

Effect of repeated climatic impacts on a coral community: a simulation study

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Abstract

The impact of climate change on coral communities remains unknown, though this phenomenon represents a major contemporary threat to coral reefs. While immediate responses of corals to anomalous sea temperatures (bleaching and mortality) have been well reported for many areas, long-term changes to coral populations and communities are less well understood. We addressed this by employing a previously developed and tested simulation model in conjunction with species-specific thermal responses of corals and predictions of future climate. The model is spatially explicit and has a probabilistic cellular automaton core. Life history processes of corals such as recruitment, growth, aggression and background disturbance are implemented deterministically. Corals were assumed unable to adapt to temperature change fast enough to keep pace with predicted trends. Climate change was implemented as a sequence of anomalous sea warming events derived from HadCM3 global climate model data. Following application of this sequence, the modelled community rapidly lost its integrity. There were two main community responses: 1) a shift in community structure towards corals with an ephemeral life history (or strategy shift) at 15 years and 2) a phase shift whereby the community moved from coral- to algal-dominated at 50 years. Life history and variation in vulnerability to warming mediated the degree of vulnerability. Some species resisted repeated warming, e.g. *Agaricia* spp. and *Porites astreoides*, while others were extremely vulnerable, e.g. *Montastraea annularis*, the main reef-framework building species. We conclude that future reefs may not be dominated by this species, and that there will be resounding implications of ecological and economic significance accompanying this altered reef functioning.

Introduction

The impact of climate change on coral communities remains unknown, though this phenomenon represents a major contemporary threat to coral reefs (Wilkinson and Hodgson, 1999). Prior to 1998, concern for the degradation of reef systems was focussed on the effects of local agents, mostly induced by human activities, and conservation and management objectives were often the direct mitigation of these activities (Hughes and Connell, 1999). In the wake of the 1998 global coral mortality event, attention has moved to encompass global impacts, namely sea warming. While immediate responses of corals to anomalous sea temperatures, manifest as bleaching and mortality, have been well reported for many areas of the Western Atlantic (Lang et al., 1992, Meesters and Bak, 1993, Fitt et al., 1993, Ghiold and Smith, 1990, Lang et al., 1988, Cook et al., 1990, McField, 1999, Kramer and Kramer, 2000, Wilkinson and Hodgson, 1999), long-term impacts in terms of changes to coral populations and communities are less well understood. Furthermore, is not known how changes in community structure may affect the functionality of coral reef communities. At present, there is no comprehensive system is available for predicting effects of global impacts manifest at local scales, and our understanding of community and population responses is generalised (Bak and Meesters, 1999, Done, 1999, Hoegh-Guldberg, 1999).

Coral bleaching can be functionally defined as the loss of the normal brownish colour characteristic of healthy corals, due to mass expulsion of symbiotic zooxanthellae from coral tissues and/or the decrease in photosynthetic pigments within individual zooxanthella (Hoegh-Guldberg, 1999). Bleaching is a stress response of corals to a range

of environmental stresses e.g. cold, salinity changes, light changes, low tides, sedimentation and pollution, though it has received most attention as a response to increased sea temperature (Glynn, 1996, Hoegh-Guldberg, 1999, Wilkinson and Hodgson, 1999). This may occur at local scales, (e.g. parts of reefs, Goreau, 1992) or at geographic scales that may involve whole reef systems (e.g. mass bleaching, Williams and Bunkley-Williams, 1988, Hoegh-Guldberg, 1999, Glynn, 1996). Frequently corals recover from bleaching (Fitt et al., 1993, Lang et al., 1992, Mumby, 1999), but death may result if the stress is extreme or prolonged, as occurred over large areas of reefs in the Indian Ocean during 1998 (Sheppard, 1999, Wilkinson and Hodgson, 1999). Bleaching is elicited by sea temperature above expected climatology (maximum monthly mean, MMM) for a period of time, e.g. ≥ 10 degree heating weeks (cumulative number of weeks where the sea surface temperature (SST) is $\geq 1^\circ\text{C}$ above the MMM) are accompanied by severe bleaching followed by mortality (see www.osdnpd.noaa.gov/PSB/EPS/method.html for details).

