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REPORT

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Future coral reef habitat marginality: temporal and spatial effects of climate change in the Pacific basin

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Abstract Marginal reef habitats are regarded as regions where coral reefs and coral communities reflect the effects of steady-state or long-term average environmental limitations. We used classifications based on this concept with predicted time-variant conditions of future climate to develop a scenario for the evolution of future marginality. Model results based on a conservative scenario of atmospheric CO_2 increase were used to examine changes in sea surface temperature and aragonite saturation state over the Pacific Ocean basin until 2069. Results of the projections indicated that essentially all reef locations are likely to become marginal with respect to aragonite saturation state. Significant areas, including some with the highest biodiversity, are expected to experience high-temperature regimes that may be marginal, and additional areas will enter the borderline high temperature range that have experienced significant ENSO-related bleaching in the recent past. The positive effects of warming in areas that are presently marginal in terms of low temperature were limited. Conditions of the late 21st century do not lie outside the ranges in which present-day marginal reef systems occur. Adaptive and acclimative capabilities of organisms and communities will be critical in determining the future of coral reef ecosystems.

Keywords Saturation state · Sea surface temperature · Future habitats · Reef stress

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Introduction

Background

Coral reefs and reef communities have been defined in many different ways (Kleypas et al. 2001), and there is no consensus for determining the condition under which a coral assemblage is judged marginal in terms of ecosystem function, nor for assessing marginality of habitat independent of what happens to be living there at any given moment. Similarly, the term “marginal” is itself subject to different definitions and interpretations. Marginality may be defined:

1. In a purely statistical sense, identifying the subset of reef communities or conditions that are near the extreme of a particular suite of environmental variables or community conditions.
2. On the basis of proximity to an environmental condition known or reasonably assumed, based on physiological or biogeographic evidence, to place an absolute limit on the occurrence of reef communities or key classes of reef organisms.
3. In terms of organism and community condition (cover, composition, diversity, health) or metabolism. We address the interacting concepts of community and marginality below.

Kleypas et al. (1999b) used cluster analysis to define marginal reef categories at a global scale in the statistical sense. Many of the marginal categories defined coincide well with marginality in terms of definitions 2 and 3 above. These marginal groupings generally represent the low ends of the environmental distributions—low temperature, low salinity, low light, and low aragonite saturation state. At the global scale, high-value clusters generally do not abut or grade into areas of clear absolute limitation, although high extremes of temperature, salinity, and light (or their combinations) can be shown to be stressful (hence potentially limiting) at local scales or in the laboratory. This emphasizes the importance of specifying spatial and temporal (both duration and frequency) scales in discussions of marginality. The definition of future marginality used in this paper refers to those reefs that are in danger of becoming marginal [i.e. being pushed beyond their "normal" environmental limits (Kleypas et al. 1999b) due to increasing sea surface temperatures and decreasing aragonite saturation state].

A community with high cover and high diversity of healthy, zooxanthellate, scleractinian corals, with hydrocorals and reef-associated calcifying algae, would meet almost any standard for a non-marginal reef community. As diversity, cover, and health decline, the community itself becomes more marginal; this may or may not mean that the habitat (local or regional environment) is necessarily more marginal in a general or long-term sense. One specific example may be drawn from the observations of Done (1999), who described coral communities on the Great Barrier Reef (GBR) as a "shifting steady-state mosaic." Overall, the GBR is far from most people's concept of a marginal reef environment, but it is one with a high level of dynamic disturbance and recovery. Over decadal averages or spatial scales of hundreds to thousands of kilometers the reefs are healthy—but at any given moment a specific reef site may look very marginal as the result of cyclone damage, *Acanthaster* predation, or bleaching (definition 3). By contrast, Harriott and Banks (2002) describe the systematic and consistent increase in marginality with increasing latitude south of the GBR. The latter case—a large-scale geographic marginality gradient that clearly relates to habitat characteristics—has the potential to help us understand biogeography and physiological limits on climatic and evolutionary time scales.

