

# How much time can herbivore protection buy for coral reefs under realistic regimes of hurricanes and coral bleaching?

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## Abstract

Coral reefs have been more severely impacted by recent climate instability than any other ecosystem on Earth. Corals tolerate a narrow range of physical environmental stress, and increases in sea temperature of just 1 °C over several weeks can result in mass coral mortality, often exceeding 95% of individuals over hundreds of square kilometres. Even conservative climate models predict that mass coral bleaching events could occur annually by 2050. Unfortunately, managers of coral-reef resources have few options available to meet this challenge. Here, we investigate the role that fisheries conservation tools, including the designation of marine reserves, can play in altering future trajectories of Caribbean coral reefs. We use an individual-based model of the ecological dynamics to test the influence of spatially realistic regimes of disturbance on coral populations. Two major sources of disturbance, hurricanes and coral bleaching, are simulated in contrasting regions of the Caribbean: Belize, Bonaire, and the Bahamas. Simulations are extended to 2099 using the HadGEM1 climate model. We find that coral populations can maintain themselves under all levels of hurricane disturbance providing that grazing levels are high. Regional differences in hurricane frequency are found to cause strikingly different spatial patterns of reef health with greater patchiness occurring in Belize, which has less frequent disturbance, than the Bahamas. The addition of coral bleaching led to a much more homogenous reef state over the seascape. Moreover, in the presence of bleaching, all reefs exhibited a decline in health over time, though with substantial variation among regions. Although the protection of herbivores does not prevent reef degradation it does delay rates of coral loss even under the most severe thermal and hurricane regimes. Thus, we can estimate the degree to which local conservation can help buy time for reefs with values ranging between 18 years in the Bahamas and over 50 years in Bonaire, compared with heavily fished systems. Ultimately, we demonstrate that local conservation measures can benefit reef ecosystem services but that their impact will vary spatially and temporally. Recognizing where such management interventions will either help or fail is an important step towards both achieving sustainable use of coral-reef resources and maximizing resource management investments.

**Keywords:** climate change, coral bleaching, coral reef dynamics, global climate model, grazing, hurricanes

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## Introduction

Concern over the degradation of coral-reef ecosystems has risen sharply in recent decades (Birkeland, 1997;

Dight & Scherl, 1997) because such local and direct human activities as habitat modification, poor sewage treatment, and resource extraction increasingly alter the natural capital and services associated with reef ecosystems (Connell, 1997). More importantly, such degradation increases the vulnerability of coral reefs to changes in temperature, storms, and ocean chemistry (Hoegh-Guldberg *et al.*, 2007). As many of the global or regional stressors cannot yet be mitigated directly, managers

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typically have to limit their toolbox of local interventions to the management of local factors alone. A key question facing managers is 'to what extent can the management of local stressors influence the response of reefs given the inevitable impacts of climate change?' Many managers expect that local interventions could have a credible impact of 'buying time' but have no means to judge in which areas such measures will be sufficiently effective (P. J. Mumby, personal observations).

The principal climate change drivers on Caribbean coral reefs are rising sea temperatures, which cause coral bleaching (Donner, 2009), possibly a weak increase in the severity of hurricanes (Emanuel, 2005; Webster *et al.*, 2005), and ocean acidification (Kleypas & Langdon, 2007). Thermal stress causes coral bleaching, which frequently results in mass coral mortality (Wilkinson, 1998), and may facilitate outbreaks of coral disease (Muller *et al.*, 2008; Rogers, 2008). Hurricanes are an integral part of coral-reef ecology (Connell, 1978) and their impacts are notoriously patchy on many spatial scales (Done, 1992; Bythell *et al.*, 2000). Hurricanes may also alleviate thermal stress on coral reefs through a reduction in sea temperatures caused by wind-forced vertical mixing (see Manzello *et al.*, 2007).

Ocean acidification principally decreases coral calcification rates (Langdon & Atkinson, 2005; Silverman *et al.*, 2009), although the ecological consequences of this are not yet clear (Jury *et al.*, 2010). Additionally, acidification may decrease secondary cementation of reefs (Manzello *et al.*, 2008) and increase bioerosion. Declining aragonite saturation state will likely reduce the growth rate of some corals and perhaps the skeletal density of others, rendering them more vulnerable to hydrodynamic disturbances (Madin *et al.*, 2006). Reduced cementation also reduces the structural integrity of reef structures (Manzello *et al.*, 2008). Both of these can make reefs more vulnerable to natural hurricane activity, perhaps by making corals and reefs more vulnerable to breakage and definitely through slowed growth during poststorm recovery. Short-term experimental studies have found high CO<sub>2</sub> to act synergistically with warming to lower thermal bleaching thresholds (Anthony *et al.*, 2008), but whether these results extend to field situations has not yet been determined.

Two common direct approaches to manage coral reef resources are improving watershed and fishery management. Watershed management can reduce levels of sediment and nutrients reaching the reef and reduce factors that cause chronic stress to coral-reef ecosystems (Birrell *et al.*, 2005; Richmond *et al.*, 2007). Sewage treatment can reduce nutrification, helping to keep the balance between the growth of corals and algae and

prevent algal overgrowth of reefs. However, managing the fishery, either through local no-take marine reserves or restrictions to the harvesting of key species, can enhance levels of grazing (McClanahan, 1995) and therefore keep algal populations in check. In the Caribbean, the cover of macroalgae on reefs is linearly related to the biomass of herbivorous fishes, both at regional scales (Williams & Polunin, 2000) and at local scales (Mumby *et al.*, 2006a) when no-take marine reserves have elevated the numbers of parrotfish. Macroalgae compete with corals for space, both preempting space for settlement and through direct antagonistic interactions and overgrowth (McCook *et al.*, 2001; Nugues & Bak, 2006). Therefore, a reduction in algal cover – be it caused by better management of the watershed, sewage, or fishery – should facilitate coral recovery after disturbance. Indeed, recent evidence from a series of reefs in the Bahamas showed that coral recovery was linearly and negatively related to macroalgal cover and positively related to grazing (Mumby & Harborne, 2010).

Here, we study the degree to which the implementation and enforcement of no-take marine reserves (or a ban on parrotfish harvesting) might influence the future trajectories of Caribbean reefs. We focus on marine reserves because they are the most widely used conservation measure being deployed on coral reefs (though we recognize that marine reserves also need to be supplemented by better management of fished sectors on the reef). We also focus on reserves because their impacts on herbivore density, macroalgal cover, and coral recovery have been verified empirically (Mumby *et al.*, 2006a; Mumby & Harborne, 2010). While improved sewage treatment is undoubtedly a priority for reef management, the reduction of both source and nonsource pollutants to a reef is difficult to quantify, and the magnitude of their effects on algal blooms are not yet clear. Thus, reduction of sewage cannot be modelled easily at this time.

In addition to promoting herbivory by protecting parrotfishes, we also consider the functional significance of a recovery of the long-spined sea urchin, *Diadema antillarum*. A pan-Caribbean disease decimated populations of this urchin in 1983/1984 (Lessios, 1988) and recovery is beginning at a number of sites in the Caribbean (Carpenter & Edmunds, 2006). However, recovery has rarely extended from the urchins' favoured shallow reef habitat into deeper (>5 m) parts of the reef. Nonetheless, we explore the consequences of a modest recovery of urchins (densities of approximately 1 m<sup>-2</sup>) on mid-depth reefs.

We focus on two climate impacts that are reasonably well understood; hurricanes and coral bleaching and develop spatially realistic models of disturbance.

Currently, there are too many uncertainties to include ocean acidification in this modelling effort. While ocean acidification has been shown to reduce growth of some corals, the impact varies across species (Anthony *et al.*, 2008). Additionally, spatial patterns of ocean acidification across the Caribbean and patterns between offshore and reef environments are not yet clear. Thus, our goals here are to present spatially realistic models of climate-change impacts on Caribbean reefs and ascertain the extent to which local changes in grazing, be it through marine reserves or urchin recovery, can influence their dynamics. Specifically we ask the questions:

1. What are the predicted return times for bleaching and hurricane events in different regions of the Caribbean? At what spatial scale do return times change?
2. What are the relative effects of hurricanes and coral bleaching in creating spatial variance in the health of coral reefs?
3. To what extent can grazing fishes and urchins compensate for the impacts of disturbances and essentially buy time for reefs?
4. What are the implications of the results for managing coral-reef resilience?