Coral species differ in their susceptibility to anomalous sea temperatures (Williams and Bunkley-Williams, 1988); generally corals with the highest rates of skeletal growth and respiration are most susceptible (Glynn, 1996). Furthermore, within populations of the same species bleaching responses are also different with bleached lone corals or groups of corals interspersed with normal coloured conspecifics (Jokiel and Coles, 1990, Williams and Bunkley-Williams, 1988), which may be related to genotypic differences (Edmunds, 1994), depth (Fisk and Done, 1985, Ghiold and Smith, 1990) or individual history (Sheppard, 1999, Brown et al., 2002).

Bleaching can have profound physiological consequences, even when colonies survive growth may be compromised (Goreau and Macfarlane, 1990, Leder et al., 1991, Suzuki et al., 2000), fecundity reduced (Szmant and Gassman, 1990, Omori et al., 2001, Sheppard et al., 2002), competitive ability (Diaz-Pulido and McCook, 2002) and the capacity to regenerate lost tissue or skeleton impaired (Mascarelli and Bunkley-Williams, 1999, Meesters and Bak, 1993), and such physiological stress may compromise host resistance leading to increased frequencies of opportunistic diseases (Harvell et al., 1999, Hayes and Goreau, 1998, Kramer and Kramer, 2000, McField, 1999). These changes may last for more than 1 year following a warming event.

The overall objective of this work was to employ a previously developed and tested simulation model (Langmead, 2002, Langmead and Sheppard, 2004, Langmead and Sheppard, *submitted*) in conjunction with species-specific thermal responses of corals and predictions of future climate to gain insight into how coral populations and communities are likely to change over the course of the next 100 years. Assumptions were based on known immediate responses of individual corals to recent real warming events, as outlined above, in order to expand our understanding of how an interacting, multi-species community may respond to repeated and intensifying warming events.

Materials and Methods

Coral community model

The impact of repeated warming events was simulated using a coral community model previously developed and validated (full details in Langmead and Sheppard, 2004, Langmead, 2002). The model is spatially explicit and at its core is a probabilistic cellular automaton. It represents a 9 m² plot of homogeneous reef substratum on a Caribbean fore-reef slope. Life history processes of corals such as recruitment, growth, aggression and background disturbance are implemented deterministically. The model was previously tested against field data and found to be capable of accurate predictions of both community dynamics and high-resolution demographic patterns (Langmead and Sheppard, 2004).

Previous studies on the effects of single warming events investigated coral community resilience under various intensities of impact and local settings (Langmead and Sheppard, *submitted*). Immediate warming responses of corals were based on recent real events. The current work builds on this by expanding the scope to repeated impacts of warming events by combining predictions of future warming episodes from a global climate model together with previously characterised species-specific thermal responses.

‘Algae’ in the model includes all benthic types, it can occupy vacant space and colonise new space, is vulnerable to removal during disturbances (Ostrander et al., 2000), and while it cannot overgrow healthy corals (Bak et al., 1977, de Ruyter van Steveninck et al.,

1988, McCook et al., 2001, Meesters et al., 1994), it is able to outcompete bleached corals (Diaz-Pulido and McCook, 2002, McClanahan et al., 2001, Shulman and Robertson, 1996) (full details in Langmead, 2002).

Warming responses by corals were simulated by allocating coral species probabilities of bleaching or dying during warming events of varying intensities, based on recent real events (Langmead and Sheppard, *submitted*, Langmead, 2002). Bleached corals remained bleached for 1 year after which they either returned to a healthy state or died. Coral species had differential susceptibility to bleaching, but once in a bleached state, they were not able to grow, reproduce, repair damaged tissue and their competitive abilities were impaired. Further assumptions include: 1) corals do not adapt or acclimatize to temperature change at the speed needed to respond to current trends, 2) coral bleaching is induced solely by high sea temperature (UVR and PAR have a role in bleaching responses, but are not included here because of lack of predictions of light levels) and 3) climate change is manifest only as increased SST (aragonite saturation level (Kleypas et al., 1999), sea level rise (Done, 1999) and storm frequency/intensity changes (Pittock, 1999) are also likely to change with climate, but are not included here again due to a lack of clear predictive data).

