHW>8) and live in areas with annual mean open ocean seawater aragonite

saturation above 3.3. *Orange reefs* are thermally stressed experiencing a severe bleaching event at least once every 10 years. *Light blue reefs* are chemically stressed (annual mean seawater aragonite saturation below 3.3), and reefs in red are both thermally and chemically stressed

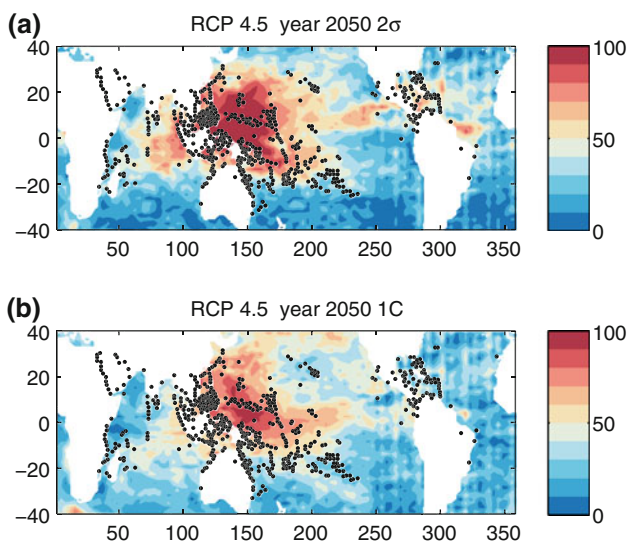


Fig. 5 Probability of a severe bleaching event (DHW>8) occurring at year 2050 in our RCP 4.5 simulation. 2σ threshold is shown in **(a)**, 1°C threshold in **(b)**

Finally, Fig. 5 shows two probability maps of severe bleaching events at year 2500 for our RCP 4.5 simulation; the upper panel follows the 2σ threshold (Boylan and Kleypas 2008) while the lower panel uses a spatially constant threshold of 1°C widely used operationally (http://www.noaawatch.gov/themes/coral_bleaching.php) in the literature. Using the 2σ threshold leads to higher bleaching probabilities in regions with lower natural variability (e.g., the Indian Ocean).

Discussion

When considering the adaptive ability of coral reef communities, it is necessary to consider rates of change in addition to absolute changes as communities have survived greater absolute changes in the past than are projected for the future. For example, over a 95,000 year interval, coral communities in the Huon Peninsula were able to survive sea level variations of up to 120m and temperature variations

of up to 6°C (Pandolfi 1996), and coral reefs have prevailed through glacial and interglacial periods (Jackson 1992). However, rates of change have never met or exceeded rates that are expected to occur over the next century (Veron 2008). While some authors report a decrease in ecological resilience with time and increasing temperatures (Hoegh-Guldberg 2008), others suggest that coral acclimatization and adaptation to extreme warming events will increase thermal tolerance (Brown et al. 2002; Castillo and Helmuth 2005). Glynn (1991) suggests that some species have already died out due to the thermal tolerance being breached, and remaining species have reached the thermal tolerance limit and so are unlikely to survive increasing temperatures.

Our simulations show that annual mean open ocean surface seawater aragonite thresholds will be exceeded within the first half of this century if we follow a RCP 4.5 or more intensive pathway. Only the low emission scenario (RCP 3PD) ensures that annual mean open ocean seawater aragonite saturation stays above 3.3 in most locations where present-day corals are found (Fig. 4). The most severe mass bleaching events in the recent past occurred during El Niño events. A famous example is the 1997–1998 event. 1998 was the warmest year on record at that time (McPhaden 1999), and the El Niño of 1997–1998 caused the greatest thermal stress ever recorded at many coral reef sites (Veron et al. 2009). When present-day observed inter-annual variability is added to our simulations, we find that, depending on the emission scenario, 66–85% of the reef locations considered in this study become thermally marginal by year 2030 (i.e., a severe bleaching event occurring at least once every 10 years). By year 2050, 100% of the reef locations become marginal when forced with the RCP 8.5 scenario, while for our RCP 4.5 simulation, only four reefs are below our SST threshold resulting in 99% of the reefs under stress (not shown). The most optimistic scenario (RCP 3PD) results in 98% of the reefs stressed by 2050. It is interesting to note that our results are more pessimistic than the findings of Tevena et al. (2011) but align well with Donner et al. (2005). There are three main differences between the present study and the analysis of Tevena et al. (2011): while we add observed present-day ENSO-related variability to our simulations, Tevena et al. (2011) analyze model output from three models that display their own simulated ENSO variability. Furthermore, their analysis is based on DHM instead of DHW, which is common for modeling studies that are based on monthly output data (e.g., Donner et al. 2005), but might lead to an underestimation of risk (Tevena et al. 2011). Finally, Tevena et al. (2011) analyze the SRES A1B scenario, which is more carbon intensive than RCP 4.5.