In the present "coral reef crisis" (Wilkinson 2000) there is great concern that many reef communities are passing very rapidly from healthy to marginal (in the sense of definition 3 above) to dead. These transitions are generally associated with increased stresses, which may be local anthropogenic, large-scale climatic and environmental, or both. The acute local forms of stress are readily identified (e.g., physical destruction, eutrophication, etc.) and are potentially controllable. What is less clear is the role of "background" environmental change in increasing marginalization (definition 2 above)—particularly the effects of changing ocean chemistry and temperature. The roles of temperature, salinity, nutrients, light, water motion, and carbonate saturation state in defining the geographic limits of coral and reef occurrence are well established (Smith and Buddemeier 1992; Veron 1995; Kleypas 1997; Guinotte 1999; Kleypas et al. 1999b), although for most of these, the mechanisms of how they limit coral reefs (both environmentally and geologically) are not necessarily well understood.

Among current concerns is the question of how these environmental controls will change over time and space, and of the significance of the changes to ecosystems. Within the present century, Earth is predicted to attain conditions of temperature and carbon dioxide concentration that have not co-occurred since the evolution of modern reef systems after the Eocene (Wood 1999; B. Opdyke, personal communication); our present and future environment has been referred to as the no-analog earth (Steffen and Tyson 2001). Throughout Earth's history, low temperatures have placed an absolute limit on reef development. Today, high as well as low temperatures place an absolute limit on reef occurrence, or create marginality in the cases of definitions 2 and 3. Much effort is currently being devoted to conservation, threat mitigation, and management; however, without some basis for estimating future environmental baselines and probable changes in marginality of local habitats, long-term success is unlikely in a rapidly changing world (Buddemeier 2001).

We systematically extend the work of Kleypas et al. (1999b) on contemporary marginal environments (definitions 1 and 2) to consider the global-scale effects of CO_2 increase and global warming up until 2069. Kleypas et al. (1999b) found that contemporary geographic variations in light, temperature, and aragonite saturation state accounted for most of the variation in reef occurrence at the global scale. Since day length and sun angle (two of the major controls on available subsurface light) will not change over this time, and the effects of changing cloud cover or water transparency cannot be predicted at the global scale, we consider only the effects of temperature and saturation state.

CO_2 concentration in the surface ocean is largely controlled by the combination of atmospheric concentration and temperature; and since CO_2 is well-mixed in the atmosphere, aragonite saturation state is highly correlated with sea surface temperature. Temperature has long been considered the factor limiting reef development to tropical and subtropical environments, but recent evidence indicates that calcification rates of reef-building corals and algae are positively correlated with aragonite saturation state (reviewed by Gattuso et al. 1999; Gattuso and Buddemeier 2001; Kennedy et al. 2002; Langdon 2003). There is no evidence that high saturation state limits coral growth or reef development, but low saturation state can be limiting at biological, ecological, and geological levels. Reef-building corals and algae are obligate calcifiers, and reduced skeletogenesis not only will reduce their ability to compete for space and withstand erosion, but can be expected to interact with other aspects of life history and ecological function. The three-dimensional structures and resultant niche diversity provided by corals are important factors in the high general biodiversity of reef communities, and these depend heavily on coral skeletal growth. At geological scales, carbonate accumulation and lithification—the processes that distinguish true reefs and coral communities (Buddemeier and Smith 1999)—would be reduced by lowered calcification rates.

Although low temperature and low saturation state appear to represent "marginal" conditions by both definitions 1 and 2 above, high temperature is a more complicated issue. Elevation of temperature is clearly stressful to corals, and there are clear metabolic responses to temperature and its change (Gates and Edmunds 1999). However, there is also evidence that corals can adapt and acclimatize to temperature (reviewed by Jokiel and Coles 1990; see also Gates and Edmunds 1999), and there is currently no solid basis for determining an absolute upper temperature limit. In view of the abundant evidence for thermal stress as a factor in bleaching and mortality, we chose the statistical definition of high temperature marginality used by Kleypas et al. (1999b) to illustrate patterns of change over time and to assess habitat change.

We examine a time-series of changing saturation state and temperature conditions in the Pacific Ocean region, and specifically the expansion of these conditions that we currently associate with reef marginality, in order to identify specific regions that may experience early, extreme, or multiple stresses as a result of climate change. The Pacific region reefs vary broadly in diversity, geographic connectivity, and anthropogenic impacts, and provide an opportunity to examine pronounced gradients in both climatic and non-climatic factors associated with habitat marginality.