Application of HadCM3 SST data

SST predictions (as monthly means) from a global climate model, HadCM3, were used to indicate future frequency and intensity of warming events (details of the model can be found at www.metoffice.com/research/hadleycentre/models/HadCM3.html). Data from Belize (83°30' - 87°15'W, 15°00' - 17°50'N) was extracted for 3 reasons: climatic details

are known, there are several bleaching reports from this area which were used to estimate coral responses (Langmead and Sheppard, *submitted*) and field measurements of coral competition were from this area (Langmead, 2002). The maximum monthly mean (MMM) for a 20-year period between 1980-1999 was calculated and compared to a historical dataset (HadISST, see www.metoffice.com/research/hadleycentre/obsdata/GISST.html for details) for the same area and time to check for accuracy of the model data, and the latter was corrected (Langmead, 2002). Degree heating months (DHM) were extracted from the full dataset (1950-2100) by firstly calculating anomalies (subtracting the MMM) to identify the magnitude of warming events, and where the monthly mean SST was 1°C above the MMM, this was considered 1 DHM, 2 DHMs was either two consecutive months of the monthly mean 1°C above the MMM, or one month of 2 °C above the MMM. Thresholds were set so that 1 DHM was categorised a ‘mild’ event, 2-3 DHMs ‘moderate’ and anything above this was considered ‘severe’.

Experimental design

The coral community model was run for 300 years to allow coral communities to stabilise prior to applying impacts from the derived warming sequence. This initial part of the run was not used in analyses, and year 0 corresponds to immediately prior to warming sequence application. 20 replicate simulations were run to account for inbuilt model stochasticity, with results taken as percent cover every year, and the number and size of colonies at 10 year intervals. Coral species were grouped according to their responses to the warming sequence; *Montastraea annularis*, *M. cavernosa* and *Stephanocoenia michelinii* formed one group, while *Agaricia* spp., *Porites astreoides* and *Colpophyllia*

natans composed another. A Bray-Curtis similarity matrix (Bray and Curtis, 1957) was constructed from mean percent cover at 2 year intervals and this was used to plot a multidimensional scaling (MDS) ordination to represent community trajectories. Population size structure analyses were done by pooling colony sizes for all replicates and then dividing them into broad size classes on a log-scale, with the proportion of the population calculated by species and time increment.

Results

Following application of the warming sequence, the community rapidly lost its integrity, and shortly after 10 years there was an unprecedented decline in *Montastraea annularis* (the spatially dominant species) and also declines in *M. cavernosa* and *S. michelinii* (Fig. 1). Other species increased in abundance, between 15 and 50 years *P. astreoides*, *C. natans* and *Agaricia* spp. opportunistically expanding into space freed by the decline of the large reef-building species. This change in coral type can be viewed as a 'strategy shift' (*sensu* Done, 1999), as there is a change in dominance from slow-growing, large, long-lived species to highly fecund, ephemeral, small, fast-growing species. However, at around 50 years, these corals also declined and were replaced by algae, constituting a phase shift (Hughes, 1994).

Breakdown of community integrity is evident from the MDS ordination (Fig. 2), where the main decline runs from left to right, but is complicated by a diagonal pattern of disturbance and recovery. Disturbance is characterised by peaks in algal abundance immediately following warming events and initial recovery processes are marked by increases in *Agaricia* spp. It is clear that under the predicted sequence of warming events, the coral community departs its characteristic structure at around 10 years, and does not return to this starting state, instead is pushed further and further away from it with successive warming events. No differences in community structure can be determined after 70 years; at this point the community is entirely degraded and cannot be further degraded.