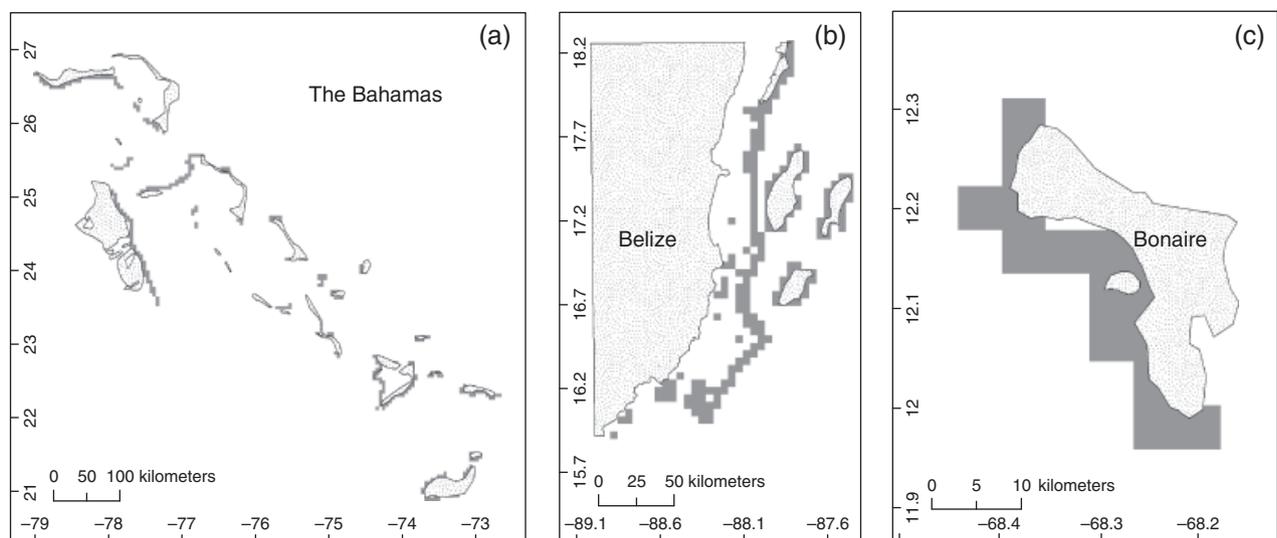
### Materials and methods

An individual-based model of the *Montastraea annularis* zone of a Caribbean coral reef was used to model the ecological dynamics and subject coral populations to spatially realistic regimes of disturbance. Future disturbance events were predicted at a resolution of 4 km by 4 km, and the model simulated for all 4 km grid squares containing *Montastraea* reefs. No

other model parameters were modelled to vary with location. Coral reefs were simulated in three contrasting regions of the Caribbean (Fig. 1). The simulation model was originally designed to represent mid-depth *Montastraea*-dominated fore-reefs, which typically harbour the highest biomass and diversity of reef organisms. Since white-band disease has depleted populations of large, branching corals (Aronson & Precht, 2001) stylized massive growth forms of coral were simulated together with rates of recruitment, growth, reproduction and mortality. The model is a square lattice of 2500 cells, each of which approximates 0.25 m<sup>2</sup> of reef, and can be occupied by a mixture of living and dead substrata (Table 1). Although the reef has a continuous (toroidal) lattice of 2500 cells, the lattice structure merely helps define probabilistic rules of coral recruitment and coral and algal growth. Individual cells comprise multiple coral colonies and algal patches so interactions occur at colony scales as they do *in situ*. Corals can recruit to individual patches of cropped algae (which in this model harbor little sediment) but not on species of macroalgae. Earlier studies have conducted sensitivity analyses and compared model predictions to a 20-year time series of data from Jamaica (Mumby *et al.*, 2007). Full details of the model and parameters are provided in Appendix S1 but extensions to the model, to simulate more realistic disturbance events, are described here in full.

### Bleaching events

Observed climatologies [Pathfinder 4 satellite-based weekly sea surface temperatures (SSTs) from 1985 to 2005, with quality flags 4 and above] were acquired from NOAA at a 4 km scale (<http://www.nodc.noaa.gov/sog/pathfinder4km/>, Kilpatrick *et al.*, 2001). Future SSTs were derived from the SRES A1 scenario (Nakicenovic *et al.*, 2000) run of the UK Hadley Centre Global Environmental Model HadGEM1 (Johns *et al.*, 2004). HadGEM1, a coupled atmosphere-ocean general circulation



**Fig. 1** Shaded areas represent 4 km grid squares containing reefs in (a) the Bahamas (356 sites), (b) Belize (206) and (c) Bonaire (15).

**Table 1** Contents of individual cells (0.25 m<sup>2</sup>) within the model

Substratum	Constraints	Range (cm <sup>2</sup> )
Brooding coral (BC) (e.g. <i>Porites astreoides</i> )	Up to three individuals per cell	$1 \leq BC \leq 2500$
Spawning coral (SC) (e.g. <i>Siderastrea siderea</i> )		$1 \leq SC \leq 2500$
Cropped algae [filamentous, coralline red algae, and short turfs (<5 mm height)], 0–6 months (A <sub>6</sub> )		$0 \leq A_6 \leq 2500$
Cropped algae, 6–12 months (A <sub>12</sub> )		$0 \leq A_{12} \leq 2500$
Macroalgae (e.g. <i>Dictyota pulchella</i> , <i>Lobophora variegata</i> ), 0–6 months (M <sub>6</sub> )		$0 \leq M_6 \leq 2500$
Macroalgae, 6+ months (M <sub>12</sub> )		$0 \leq M_{12} \leq 2500$
Ungrazeable substratum (e.g. sand), <i>U</i>	Fills entire cell if present	$U = 0$ or $U = 2500$

All substrata represented as area (cm<sup>2</sup>).

model, predicts changes in atmospheric and SSTs at a resolution of 1° × 1°. The SRES future emissions scenarios were designed to reflect different paths of future economic development and energy use. Scenario A1 describes a future typified by rapid economic growth that only takes moderate steps to deal with climate change. Three options under the A1 scenario are distinguished by their technological emphasis: fossil-intensive (A1FI), nonfossil energy sources (A1T), or a balance across all sources (A1B). Although A1 may be considered the worst-case scenario of the four major IPCC scenarios it should be noted that at current growth rates of CO<sub>2</sub> emissions (~2 ppm yr<sup>-1</sup>) (Tans, 2010), we are currently travelling along a trajectory that exceeds not only scenario A1B, but also the disastrous fossil intensive (A1FI) scenario. We focus our analysis on the impacts before the year 2100.

Forecast temperatures rarely flow seamlessly from historical data (Sheppard, 2003). Following Donner *et al.* (2005) this was taken into account by calculating the difference between the HadGEM1 projected monthly SSTs (e.g., January 2080) and the simulated SST for 'today' (e.g., January mean for 1980–2000), known as the GCM anomalies. The monthly SST was estimated as the sum of this simulated temperature change and the observed (historical) monthly data for each location, where observations of SSTs were taken from the NOAA climatology (e.g., January mean for 1985–2002). Since the spatial resolution of the NOAA and HadGEM1 datasets was different, the location of the centre of each NOAA 4 km cell was used to identify the corresponding HadGEM1 cell.

Here the underlying cause of coral bleaching is assumed to be elevated temperatures. Bleaching was modelled to occur at a range of temperatures, but with mortality dependent on the magnitude and duration of thermal stress. Projected temperatures and historical SST climatologies were used to calculate the number of degree heating months (DHMs) (Donner *et al.*, 2005), representative of the cumulative heating stress on a coral reef throughout the year, predicted for each summer from 2010 to 2099. A DHM is equal to one month of SST that is 1 °C greater than the maximum in the monthly climatology for that grid cell.

Bleaching usually occurs in summer months and was therefore simulated at a maximum of once every other 6-month time step of the simulation model. SSTs and thus degree

heating weeks (DHW) vary with spatial location, as do storm return times.