Methods

Data used

Future ocean sea surface temperature (SST) was calculated from the NCAR Community Climate System Model CCSM v 1.0 (Boville and Gent 1998). The CCSM is a non-flux corrected model with fully coupled atmosphere, ocean, ice, and land components, and has a spatial resolution of 2.4° longitude and 1.2–2.4° latitude. Future changes in SST were determined as the difference between SST from the 'B2' computation, which used the IPCC SRES B2 emissions scenario (Nakicenovic and Swart 2000), and a control computation that used constant atmospheric conditions set at preindustrial levels. SRES B2 is based on relatively slow population growth, a rapidly evolving economy, and an increasing emphasis on environmental protection (Nakicenovic and Swart 2000). It therefore projects low-to-moderate increases in CO_2 levels (increasing from approximately 375 ppm at present to 517 ppm by 2069). These increases are more conservative than the 'classic' IS92a scenario, and in fact it is one of the most optimistic scenarios.

Model SSTs were averaged over decadal intervals between 2000 and 2069. Monthly averages were calculated for each 10-year average, from which the 10-year minimum and maximum values were determined. Differences between the B2 and control computations were determined and resampled to a 1×1° grid. Future SSTs were determined by adding the CCSM B2-Control SST differences to present-day SST derived from the Reynolds optimally interpolated SST data set (Reynolds et al. 2002). This data set incorporates remotely sensed and ship-board observations, and has provided both weekly and monthly averages since mid-1981. Monthly data were used to calculate decadal averages for the periods 1982–1991 and 1992–2001, as was done for the model data. Because the 1992–2001 averages are warmer than the 1982–1991 averages, and may be contaminated by global warming, the 1982–1991 averages were used as the "baseline" SST data set, keeping in mind that this decadal average may also have significant warming relative to preindustrial SST. Aragonite saturation state was calculated at 10-year intervals and 1×1° spatial resolution, using projected CO_2 levels from the IPCC SRES B2 scenario (Nakicenovic and Swart 2000), and the CCSM-derived projections of SST change as described above. Saturation state calculations were the same as those described by Kleypas et al. (1999a). The 1870 pCO_2 conditions were used to calculate the preindustrial baseline for this data set.

Analytical tools

The gridded SST and saturation state files were imported as ArcInfo Grids using Environmental Systems Research Institute's (ESRI) ArcInfo software. Geographic information system (GIS) analysis and cartographic displays were generated using ArcMap 8.1 and ArcView 3.3. Guinotte (1999) describes methods for spatial analysis in marine environments, mapping functionality, and visualization techniques in more detail.

Threshold identification

Saturation state. "Low saturation state reefs" were identified as those occurring where aragonite saturation state (Ω_{arag}) values were between 3 and 3.5 (Kleypas et al. 1999b). Since no reefs occurred at calculated values <3, we identify that as the threshold for "extremely marginal," and further subdivide the values of Ω_{arag} >3.5 into "adequate" (3.5–4.0) and "optimal" (>4.0) categories based on preindustrial saturation state (see Results) and coral and community calcification responses (see Discussion).

Temperature. Kleypas et al. (1999b) based their temperature classifications on maximum and minimum weekly values, while the CCSM 1.0 model results are reported at monthly resolution. Weekly and monthly averages of maximum, minimum, and average SST values for the latitude range 35°N–35°S were consistently highly correlated. Mean differences did not exceed 0.41 °C and variances were less than 0.05 °C. For the purposes of this investigation we used monthly data and adjusted the values presented in Table 5 of Kleypas et al. (1999b) according to the comparison presented in our Table 1: the high monthly average temperature is >31.1 °C and low monthly average temperature is <18.4 °C. Mean monthly and mean weekly temperatures are essentially identical.