The population dynamics of *Montastraea annularis* show a rapid decline that is complete within 20 years of warming sequence initiation (Fig. 3). At this point the population of *M. annularis* was almost non-existent, although there is sporadic recruitment, and is reflected in both the population size structure, which falls entirely within the 1-10 cm² colony size class (a drop of > 3 orders of magnitude), and the number of colonies (Fig. 3).

Discussion

The modelled coral community changed rapidly and irreversibly with the application of the HadCM3-derived sequence of warming events. The model demonstrated two community responses: firstly there was a shift in community structure from large, slow-growing, long-lived corals to ephemeral, small, fast-growing corals, and secondly a phase shift from a system state dominated by corals to one of algae. The timing for these responses was rapid, the shift in strategy occurred just 15 years into the warming sequence, and the phase shift at around 50 years. However, the timing of these community responses is likely to be conservative; (Hoegh-Guldberg, 1999), using data from several global climate models, predicted that Caribbean reef systems will experience near-annual warming events by the year 2020 compared with 2035 for the HadCM3-derived sequence used in this study. This work represents the first qualitative prediction of the pattern of coral community responses to predicted warming events.

Life history strategy and variation in vulnerability to warming mediated the degree to which Caribbean coral species were able to resist the effects of predicted climate change. Some corals such as *Montastraea* spp. and *Stephanocoenia michelinii* were extremely vulnerable, declining rapidly to near extinction with no evident recovery. This can be explained by attributes of their life histories, being relatively slow growing (Huston, 1985), large corals (Soong, 1993) with low rates of recruitment (Rylaarsdam, 1983, Hughes, 1985, Rogers et al., 1984), and also vulnerable to bleaching (Meesters and Bak, 1993, Fitt et al., 1993, Ghiold and Smith, 1990, Lang et al., 1988). This combination of traits meant that once populations were impacted by an event early in the sequence,

recovery was so slow as to be rendered undetectable and subsequent impacts further depleted populations. This is reflected in differences between required recovery time and predicted repeat time for warming events: for the largest *M. annularis* colonies at the start of the warming sequence to be replaced requires approximately 42 years, while the longest period between subsequent events was just 8 years. Similar dramatic declines in *M. annularis* populations have been reported from Jamaica, caused by impacts from hurricane damage and the results of the die-off of an echinoid grazer (Hughes and Tanner, 2000). The colony size frequency distribution shifted rapidly as large colonies were dismembered into small remnants, many of which were subsequently overgrown by algae.

The vulnerability of *Montastraea annularis* demonstrated by the model may even be underestimated, due to two further mechanisms enhanced by its life history strategy (low fecundity, propensity for asexual reproduction and longevity). 1) Allee effect (inverse density dependence at low density) which would be manifest on populations as chronic reproductive failure (Courchamp et al., 1999, Knowlton, 2001). 2) If adaptation is possible for corals within the scale of climate change, *M. annularis* is not best equipped to adapt as a) reproducing mostly asexually means there is not much opportunity for genetic recombination to generate adaptive traits (Lasker and Coffroth, 1999), b) long generation times mean a low turnover of adaptive traits, and c) as colonies shift to smaller sizes with the fragmentation of large colonies, they will no longer be fecund (Soong, 1993, Meesters et al., 2001), exacerbating all other effects. Although arguably these

mechanisms operate in all coral populations under conditions of chronic disturbance, it is likely to be of particular significance for *M. annularis*.

Agaricia spp., *Porites astreoides* and *Colpophyllia natans* increased in abundance with the onset of the warming sequence. Again, this is related to the life history of these species, being capable of high tissue turnover by possessing high growth and recruitment rates (refs). And although these species are susceptible to bleaching, the opportunity for population expansion appeared to outweigh the impacts of climate change, at least for the first part of the warming sequence. This result agrees with other modelling and field studies: *Agaricia agaricites* is highly resilient to hurricane disturbances (Andres and Rodenhouse, 1993), and *P. astreoides* actually increased in density by 9% following warming and hurricane disturbance in Belize (McField pers. comm.).