The UVic ESCM, like most global climate models, is unable to resolve processes at scales finer than a few hundred kilometers. As such, many important processes

that affect physical and biochemical properties on coral reefs are entirely absent. Boundary currents, local upwelling and enhanced temperature variability in shallow lagoons, all play a large role in controlling the reef habitat. In addition, the interdependence of reef biology and seawater carbonate chemistry is complex. Local biological and biochemical processes such as reef calcification and dissolution as well as reef photosynthesis and respiration can cause large swings in local seawater aragonite saturation, dissolved inorganic carbon (DIC), pH, and pCO₂ (e.g., Smith and Veeh 1989; Suzuki et al. 1995; Kleypas and Langdon 2006; Anthony et al. 2011; Kleypas et al. 2011). The simultaneous existence of both organic and inorganic carbon processes results in beneficial interactions between photosynthesis, calcification, and respiration (Suzuki et al. 1995). For example, the existence of macroalgae enables corals to build carbonate structures in waters with low aragonite saturation by drawing down a large amount of carbon dioxide through photosynthesis. Jokiel et al. (2008) found coral calcification decreased 15–20% over a 10-month period in an increased ocean acidification mesocosm experiment but crustose coralline algae played an important role aiding the growth and stabilization of coral reefs. The net result on local aragonite saturation is thus dependent on the composition of primary producers and calcifiers within the reef system. At the same time, calcification, dissolution, photosynthesis, and respiration all depend on the local water chemistry, introducing feedbacks between biology and chemistry into the system that are hard to quantify for future scenarios (Anthony et al. 2011). A global climate model cannot resolve these small-scale processes within coral reefs; it can only predict large-scale open ocean conditions, which might be quite different. For example, Bates et al. (2010) find that in situ Ω_{arag} values observed at Hog Reef (Bermudas) are generally ~ 0.3 lower than open ocean values recorded by BATS. Several other studies have reported differences in carbonate chemistry between open ocean and reef water (Frankignoulle et al. 1996; Gattuso et al. 1996; Ohde and Van Woessik 1999; Suzuki and Kawahata 1999; Kawahata et al. 2000; Bates et al. 2001). The magnitude of these differences can be related to water residence time, depth of reef water, and composition of primary producers and calcifiers (Suzuki and Kawahata 1999).

Although global climate models are unable to resolve these small-scale feedbacks, observations suggest that some local impacts can be modulated by large-scale changes. Bates et al. (2010) find that the change in measured skeletal density for *D. labyrinthiformis* at Hog Reef between 1959 and 1999 is very close to the decrease in calcification predicted over the same period based on measured open ocean rates of carbonate decrease ($\sim 33\%$ vs. $\sim 37\%$). Another example are major El Niño events. These events produce

large-scale patterns of bleaching across the Indo-Pacific region (e.g., Oliver et al. 2009). In addition, bleaching metrics based on SST measurements at scales much greater than individual reefs are successfully used to identify local bleaching (Donner et al. 2005). As such, the large-scale changes projected by climate models are likely to be pertinent at the scale of reefs at least in an average sense.

Finally, while this paper analyzes changes in open ocean SST and Ω_{arag} , there are numerous other important stress factors that a global circulation model cannot take into account. For example, changes in sea level represent another large-scale forcing factor that could affect coral reef viability in the near future. Coral reef ecosystems require a certain amount of light for dinoflagellate microalgae to photosynthesize (Chalker et al. 1988). Coral reef growth (accretion) has been shown to respond to large changes in sea level over geological time in order to ensure light availability (Wilkinson 1999). If the sea level rise exceeds the accretion rate, the reef drowns, a phenomenon that has been observed during past events of sea level rise (Blanchon and Shaw 1995; Webster et al. 2004). The maximum mean reef accretion rate, although highly dependent on coral type, has been recorded in the literature to be between 5 and 10 mm year⁻¹ (Buddemeier and Smith 1988; Montaggioni 2005). Coral communities have successfully relocated in the past when sea level rise exceeded accretion rate, including several events of abrupt rise exceeding 45 mm year⁻¹ during the last deglaciation (Blanchon and Shaw 1995). In our simulations, the maximum rate of steric sea level change equals 6.6 mm year⁻¹ at year 2150 for RCP 8.5, 2.8 mm year⁻¹ at year 2060 for RCP 4.5 and 2.2 mm year⁻¹ at year 2030 for RCP 3PD forcing (not shown). However, these simulations do not take melting of ice sheets into account, which will considerably increase these lower bound estimates. For example, in recent decades, the thermal contribution to sea level rise makes up less than half of the total sea level rise (Domingues et al. 2008). Thermal contributions are likely to make up an even smaller fraction of the total in the future, particularly in the event of a destabilization of the ice caps (Meehl et al. 2007).

Other examples of stress factors that cannot be taken into account in the present study include coastal development, additional nutrient input into coastal habitats via agriculture and land-use changes, changes to the freshwater balance, and overfishing and exploitation of coral reefs, all of which are important drivers to changes in coral habitat.

Reef forming corals have existed for over 200 million years, they have shown an ability to adapt to different environmental conditions in the past and thus might be able to adapt to future changes. For example, Yamano et al. (2011) found evidence of poleward expansions of coral reefs with a speed of up to 14 km year⁻¹ based on 80 years of national

records from the temperate areas of Japan. Our simulations show that for medium to high-emission scenarios, thresholds for adequate environmental envelopes in terms of seawater aragonite saturation will be exceeded in the first half of this century. Only the most optimistic pathway (RCP 3PD) will keep surface seawater aragonite saturation values at most of present-day coral reef locations above 3.3. For all three simulations, virtually every reef considered here will experience a severe bleaching event at least once every 10 years by the middle of the century. According to our simulations, even if humans choose to follow a very low emission pathway, the near-term future for coral reefs looks bleak.

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