Results

Sea surface temperature maxima

Projected future monthly SST maxima for the Pacific region (Fig. 1) illustrate progressive warming relative to the 1982–1991 observations of Reynolds et al. (2002). Contour intervals in Fig. 1 were selected to reflect the marginality cluster identified by Kleypas et al. (1999b); i.e., their maximum weekly value of 31.5 °C corresponds to a maximum monthly value of 31.1 °C. High temperature regions are identified as those where maximum

Table 1 Weekly minus monthly average values for Reynolds SST data sets, 35°N–35°S, 1982–2001

Parameter	Mean difference	Variance
Maximum SST	0.41	0.044
Minimum SST	−0.38	0.035
Average SST	0.00	0.000

monthly temperatures are >31.1 °C, transitional regions as 30–31.1 °C, and "high normal" regions as 29–30 °C. Blue dots represent documented reef locations from the Reef Base database.

It is not our intention to imply that 31.1 °C is a magic number in terms of the upper thermal tolerance of corals. This value was used because it highlights regions that are near the thermal maxima experienced by present-day coral reefs in non-enclosed oceanic regions (Kleypas et al. 1999b). The responses of coral ecosystems to temperatures above this value, particularly to episodic increases, are largely unknown. Severe past bleaching events have been recorded in regions where 1982–1991 maximum monthly SSTs were significantly cooler than 31.1 °C; in 1998 several Pacific reefs experienced bleaching where maximum monthly SSTs were in the 29–30 °C range.

The regions with maximum temperatures in the 24–29 °C range encompass optimal and suboptimal (but not low marginal) regions of reef growth; the 24 °C monthly maximum isotherm corresponds fairly closely to the 18.4 °C monthly minimum isotherm [which in turn corresponds to the low temperature marginality threshold of 18 °C for the weekly minimum temperature, determined by Kleypas et al.(1999b)]. Extreme SST maxima under the B2 scenario is projected to expand within the Pacific with both temporal and spatial variations. Coral areas showing the greatest probability of extreme SST maxima by 2069 are the Philippine Islands, Gulf of Thailand and Andaman Sea regions, the Arafura and Timor Sea regions, Tuvalu and the Solomon and southern Marshall Islands, and some areas adjacent to the coast of Central America (Fig. 1e).

Aragonite saturation state

Results of the aragonite saturation state calculations show the same general trends as past studies (Fig. 2;