If the model is accurate in its predictions with respect to coral community responses (although not necessarily timing, see above), there will be enormous ecological and economic implications. Changes in community structure to more ephemeral species and in particular the loss of the major framework building species, *Montastraea annularis*, is likely to affect reef accretion rates. This may alter the balance of reef growth vs. erosion, potentially leading to a loss of reef structural material. Not only does the physical reef framework act as a barrier to wave energy and hence coastal erosion, but also its intrinsic topographic complexity provides habitat for a vast array of organisms, including commercially important fish and shellfish species. Algal reef does not usually have the same level of 3-dimensionality required to support such high diversity. These processes

are likely to be exacerbated by 3 other predictions of climate change not included in this model, namely aragonite saturation state (predicted to decrease with increased sea temperature, leading to a 14-30% decrease in coral calcification rate by 2050 (Kleypas et al., 1999)), sea level rise (Done, 1999) and increased storm frequency and intensity (Pittock, 1999). Finally the value of reefs as tourist sites is likely to diminish. It is possible that the economies of small island states dependant on reef tourism will be affected by the degradation of reefs through climate change. Thus the ability to accurately predict its consequences is extremely important.

While this model appears to have captured the essential behaviour of reef communities (Langmead, 2002, Langmead and Sheppard, 2004), and dynamic of populations undergoing repeated impacts, ultimately it is a simplification of the system; only corals and algae are present. Real reef communities are composed of many more components interacting together and constitute one of the ecologically complex and diverse systems on the planet. Also factors not included in these simulations can play a role in intensifying impacts of warming events e.g. local stressors such as pollution, sedimentation, overfishing (Done, 1999) and secondary effects of warming such as increased disease prevalence (Hayes and Goreau, 1998, Kramer and Kramer, 2000, Ostrander et al., 2000). These factors are now operating ubiquitously across reefs of the Western Atlantic region; even the most isolated reefs, such as the atolls off the coast of Belize bear signs of multiple stressors (Kramer and Kramer, 2000). Furthermore, corals in this study were assumed to be unable to adapt or acclimatize to their changing environment. It is hoped that ongoing work into the ability of corals (Brown et al., 2002,

Brown, 1997) and/or symbionts (Baker et al. 2002) to acclimate or adapt may reveal such processes can occur more rapidly than previously thought and force us to revise our assumptions.

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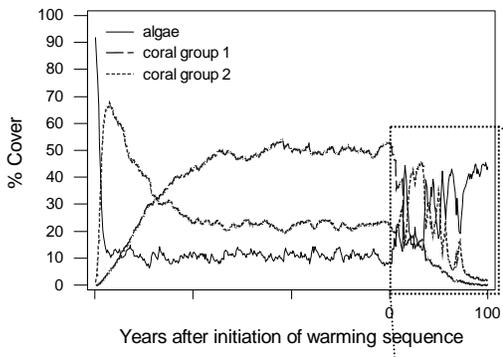
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Fig. 1. Coral community dynamics with predicted climate change. Abundance of coral group 1 (*Montastraea annularis*, *M. cavernosa* and *Stephanocoenia michelinii*), coral group 2 (*Agaricia* spp., *Porites astreoides* and *Colpophyllia natans*) and algae for the duration of the simulation. Insert shows 2 community responses to warming sequence. Percent cover, mean of 20 replicates.

Fig. 2. MDS ordination of modelled coral community trajectory during warming sequence. Triangles represent community structure at 2 year intervals, solid arrows show transitions forced by warming events, while broken arrows show partial recovery between impacts. The numbers 0-7 correspond to the timing of events, see warming sequence insert.

Fig. 3. *Montastraea annularis*. Population dynamics during warming sequence (a) colony size frequency distribution (given as proportion of total population in log size classes) and colony counts (given as mean \pm 1SD, n = 20).



strategy shift

phase shift