### Coral bleaching mortality

Probabilities of coral mortality after initial and subsequent bleaching events were derived from three datasets. Subadult (size 61–250 cm<sup>2</sup>) and adult corals (size >250 cm<sup>2</sup>) were modelled to undergo whole-colony and partial-colony mortality as a result of bleaching. Brooding and broadcasting corals were affected differently by raised temperatures, and corals that had previously been exposed to elevated SSTs were modelled to have a lower risk of mortality during subsequent bleaching events (Thompson & van Woesik, 2009).

Data on whole-colony mortality were taken from 1057 field surveys in the Caribbean, spanning the timeframe June 4, 2005 through January 21, 2006 (Eakin *et al.*, 2010). These data were collected during the most extensive coral bleaching event recorded in the greater Caribbean (Donner *et al.*, 2007; Wilkinson & Souter, 2008; Eakin *et al.*, 2010). For each data pixel, Eakin *et al.* (2010) calculated the DHW (°C weeks) values, and the date and value of the maximum DHW. The number of DHWs is calculated by accumulating HotSpots ≥ 1 that occur during a 12-week window, where a HotSpot is defined as the temperature above the monthly maximum, in the monthly climatology, for each grid cell (Liu *et al.*, 2003). For observations taken before the date of the maximum DHW value for that pixel, the DHW value at the time of the observation was used as the measure of thermal stress (°C weeks); otherwise, the maximum DHW value was used.

Mortality of colonies was related to thermal stress experienced at a site (Eakin *et al.*, 2010). There was, however, significant variability in mortality with DHW. For predicted DHWs within the range experienced by sites in 2005 (DHW < 17), data from the window (DHW–1, DHW + 1) were used to generate a distribution of mortalities, from which a value for mortality was drawn. For all windows centred on integer values (0–2 up to 16–18) the standard deviation of data within each window was calculated; these values were averaged to give an overall measure of variability *s*.

To enable simulation of thermal stress greater than that experienced in 2005 (DHWs ≥ 17), we used linear regression

analysis to establish the relationship between DHW and colonies undergoing mortality because of bleaching. The probability of mortality for predicted DHWs  $\geq 17$  was drawn from a normal distribution with mean calculated using the regression line and standard deviation  $s$ . Values of DHMs predicted by the global climate model (GCM) were converted to DHWs for the purposes of estimating mortality by multiplying by 4 [one DHM being a good proxy for four DHWs, two DHMs for eight DHWs, see Donner *et al.* (2005)].

Data on partial-colony mortality (McField, 1999) were taken from 13 sites on the Belize barrier reef during the 1995 bleaching event (Strong *et al.*, 1997). Tagged colonies (68 in total) were monitored from October 1995 to May 1996 and corals were ranked by condition (normal, pale, part bleached, bleached, and partial mortality) following methods of CARICOMP (1997) and Lang *et al.* (1992). Partial mortality corresponded to colonies being reduced in area by 30%. All tagged colonies experienced bleaching (as opposed to only 52% of all coral colonies in the surveyed area) and the data suggested that those tagged colonies may have been more severely bleached than the overall population. Taking this into account, 12% of all coral colonies were estimated to have undergone partial mortality by May 1996.

Data from Belize for *Montastraea* spp. and *Siderastraea siderea* showed that 7.4% of spawning corals underwent partial mortality. Similarly, averaging over *Agaricia tenuifolia* and *Porites* spp. gave 8.3% partial mortality for brooding corals. Brooders were thus modelled to have a slightly greater risk of partial mortality than broadcasting corals. Satellite SST data were used to determine the number of DHWs experienced at the 13 sites during the 1995 event in Belize. In the absence of data on the proportion of colonies undergoing partial mortality for other levels of thermal stress, the regression line showing the trend in mortality with thermal stress (DHWs) derived from whole-colony mortality data described above was used to adjust partial mortality accordingly. This was achieved by keeping the slope of the linear regression, but changing the intercept, so that the partial mortality observed during the 1995 bleaching event was predicted by the number of DHWs calculated for Belize at that time.

#### *Heterogeneity of response of corals to bleaching*

The response of corals to successive bleaching events has not yet been monitored in the Caribbean. However, the fate of 12 Pacific coral species during a period in which two bleaching events occurred was monitored in Okinawa from 1998 to 2002 (van Woesik *et al.*, 2004). No coral species monitored were common to both the Pacific and Caribbean and therefore we focused on the response of nonacroporid Pacific species that best compared with the massive and encrusting morphology of most reef-building corals in the Caribbean. Population responses of *Porites lutea*, *Favia pallida* and *Favia fava* over six time periods (September 1998–May 2002) were used to derive the proportion of corals that were resistant (no discernable bleaching), resilient (bleached and recovered) or killed as a result of each bleaching event. The proportion of coral colonies killed as a result of bleaching was lower for the second bleach-

ing event for all three species. Averaging over these species, the risk of mortality because of the second event was approximately 30% of that due to the first event. Whilst the actual risk of mortality will vary with species and with thermal stress, it is assumed that a similar reduction in mortality risk could be applied to Caribbean corals in the model if they have been previously exposed to elevated temperatures.

#### *Storm return periods*

In earlier versions of the coral-reef model (Mumby, 2006; Mumby *et al.*, 2006b), hurricanes were modelled to be of equal intensity and to occur on average once per decade, 20, 40, or 60 years. However, reefs across the Caribbean will differ in their exposure to hurricanes of different strengths and as such will not incur the same level of coral mortality each time a hurricane strikes. Data on the frequency of past storms were used as a proxy for simulating predicted environmental conditions at specific reef locations across the Caribbean.

Whilst few storm tracks pass directly over reefs, storms hundreds of kilometres from reefs are capable of generating waves that can damage corals (Gardner *et al.*, 2005). The dimensions of each category of storm, defined by the Saffir–Simpson scale (Simpson & Reihl, 1981), were considered using the model of Keim *et al.* (2007). These dimensions, derived from predictions of the average size of storms, take the form of regions of storm-forced winds, for different categories of storm, while taking into account that Northern Hemisphere storms are more extensive and severe on the right side of the storm's centre, and less developed on the left-hand side. Although storm-force winds may extend hundreds of kilometres from a track, wind speeds decrease with distance from the eye wall (where the maximum wind speeds are observed). Only reefs within a given distance of the track will therefore experience winds equivalent to the hurricane category. To model the impact of hurricanes on reefs, we incorporated the reduction in wind speed with distance from the eye wall by creating a series of zones of winds.

Keim *et al.* (2007) divide the extent of storm-force winds into major hurricane conditions, weaker hurricane conditions and tropical storm conditions. Here we segregate these further into zones for each category of hurricane (Table 2). The creation of such zones is dependent upon knowing the relative wind speeds of the different hurricane categories. Those hurricanes with the greatest recorded wind speeds, classified as category 5 hurricanes; however, are only defined by the Saffir–Simpson scale as having wind speeds  $>249 \text{ km h}^{-1}$ . Here the estimated maximum sustained winds observed in the strongest tropical cyclones:  $305 \text{ km h}^{-1}$  (National Hurricane Center: <http://www.aoml.noaa.gov/hrd/tcfaq/E1.html>) was used as the maximum wind speed for category 5 hurricanes.

A linear relationship between wind speed and the extent of storm-force winds was assumed for each zone defined by Keim *et al.* (2007). For example, major hurricane conditions, corresponding to category 3–5 storms, were specified as extending 40 km to the left of a major hurricane's central path. We divided this into three zones: a 17.4 km zone for category 5 winds, a 12.6 km zone for category 4 winds, and a 10 km zone

**Table 2** Extent of storm forced winds for each category of storm

Storm category	Left buffer (km)	Right buffer (km)
Hurricane category 1	23.6	47.2
Hurricane category 2	16.4	32.8
Hurricane category 3	10	20
Hurricane category 4	12.6	25.2
Hurricane category 5	17.4	34.8

This table 'cascades upwards', so that a category 3 hurricane, for example, extends 10 km to the left as category 3, a further 16.4 km to the left as category 2, and finally 23.6 km to the left as category 1.

for category 3 winds (Table 2). Similarly, the zone corresponding to minor hurricane conditions from Keim *et al.* (2007) was divided into zones for storm categories 1 and 2. The storm category at a reef site can then be calculated for any hurricane based on its position relative to the storm track.