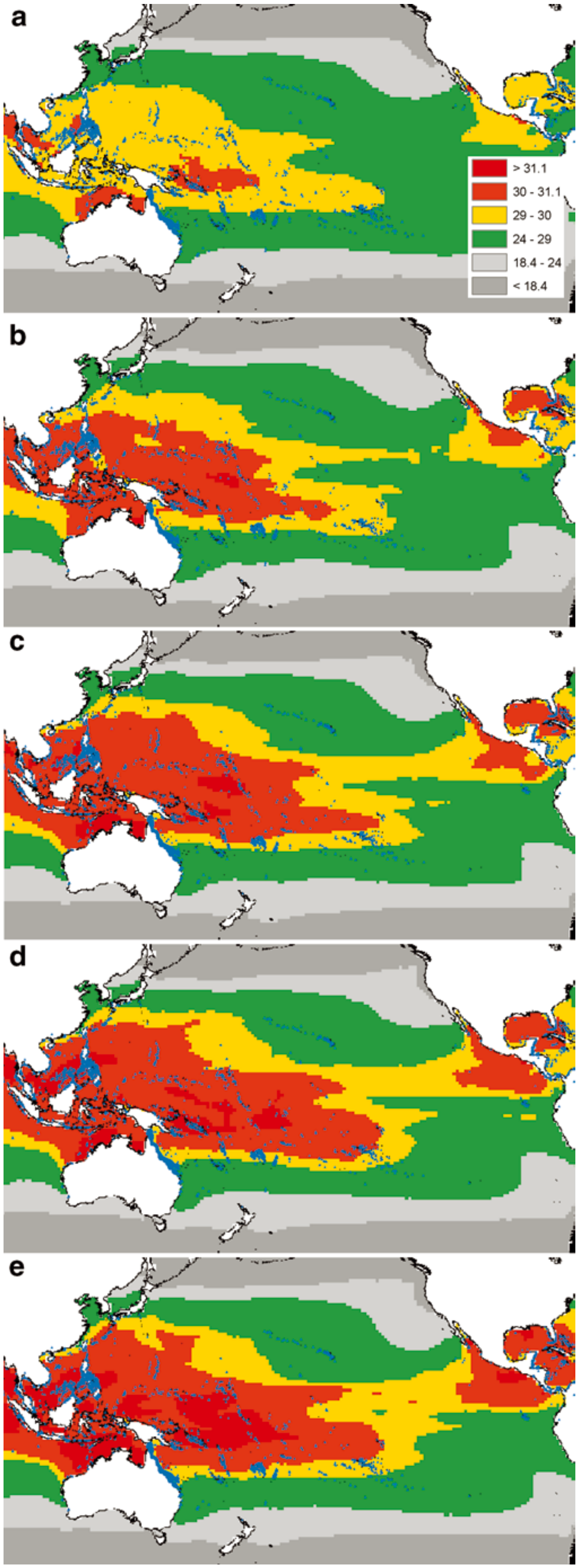

Fig. 1 Maximum monthly sea surface temperature values. **a** Observed 1982–1991 temperatures (Reynolds et al. 2002). **b** Projected values, 2000–2009; $pCO_2 = 375$ ppmv (see text for description of methods). **c** Projected values, 2020–2029; $pCO_2 = 415$ ppmv. **d** Projected values, 2040–2049; $pCO_2 = 465$ ppmv. **e** Projected values, 2060–2069; $pCO_2 = 517$ ppmv. [Depiction of the full decadal time series (2000–2069) may be found in the electronic supplementary material for this paper at the link Springer 10.1007/s00338-003-0331-4]

Kleypas et al. 1999a, 2001)—the pools of optimal and adequate saturation states contract inward from higher to lower latitudes and from the ocean basin margins toward the center. This analysis also highlights some additional important features for the Pacific region:

1. Only the very high latitude reefs (generally those presently deemed marginal) fall into the ''extremely marginal'' (Ω_{arag} < 3.0) category by 2069 (Fig. 2e).
2. By 2069, only a few regions in the tropical oceanic south Pacific remain in the ''adequate'' category (Fig. 2e).
3. The Indo-West Pacific center of reef biodiversity enters the ''marginal'' saturation state category over the period 2020–2049 (Fig. 2c and d).

Discussion

Projections, predictions, and uncertainty

The future scenarios presented in this paper are projections of what is likely to occur if the assumptions and models used are valid. At a general level of accepted physics and oceanography, saturation state and temperature will almost certainly continue to decrease and increase, respectively, and broad latitudinal and longitudinal features of the patterns are probably realistic. Exact rates, final extent, and detailed geographic distributions of change are much less certain. Also, the models and data sets used are primarily oceanic, and are less likely to accurately predict coastal zone conditions.

Controversy surrounds the issue of whether rising atmospheric CO_2 will reduce calcification or buffer the system by dissolving existing carbonate reservoirs in the ocean. Halley and Yates (2000) have conducted field experiments demonstrating that elevated CO_2 may enhance dissolution of high-Mg calcite sediments, which could in turn partially buffer saturation state reductions. This process is likely to be significant only in areas of permeable sediments and restricted circulation (e.g. reef flats), not in the well-flushed areas of highest calcification (e.g. reef slopes).

Future behavior of other climatic and oceanographic factors should also be considered when interpreting these results. For example, recent major bleaching events occurred during El Niño years, but it is not clear whether El Niño intensity and duration will change in response to global climate change (Enfield 2001). Future