Hurricane tracks were obtained from the US National Oceanographic and Atmospheric Administration (NOAA). These data are available online [see Jarvinen *et al.* (1984) and Neumann *et al.* (1999)] and include 6-hourly track information on the position of storms, their pressure, wind speed and Saffir–Simpson category from 1851 to 2005. For each of the *Montastraea* reef sites the frequencies of different intensity storm categories were determined based on their distance from storm tracks as described above and summarized over the 156 year record. Owing to uncertainty regarding how climate change might influence future storm trajectories this information on past events was used to derive the (site-dependent) probabilities with which storms of differing strengths occur in the future. While the long-term incidence of hurricanes was fixed, their implementation was stochastic, such that higher and lower frequencies occurred over shorter time-scales as they do in nature (Webster *et al.*, 2005). The Atlantic hurricane season ranges from the 1st June to 30th November and encompasses more than 97% of tropical activity (Neumann *et al.*, 1993). Hurricanes were therefore simulated a maximum of every other 6-month time step in the coral-reef model.

### Hurricane impacts on corals

Whole-colony mortality on adolescent and mature corals  $P_{\text{hur}}$  was modelled to be a function of colony size and storm strength. For the most severe, category 5, storms whole-colony mortality was represented using a quadratic function where  $x$  is the cross-sectional basal area of the colony in  $\text{cm}^2$  (Bythell *et al.*, 1993; Massel & Done, 1993)

$$P_{\text{hur}} = -0.0000003x^2 + 0.00007x + 0.0551, \quad (1)$$

see Mumby (2006) for further details. Small colonies avoid dislodgement because of their low drag; intermediate-sized corals have greater drag and are light enough to be dislodged,

whereas large colonies are heavy enough to prevent dislodgement. In the absence of data on coral mortality for less severe storms, this function was modified by lowering the peak by the predicted impacts of each category of storm relative to the impacts of a category 5 storm. These relative predicted impacts ( $w_k$  where  $k = 1, \dots, 5$ ) were determined by defining a simple relationship between storm intensity (wind speed), wave height, and predicted dislodgement. Tropical storm conditions were predicted to result in negligible coral mortality and were thus not simulated in the model.

Predictions from oceanographic models (Madin *et al.*, 2006) integrated with engineering theory were used to predict the dislodgement of corals (here assumed to be a proxy for mortality) during hydrodynamic disturbances as a function of wave energy (Madin & Connolly, 2006). Assuming that the reef is dominated by massive corals (whose basal area is assumed to be similar to their height) the model predicts the percentage of an assemblage of corals that would undergo dislodgement because of a hurricane to be an exponential function of wave height (see Appendix S2). Assuming a linear relationship between wind speed and wave height [as obtained by Cornish (1912) and Zimmerman (Patton & Marmer, 1932)] this enabled the relationship between hurricane category (wind speed) and coral mortality (predicted dislodgement) to be determined. The maximum whole-colony mortality due to hurricanes of categories 1–4 was predicted to be 4.6%, 11.8%, 25.0%, and 56.7% of the maximum for category 5 hurricanes, respectively.

For hurricanes of category 5, the extent of partial mortality,  $M_{\text{hur}}$  on mature corals ( $>250 \text{ cm}^2$ ) was modelled using a Gaussian distribution with a mean of 0.30 and standard deviation of 0.20 (Mumby, 2006). Each value of  $M_{\text{hur}}$  represents the percentage of original colony tissue that is lost due to the hurricane. If  $M_{\text{hur}} \leq 0$ , there is no mortality; if  $M_{\text{hur}} \geq 1$ , the entire colony is lost (though this is a rare event). For less severe storms the mean of  $M_{\text{hur}}$  was modified by the relative predicted impacts of the different hurricane categories as defined above.

A hurricane metric  $\lambda$  was used to characterize a site's exposure to hurricane disturbances. For each  $4 \times 4 \text{ km}$  reef site  $i$

$$\lambda(i) = w_1T_{i,1} + w_2T_{i,2} + w_3T_{i,3} + w_4T_{i,4} + w_5T_{i,5}, \quad (2)$$

where  $T_{i,j}$  ( $j = 1, \dots, 5$ ) is the total number of hurricanes of category  $j$  experienced at site  $i$  during the 156-year period, and  $w_k$  ( $k = 1, \dots, 5$ ) is the predicted impact on corals of category  $k$  hurricanes relative to category 5 hurricanes, as described above.

### Relationships between disturbance events

The passage of a hurricane can alleviate thermal stress on coral reefs, highlighting the potential for hurricane associated cooling to mitigate climate change impacts (Manzello *et al.*, 2007). As a simplification, we assumed for the model that if a hurricane occurs in any given year then bleaching will not occur.

### Scenarios simulated

To obtain an insight into the contribution of bleaching, storms and local impacts (exploitation of grazing fish) to coral reef community dynamics, we assessed gross changes in coral cover for a 90-year period in which bleaching and/or hurricanes occur. We assumed that total-coral cover was initially at intermediate levels for the Caribbean (30%) and was equally dominated by brooding and broadcasting corals. Since this initial coral cover is likely to overestimate the current state of some Caribbean reefs we have also discussed simulations with coral cover starting at 10% (see also Figure C1 in the Appendix). Variation in the response of coral reefs to disturbances was investigated under two different levels of fish grazing: in the presence (10% of the reef grazed per 6 months) and absence of exploitation (40% of the reef grazed per 6 months) upon scarids, see Appendix S1 for further details. Simulations also explored the presence (40% of the reef grazed per 6 months) or absence of urchins. The core response variable was coral cover in percentage units, which includes both broadcasters and brooders.

Spatial variation in predicted coral cover was investigated with the use of semivariograms. The semivariogram is a graph describing the variance in coral cover with distance between all pairs of sites in a region. The semivariance  $\gamma(h)$  for lag distance  $h$  is defined as one-half the average squared difference of coral cover values  $z$ , separated approximately by  $h$ :

$$\gamma(h) = \frac{1}{2N(h)} \sum_{i=1}^{N(h)} [z(u_i) - z(u_i + h)]^2,$$

where  $N(h)$  is the number of pairs of sites for lag distance  $h$ ,  $z(u_i)$  is the percentage coral cover at location  $u_i$ , and  $z(u_i + h)$  is the percentage coral cover at a point which is at distance  $h$  from  $u$ . In practice, pairs of data separated by distances within a certain lag are averaged. Typically, a semivariogram displays an increase in variance as the lag distance increases, and typically reaches an asymptote when data separated by large distances become spatially independent.

## Results

### Characterizing thermal and hurricane regimes

The frequency of predicted thermal stress events increased with time; more extreme events (corresponding to high numbers of DHMs) were observed in the later years (2070–2099) (Fig. 2). The level of DHMs exceeded ranged from 0 to 5 in the first 30 years, 0–7 between 2040 and 2069, and 0–11 between 2070 and 2099 (Fig. 2). No severe bleaching events (DHMs > 2) were predicted for the Bahamas between 2010 and 2039 (Fig. 2a). By 2070; however, Bahamas sites were exposed to almost annual severe bleaching events. Similarly, sites in Belize experienced up to 25 severe bleaching events in the last 30 years of the time series (Fig. 2b). Sites in Bonaire experienced few severe events before 2070 (Fig. 2c).

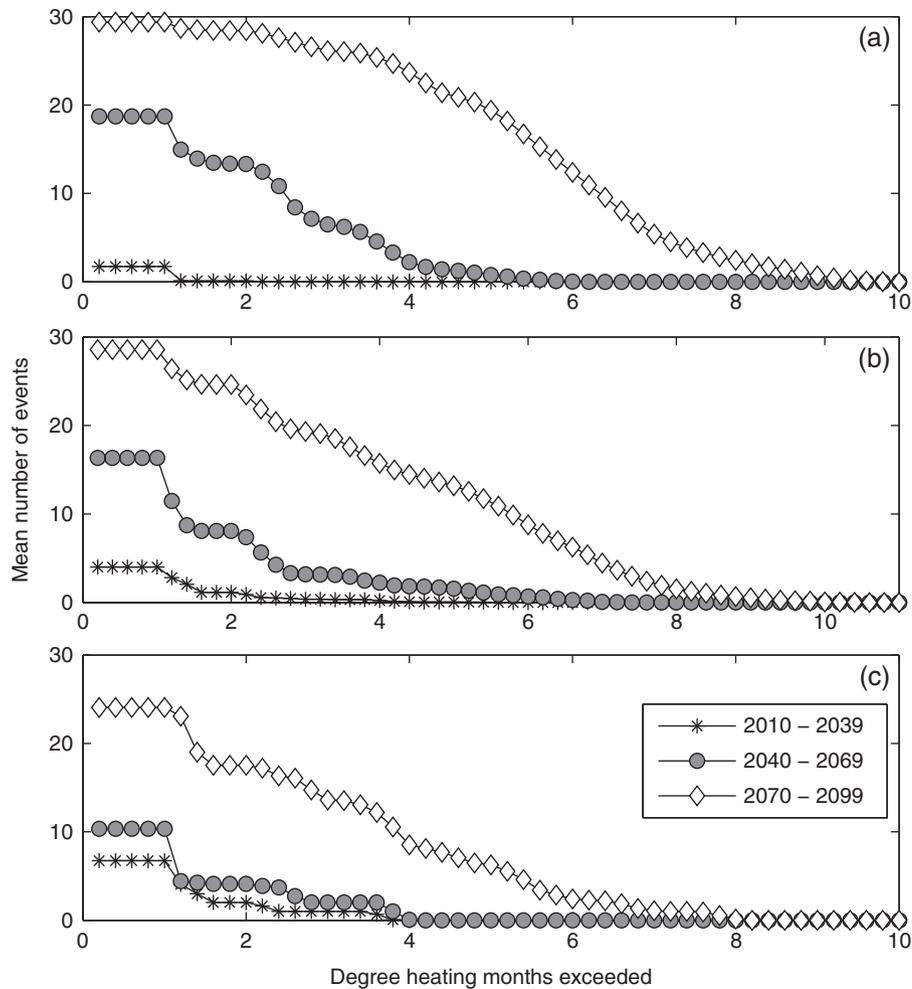
The minimum return time of hurricanes varied from 5 years in the Bahamas to 50 years in Bonaire (Fig. 3). Sites in the Bahamas were, on average, disturbed by hurricanes on a decadal basis in comparison with average return times of ~20 and 80 years for sites in Belize and Bonaire, respectively. Bahamas sites also experienced a higher frequency of the more severe hurricanes (categories 3–5) than sites in Belize (Table 3). Bonaire did not experience severe hurricanes.

### Impact of protecting herbivorous fishes in marine reserves (in the continued absence of urchins)

The hurricanes-only scenario, representing reef dynamics before coral bleaching began in the 1980s, permitted rapid but variable coral growth when scarids were protected, with coral cover fluctuating around an equilibrium level of approximately 75% from 2050 onwards (Fig. 4). Individual runs of the model show that coral cover fell as low as 30% immediately following extreme hurricane events and that recovery to pre-disturbance levels took up to 30 years. Hurricanes allowed net-reef recovery in all three areas of the Caribbean studied although, not surprisingly, the cover of coral was generally lower and more variable in the areas with high rates of hurricane incidence.

When grazing was carried out by an unexploited community of parrotfishes and reefs were only subjected to coral bleaching, coral cover fluctuated around the initial cover for approximately 40 years, after which a steady decline was observed with cover falling below 10% by 2100 at all sites in Belize (Fig. 4). A similar pattern occurred in the Bahamas although reefs in Bonaire exhibited relatively modest declines in health under a bleaching-only scenario. The response of reefs to individual bleaching events was less pronounced than the response to hurricanes, with there being no sudden declines in coral cover observed. There was therefore less variation among runs of the model for this bleaching-only scenario.

Although simulated hurricane events could cause a rapid decline in coral cover, the frequency of severe events was low enough that net recovery was always observed. However, when hurricanes were modelled in combination with bleaching events, reefs in each region of the Caribbean exhibited net decline. In the Bahamas, the decline began almost immediately but accelerated after 2050. A similar pattern occurred in Belize but the acceleration of degradation began later at about 2060. Bonaire was relatively resistant to disturbance for about 50 years, only exhibiting a modest decline to about 20% coral cover by 2060. Beyond 2070; however, reef degradation accelerated as it did at other sites, albeit some 10–20 years later (Fig. 4c).



**Fig. 2** Number of thermal stress events with level of thermal stress (degree heating months exceeded) for three time periods: 2010–2039, 2040–2069, 2070–2099 for (a) the Bahamas, (b) Belize and (c) Bonaire. Each line represents the mean number of events for the region (averaged over all sites).

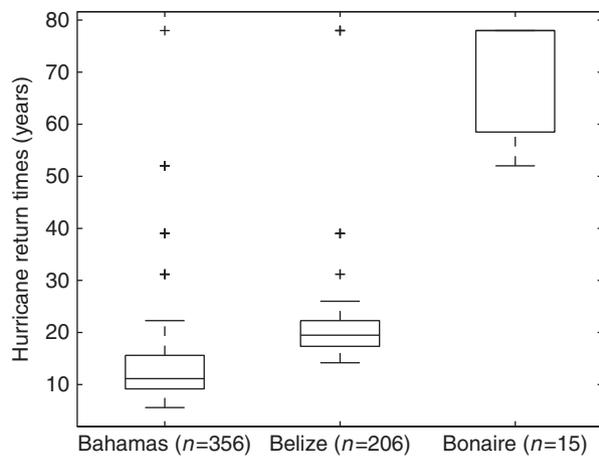
The hurricane metric  $\lambda$ , used to characterize a site's exposure to hurricane disturbances, varied between 0 and 4 (Fig. 5). A negative linear relationship was observed between  $\lambda$  and predicted coral cover in 2040 (Fig. 5). In the absence of urchins and with no exploitation of scarids, coral cover in 2040 varied from 46% to 72% under the hurricanes only scenario (Fig. 5a). Sites in Bonaire experienced little variation in  $\lambda$  and had the greatest predicted coral cover in 2040. Coral cover in Belize ranged from 59% to 72%. The Bahamas region showed the greatest variation in both the metric  $\lambda$  and coral cover (ranging from 46% to 71% of the reef).

Despite the spatial variation in predicted bleaching events (Fig. 2), a clear negative linear relationship was still observed between coral cover and the hurricane metric  $\lambda$  when both bleaching and hurricane distur-

bances were modelled (Fig. 5b). The number and strength of hurricanes may therefore be used to predict how sites within a region will fare in relation to each other (although the actual predicted coral cover will depend upon a combination of disturbances).

#### *Effects of fishing parrotfishes on coral reef dynamics*

Reducing the efficacy of parrotfish grazing from 40% to 10% of the reef led to fundamentally different reef communities even in the hurricanes-only scenario. Well-grazed coral reefs were able to withstand the entire range of hurricane regimes observed in the three regions (Fig. 5a), whereas overfished reefs always resulted in coral decline with <5% cover within 20–30 years [Fig. 4a(ii), b(ii), and c(ii)].



**Fig. 3** Box and whisker plot showing predicted return times (in years, averaged over hurricane categories 1–5) for storms at individual sites in each of the three regions shown in Fig. 1. Boxes show the lower and upper quartiles and median return times. Outliers (crosses) represent data points that are more than 1.5 times the inter-quartile range from either end of the box. The median, upper quartile and maximum return times for Bonaire are all 78 years.

#### *Effects of urchin recovery on future coral cover*

Retaining a functional community of urchins did not prevent reef decline under global warming (Fig. 6). Not surprisingly, the rate at which reef health declined increased from Bonaire to Belize to the Bahamas and the results were qualitatively similar to those under high levels of parrotfish grazing.

#### *Effects of initial conditions*

Simulations beginning with low coral cover (10% of the reef) gave qualitatively similar results to those in which reefs were initially healthy (30% coral cover), but the times taken for coral cover to reach equilibrated levels were highly dependent on the initial state of the reef. For example, in simulations with hurricanes and no bleaching with herbivores protected coral cover fluctuated around equilibrated levels of 75% by 2050 with high initial coral cover, but not until the end of the 21st century with low initial coral cover (see Figure C1 in the Appendix).