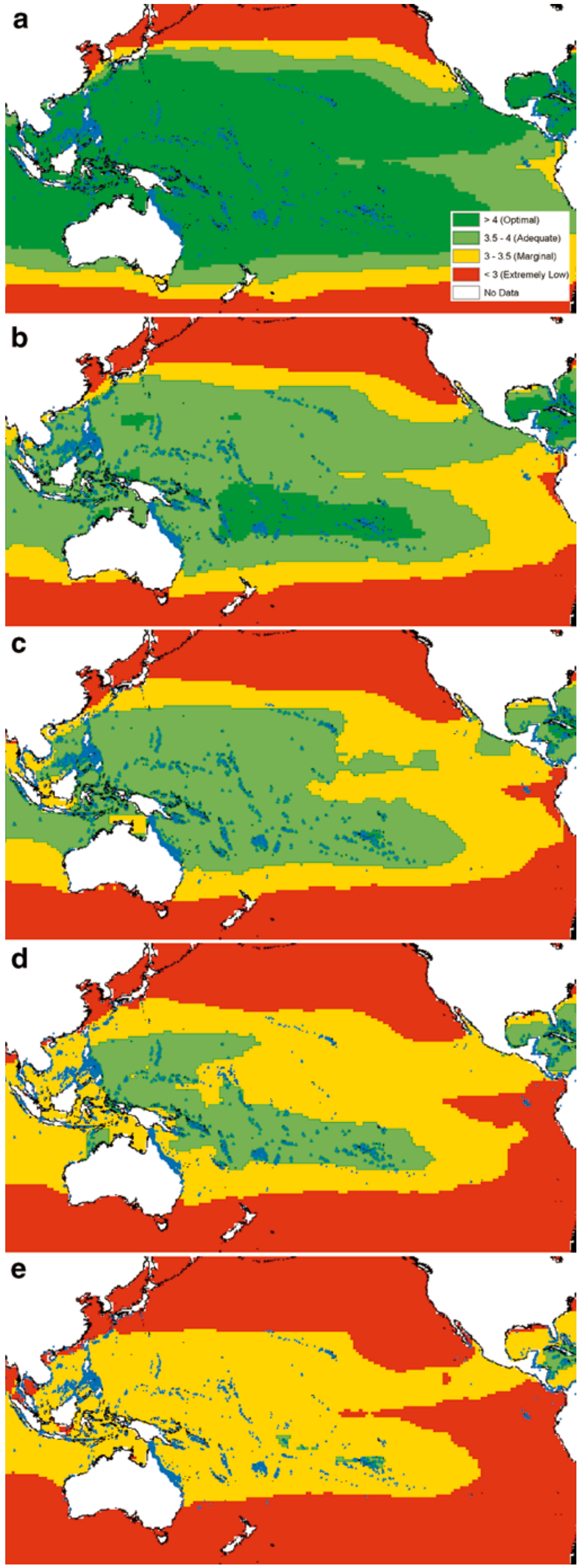

Fig. 2 Aragonite saturation state. **a** Calculated preindustrial (1870) values; $pCO_2 = 280$ ppmv. **b** Projected values, 2000–2009; $pCO_2 = 375$ ppmv (see text for description of methods). **c** Projected values, 2020–2029; $pCO_2 = 415$ ppmv. **d** Projected values, 2040–2049; $pCO_2 = 465$ ppmv. e Projected values, 2060–2069; $pCO_2 = 517$ ppmv. [Depiction of the full decadal time series (2000–2069) may be found in the electronic supplementary material for this paper at the link Springer 10.1007/s00338-003-0331-4]

changes in circulation, wave energy and storm regimes, and upwelling intensity are less predictable features of climate change.

Optimism vs. pessimism

At the global scale, most climate system models show significantly less warming in the tropics than elsewhere on the globe. There is also evidence that various ocean–atmosphere feedbacks will regionally limit the extent of open ocean warming. The ''thermostat hypothesis'' (Ramanathan and Collins 1991; Collins et al. 2000), for example, states that once SSTs rise above a threshold temperature of ~30 °C, convective processes produce both storms and cirrus clouds which shade the surface and curtail further heating. Recent studies suggest that ocean dynamics also play an important role in regulating tropical SST (e.g. Li et al. 2000; Loschnigg and Webster 2000). At the reefal scale, a number of reef areas in nearshore regions or within enclosed seas currently tolerate weekly maximum temperature values ranging from 31.5 to 34.4 °C (Kleypas et al. 1999b). Temperatures within the middle of that range should be within the adaptive and acclimative ranges of at least some reef communities and organisms.

We have used a conservative (= optimistic, from the standpoint of environmental impacts) CO_2 increase scenario, which influences both the rate and extent of temperature and saturation state change. Such a scenario could be a realistic projection, since either coherent international action to reduce emissions or the disruptive consequences of wars or economic depression could act to reduce rates of energy generation from fossil fuels. For the environmental pessimists this holds out the image of a possible future worth working toward; for the environmental (or economic) optimists, it portrays the minimum level of risk and impact that can be expected.