Similar rates of decline in coral cover were observed under the different initial conditions when simulations included coral bleaching. In both the Bahamas and Belize coral cover declined to <1% by 2070 in 10% of runs beginning with low coral cover [Fig. C1A(i) and B(i)], but it took a further 20 years for such conditions to occur in simulations beginning with healthy coral cover [Fig. 4a(i) and b(i)]. When scarids were heavily exploited, a decline to <5% coverage was observed

**Table 3** Average number of storms, by storm category and region

	Bahamas ( <i>n</i> = 356)	Belize ( <i>n</i> = 206)	Bonaire ( <i>n</i> = 15)
Category 1	5.50 (5.78)	3.54 (4.05)	0.93 (1.21)
Category 2	5.73 (10.11)	2.76 (1.08)	1.33 (0.52)
Category 3	1.57 (1.32)	0.68 (0.64)	0 (0)
Category 4	0.84 (0.91)	0.28 (0.20)	0 (0)
Category 5	0.21 (0.19)	0.32 (0.22)	0 (0)

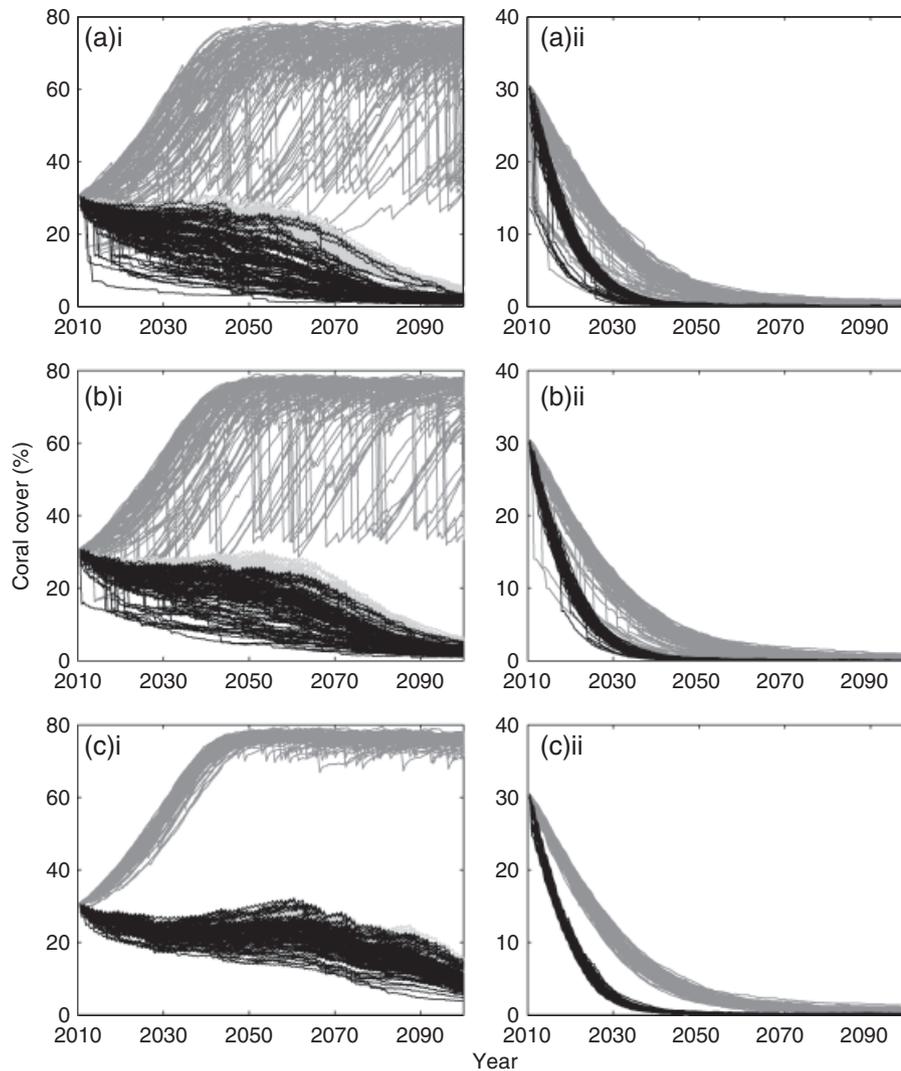
Data represent mean number of storms (averaged over *n* sites), with variance in brackets.

after only 5–10 years with low initial coral cover [Fig. C1A(ii), B(ii), and C(ii)], in comparison with 20–30 years when initial coral cover was high [Fig. 4a(ii), b(ii), and c(ii)].

#### *Local, within-region, variation in disturbance regimes across the seascape*

At a Caribbean scale, regions exhibiting very different physical disturbance regimes had a concomitant difference in their dynamics. For example, under the 'natural' hurricanes-only scenario, coral cover in the Bahamas fell as low as 20% following extreme hurricane events, and took up to 40 years to recover to predisturbance levels. In contrast, the few, low intensity, hurricanes predicted for Bonaire caused only minor decreases in coral cover, and recovery was almost immediate (Fig. 4).

Local variation in hurricane disturbance regimes within the Bahamas resulted in significant spatial variation in predicted coral cover. After only 30 years coral cover at sites in the Bahamas ranged from 46% to 71%, and distinct patterns occurred with latitude (see Fig. 5a and Fig. C3 in the Appendix). Reefs in the northern Bahamas (e.g., at Grand Bahama, Abaco and New Providence) had the lowest predicted coral cover (ranging from 46% to 56%); coral cover was highest in the southern (66–71% at Great Inagua and Little Inagua) and western Bahamas (58–68% at Andros). Indeed, a regression of predicted coral cover in 2040 against latitude across the Bahamas was strongly negative ( $R^2 = 0.75$ ,  $P < 0.01$ ), under a hurricanes-only scenario with unexploited parrotfishes. Looking at patterns across a continuous range of spatial scales (i.e., semi-variance with lags), spatial correlation in coral cover was observed when hurricanes were the only disturbance simulated. Sites in the Bahamas that were close together displayed little variation in coral cover, probably a result of them being exposed to similar hurricane disturbances; sites at opposite ends of the archipelago experienced the greatest differences in coral cover (Fig. 7a). Variation in coral cover was similar at



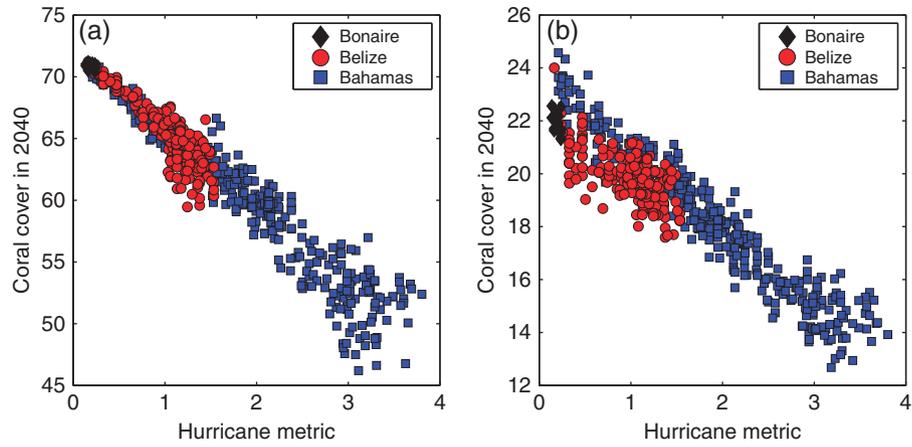
**Fig. 4** Dynamics of coral communities from 2010 to 2099 at a single site in (a) the Bahamas, (b) Belize and (c) Bonaire under three disturbance scenarios with urchins absent and (i) scarids unexploited and (ii) scarids exploited. Each line represents coral cover from a single run of the model. The bleaching only scenario is represented in light grey, hurricanes only in dark grey and the scenario with both hurricanes and bleaching is denoted with black lines.

intermediate distances (between 180 and 500 km). A similar pattern with distance was observed under the bleaching and hurricanes scenario, although variation in coral cover was lower.