Overview of findings and implications

Based on SST and Ω_{arag} thresholds for reef marginality, essentially all present-day reef habitats in the Pacific Ocean will be ''marginal'' within the next several decades (Fig. 3). The poleward shift of the 18 °C isotherm

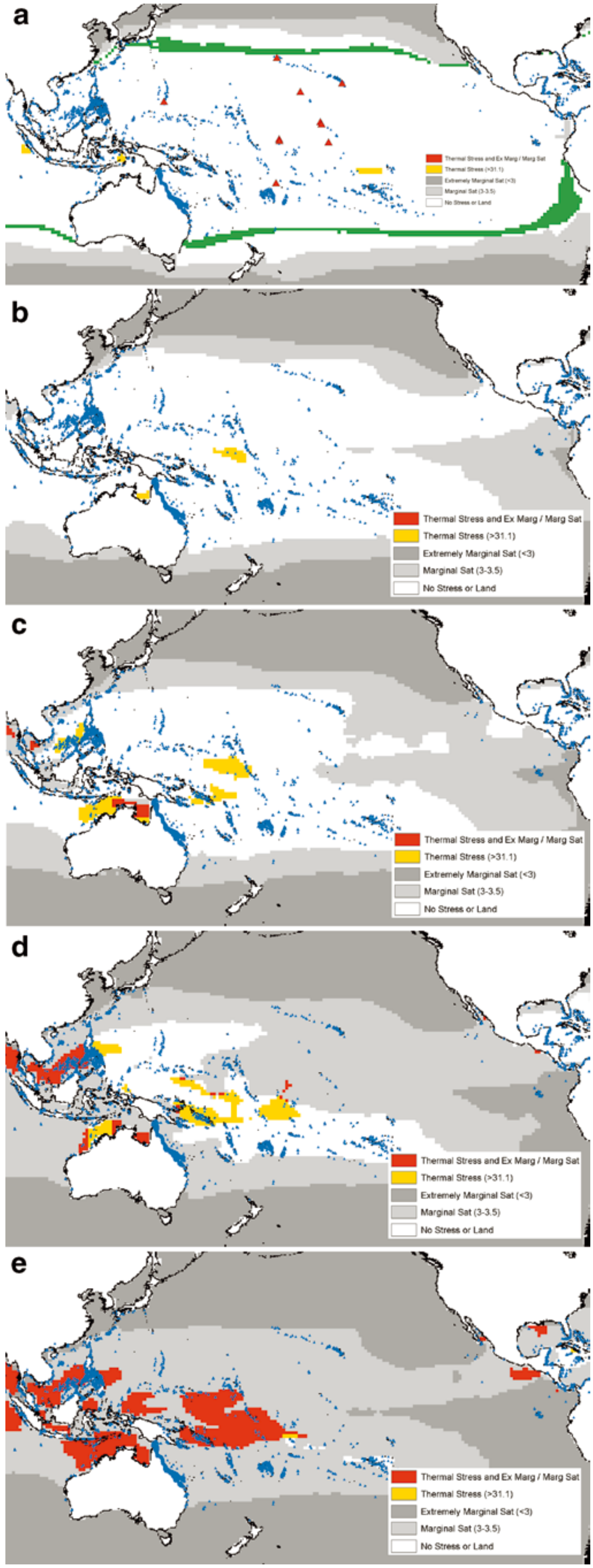

Fig. 3 Index map and composite marginality. **a** Map of preindustrial SST and Ω_{arag} marginal ranges, showing locations of US National Wildlife Refuges and Marine Sanctuaries (red triangles) and range of pole-ward shift of the 18 °C low temperature marginality isotherm (green area), present to 2069. **b** Projected values, 2000–2009; $pCO_2 = 375$ ppmv. **c** Projected values, 2020–2029; $pCO_2 = 415$ ppmv. **d** Projected values, 2040–2049; $pCO_2 = 465$ ppmv. **e** Projected values, 2060–2069; $pCO_2 = 517$ ppmv. [Depiction of the full decadal time series (2000–2069) may be found in the electronic supplementary material for this paper at the link Springer 10.1007/s00338-003-0331-4)

represents only a small increase in potential reef habitat "gained" by global warming. However, the finding of increased reef marginality is not the same as predicting the complete demise of reefs. Within all of the "marginal" categories of Kleypas et al. (1999b), there are significant reef occurrences. Further, the two dimensions of marginality considered represent very different types of stresses. Saturation state reduction will gradually lead to less carbonate accumulation on average, probably to slower extension rates or weaker skeletons in some corals, and possibly to reduced cementation and reef structure stabilization. This suggests that the future will hold more non-framebuilding communities and fewer net accretionary reefs (Kleypas et al. 2001). The expected gradual shift in organism and community behavior due to saturation state change contrasts with the typically episodic response of coral reefs to high temperature stress.