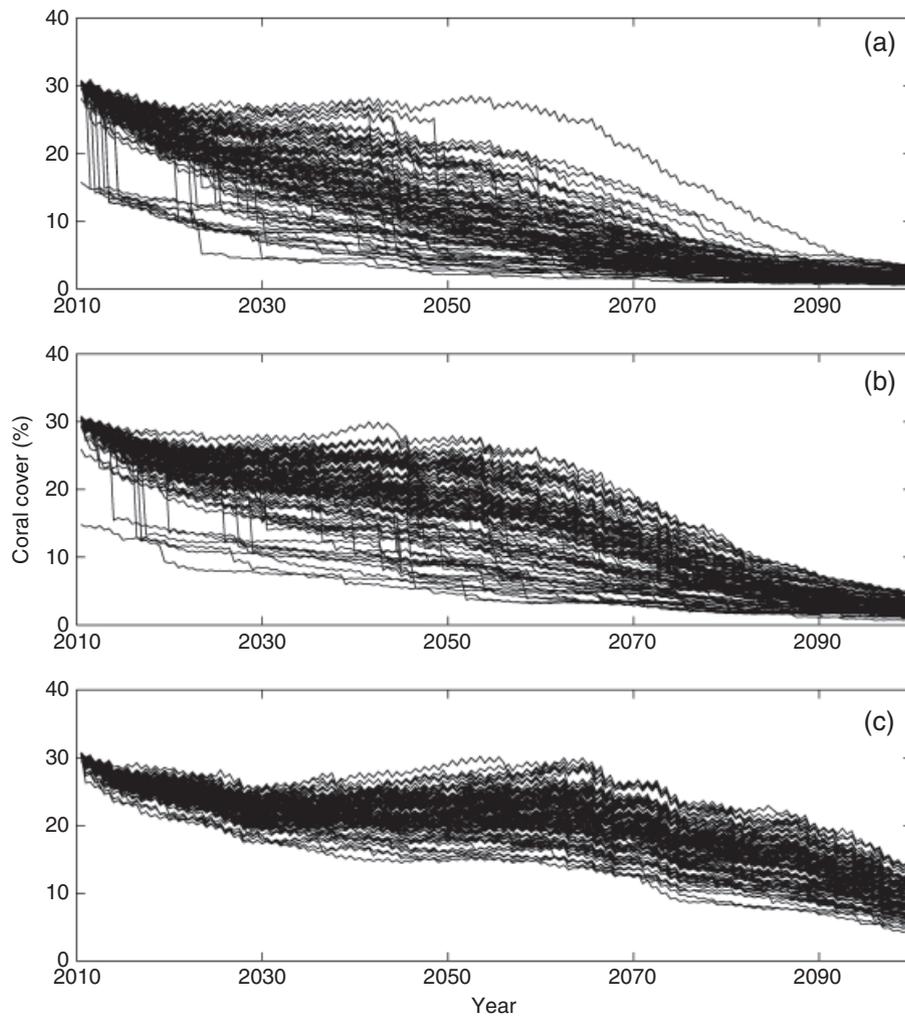
Although variation in coral cover was observed when bleaching was included in simulations (Fig. 5b), only limited spatial patterns were discernible in the Bahamas under either the bleaching only or bleaching and hurricanes scenarios. For example, the regression of coral cover, in 2040, against latitude fell from a coefficient of determination of 0.75 under hurricane disturbance to only 0.13 ( $P < 0.01$ ) when bleaching was added. Similarly, semivariance in predicted coral cover in 2040 showed

little variation with distance under the bleaching only scenario in either the Bahamas or Belize (Fig. 7).

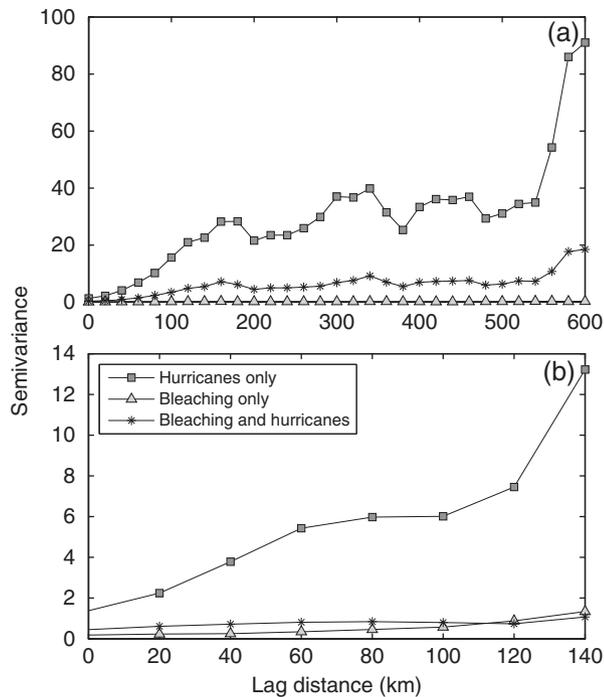
As in the Bahamas, spatial correlation in coral cover was only observed in Belize when hurricanes were simulated alone (Fig. 7b). The Bahamas and Belize differ in their overall size (Bahamas being much larger) but at comparable lags of  $< 150$  km, a striking difference in spatial variance occurred. An initial plateau of variance was reached in the Bahamas at a scale of 120 km whereas the equivalent plateau occurred at the finer scale of 60 km in Belize (Fig. 7). This result implies that the spatial patchiness of hurricane impacts is approximately twice the size in the Bahamas than it is in Belize.



**Fig. 5** Observed relationship between hurricane metric [Eqn (2)] and mean coral cover (based on 100 simulations) in 2040 for each of 577 sites under (a) hurricanes only scenario and (b) hurricanes and bleaching scenario, where urchins are absent and scarids are unexploited.



**Fig. 6** Dynamics of coral communities from 2010 to 2099 under hurricanes and bleaching scenario with urchins present and scarids unexploited. Each line represents coral cover from a single run of the model at a single site in (a) the Bahamas, (b) Belize and (c) Bonaire.



**Fig. 7** Semivariogram showing semivariance in coral cover with distance between pairs of sites within (a) the Bahamas and (b) Belize in 2040 under three disturbance scenarios with scarids unexploited.

## Discussion

In a previous paper, the effects of herbivores on reef dynamics under simple fixed rates of hurricane incidence were examined (Mumby, 2006). Here, we extended the earlier analysis to include a spatially and temporally realistic representation of hurricane disturbance and the additional impact of coral bleaching, parameterized from an extensive field dataset and rare studies of the impact of consecutive bleaching events on coral populations. We find that climate change impacts are detrimental throughout the Caribbean but that the rates of decline vary substantially with geographic location. While practical steps to protect grazers are by no means a panacea for conservation, we find that they can retard the rate of reef degradation dramatically, essentially buying time for local societies to adapt to depleted ecosystem services and buying time for mitigation measures on greenhouse gas emissions to take effect. For example, if we contrast the time it takes for coral cover to fall from 30% to 10% in the presence of bleaching and hurricanes, the addition of a full complement of parrotfishes (grazing of  $\sim 40\%$ ) delays the degradation by 18 years in the Bahamas and over 50 years in Bonaire (compared with an overfished system with only 10% grazing). The time taken for reefs to become degraded also depends upon the initial state of the reef.

## Relative effects of hurricanes and coral bleaching in creating spatial variance in the health of coral reefs

The frequency with which individual reefs have been disturbed by hurricanes displays substantial spatial variation. Spatial variation in both storm strength and storm return times led to significant within-region differences in disturbance regimes in the Bahamas and Belize. In contrast, reefs in Bonaire, being few and separated by only short distances, experienced similar disturbance events.

Coral-reef trajectories within each region were influenced by the size of the region and by the range of hurricane disturbance events that occurred. Spatial variation in trajectories was therefore most substantial in the largest region, with reefs in the southeast Bahamas possessing up to 25% higher coral cover than in the northwest Bahamas.