Increasing temperature thus represents an acute stress, whereas lowering of saturation state is a chronic reduction of habitat suitability. Their effects will play out over different time periods, and although they will certainly interact, neither humans nor corals have any experience with that interaction. Under the conditions of the last several million years, temperatures at the upper limit of coral tolerance would seldom if ever have had widespread occurrence at the same times and locations as aragonite saturation states below 4.0.

Implications for reef research, management, and conservation

Human alteration of the oceanic climate is a biophysical experiment that, although unplanned, is neither unpredictable nor lacking in opportunities for adaptive research, monitoring, and management of the affected ecosystems. The projections illustrated in this paper depict a shift in saturation state which will gradually modify reef carbonate accumulation and probably community structure, and which has a distinctive geographic time course. They also show a probable development of regions where maximum temperatures will exceed the normal tolerances of present-day reefs. If these regions also experience episodic extremes (e.g. as associated with El Niño events), then we can also expect increases in mortality. The spatio-temporal evolution of reef marginality that results from the overlapping of these two variables offers some guidance toward understanding the responses of reef organisms and ecosystems to global change, and for incorporating that understanding into management and conservation plans. We suggest three specific areas for development of critical sustained research efforts:

Biodiversity: An important research step will be to quantify the spatial overlap between regions of coral biodiversity ("hotspots") in the Indo-Pacific region (Roberts et al. 2002) and projected marginality in terms of future SST and aragonite saturation state. This undertaking would have two products: (1) to identify regions with high biodiversity at risk; and (2) to identify regions of low biodiversity where reef occurrence may be at risk due to lack of functional replacements for specific vulnerable organisms or guilds.

Terrigenous vs. oceanic effects: Terrestrial influences play a large role in determining community structure of nearshore reefs that are distinct from those associated with oceanic reefs (see Buddemeier and Fautin 2002). The oceanic models used in this study are less reliable in nearshore environments, where terrestrial runoff and local climatic differences can result in local conditions that are significantly modified from those of the adjacent open-ocean water mass. The Australian Great Barrier Reef spans a wide range of latitudes and has well-characterized differences between inner- and outer-shelf reef communities (Harriott and Banks 2002; Ninio and Meekan 2002). The GBR is an ideal location to investigate the spatio-temporal distributions of environmental conditions and their effects on coral communities.

"Space for time" longitudinal studies of climate change effects: Across the oceanic central Pacific, marginal temperature and saturation conditions develop with different rates and patterns. Systematic observation of conditions and ecosystem responses at a network of relatively undisturbed reef sites (e.g. the system of US National Wildlife Refuges and Sanctuaries in the Pacific, illustrated in Fig. 3a) would enhance future evaluations of the individual and synergistic effects of changing temperature and saturation state.

Conclusions

Rising atmospheric CO_2 concentrations will reduce the saturation state of carbonate minerals in the surface ocean over the next 70 years until nearly all locations are in the category identified as marginal by Kleypas et al. (1999b). This will probably result in long-term, gradual decreases in calcification and reef accumulation, and changes in community structure.

Rising oceanic SST will place a number of areas into a temperature category that may be marginal in terms of a maximum threshold, including much of the Indo-Pacific center of reef biodiversity. Most of the tropical Pacific will be in a borderline temperature category based on either absolute temperatures or ranges of variation (Kleypas et al. 1999b).

Probable caps on SST and the gradual reduction in saturation state mean that organisms and communities may be able to adapt or acclimatize to changing conditions. A major caveat in this regard concerns regions of high temperature and low saturation state; this combination of stresses has probably not occurred in evolutionary history, at least over the Plio-Pleistocene.

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