Different hurricane disturbance regimes were also found to generate different emergent patterns in reef health. In the Bahamas, for example, hurricanes generated an overall patchiness in reef health such that health tended to be comparable at scales of  $< 120$  km, and differ more dramatically at larger scales. In Belize, where hurricane return times are, on average, about twice that in the Bahamas, the spatial patchiness of reef health was about twice as high (homogenous within 60 km sections rather than 120 km sections). A scale of 60 km closely matches the overall extent (width) of many hurricane tracks (Gardner *et al.*, 2005), implying that the seascape in Belize is essentially comprised of a series of individual hurricane 'scars', and that individual hurricane impacts have time to recover (heal) before subsequent events. In contrast, the disturbance regime in the Bahamas is more intense and the impacts of multiple, overlapping hurricanes can be seen across the seascape. Differences in such patchiness could have important consequences for the level of connectivity of reef organisms. In the Bahamas, patches of 'degraded' (recovering) habitat occur over a larger spatial scale, which may cause larger-scale Allee effects than in the Belize example. Future studies will investigate these mechanisms explicitly.

Patterns of coral bleaching had little deterministic spatial structure and served to attenuate spatial patchiness of reef health. This does not imply that coral bleaching is entirely homogenous, but in this case, the overall impact on corals showed little consistent structure. Because of the coarse scale of the HadGEM1 model, it would be useful for future studies to investigate the effect of downscaling the GCM output on spatial patterns of coral cover.

Our analyses showed that Bonaire has the most benign disturbance environment of the three regions studied. It also predicted that reefs in Bonaire would

remain healthier for longer than areas experiencing more intense hurricane disturbance. These simple predictions have some support empirically in that reefs in Bonaire are currently among the healthiest in the Caribbean (Kramer, 2003). While the health of reefs in Bonaire is likely also because of careful management, the infrequent disturbance environment is likely to be an important consideration in explaining their relatively healthy state (at least from a coral perspective).

#### *Limitations of study*

The predictions of reef health are conservative in that they are based only on the frequency of past hurricane events and do not take into account that the frequency or severity of storms may change in the future. Temporal variations in the frequency and intensity of storms, in association with increased SST, have been well documented (Goldenberg *et al.*, 2001; Emanuel, 2005; Webster *et al.*, 2005; Elsner, 2006; Holland & Webster, 2007; Elsner *et al.*, 2008), but the impact of global warming on hurricane formation remains unknown and no theoretical basis yet exists for projecting changes in tropical-cyclone frequency. If the frequency of severe tropical storms were to increase under the influence of global climate change then this study will have underestimated the negative impacts of hurricanes on reef health. The importance of hurricanes in determining spatial variation in reef health increases the need to be able to predict possible future hurricane scenarios.

Many GCMs yield similar predictions, across a range of emissions scenarios up until 2050 (Donner, 2009). HadGEM1 is a 'middle of the road' GCM and is therefore useful for exploring large, qualitative trends in temperatures. Donner *et al.* (2007) compared the frequency of predicted thermal stress events using HadGEM1 to that predicted by the Geophysical Fluid Dynamics Laboratory (GFDL) GCMs CM2.0 and CM2.1 and found broad agreement. While agreement between the model predictions was lower at the beginning of the 21st century, with location in the Caribbean appearing to play a greater part in determining thermal stress, by 2070 severe bleaching events were predicted almost annually at the majority of sites in the Caribbean by both models. Owing to weaknesses of the HadGEM1 model (Johns *et al.*, 2006), our bleaching predictions were also unable to take into account future disturbances to the El Niño-Southern Oscillation, which have been found to coincide with episodes of coral bleaching (Hoegh-Guldberg, 1999).

While every ecological and biological parameter in the model has an empirical parameterization and previous papers have tested the model against independent field data (Mumby *et al.*, 2007), we could not

explicitly model every possible factor influencing reef health. Perhaps, the most significant omission at this stage is the influence of coral disease. Some postbleaching disease is included implicitly in the bleaching parameterization, where disease outbreaks were severe at a number of locations after the 2005 bleaching event (Miller *et al.*, 2006). However, routine episodes of disease that are not explicitly associated with bleaching have not been parameterized and will likely continue to play an important role in driving local levels of coral cover. It should be borne in mind, however, that one of our main goals was to compare patterns and intensities of stress across the Caribbean region and the model provides insight into this even if absolute levels of coral cover may be incorrect.

Another important constraint of our current understanding is the uncertainty over the scope for either genetic adaptation by the holobiont to warmer conditions or the limits to phenotypic acclimation over long-time scales. However, there has been some work on this topic. Using a model of coral and symbiont ecological dynamics and symbiont evolutionary dynamics, Baskett *et al.* (2010) have shown that symbiont diversity, on both the genetic and community levels, delays the collapse of coral populations and may lead to persistence over the next 100 years provided that there are sufficient reductions in greenhouse gas emissions. However, the climate may change too rapidly for corals to be able to respond (Jokiel & Coles, 1990; Glynn, 1993; Wilkinson, 1998; Hoegh-Guldberg, 1999) and indeed under the emissions scenario A1B used here Baskett *et al.* (2009a) predict a collapse of coral populations under all but the greatest levels of variation in thermal tolerance. It should also be borne in mind that the model does not yet distinguish potentially subtle spatial variation in the acclimation of corals to thermal stress. Bleaching was modelled based on the predicted size and duration of thermal anomalies at each location. While this approach allows for local variability in temperature, corals may acclimate to other aspects of temperature such as short-term variability. We anticipate that such effects will be incorporated once further physiological studies have been completed.

#### *Implications and importance of urchin and scarid grazing*

In the presence of abundant scarids, coral cover increased even under the most extreme hurricane disturbance regimes (although recovery following a single event could take decades). In contrast, coral cover declined under the hurricanes only scenario when grazing was carried out by a heavily exploited community of parrotfishes. Grazing fishes, even in the absence of urchins, were therefore able to compensate for the

impacts of hurricane disturbances. We also point out that the use of a spatially realistic model of hurricane impact, in which impacts attenuate from the eye of the storm, led to more optimistic predictions of reef health than in an earlier study that simply modelled the impacts of category 5 storms (Mumby, 2006).

Although urchin recovery is taking place in parts of the Caribbean (Carpenter & Edmunds, 2006), much of that recovery remains confined to shallow habitats that the urchins prefer. As urchin population size grows then a migration into deeper (>5 m) reef habitats may take place and generate the kind of impacts modelled here, namely, increasing grazing substantially to at least 50% of the reef. In general, however, the results reported here for urchin recovery were qualitatively similar to those where urchins remained absent but parrotfish grazing was high. This is perhaps not surprising because the upper bifurcation fold, above which bistability (Fig. 4) is replaced with continual trajectories of coral recovery (i.e., a single coral-dominated equilibrium state), lies between grazing levels of 30% and 40% (Mumby *et al.*, 2007). Thus, providing that grazing exceeds this threshold, the response of coral populations will generally be similar, though faster rates of recovery are possible at higher levels of grazing (Baskett *et al.*, 2009b). Of course, areas that experience significant harvesting of herbivorous fishes may well benefit dramatically from a recovery of urchins, although the model does not capture all of the ecological impacts of urchin recovery. Most importantly, the model does not track rates of bioerosion and therefore a system with urchin grazing will experience greater erosion, and care must be taken to avoid an urchin population explosion that can result in overgrazing and urchin barrens (Sammarco, 1980; McClanahan & Shafir, 1990).

A sobering outcome of the modelling is that coral cover declined once coral bleaching was added to the disturbance regime, even for the highest grazing scenarios. This does not mean that restoring grazing is futile in the long-term because the process can essentially buy time, and attenuate the rate at which ecosystem services are lost. But, the requirement to reduce greenhouse gas emissions and CO<sub>2</sub> in particular remains pivotal. Here, the warming consequences of greenhouse gases are enough to severely deplete coral reefs in the long-term. Adding the effects of ocean acidification will only strengthen that requirement because acidification, together with elevated temperatures, will reduce rates of coral calcification and increase the risk that reefs slip from net accretion to net erosion (Hoegh-Guldberg *et al.*, 2007).

Lastly, although our results paint a bleak portrait for the future health of Caribbean reefs, they also reveal substantial variability within regions. Such variability

has both a deterministic and stochastic basis. The deterministic elements will include differences in ocean mixing such that some reefs experience less thermal stress than others (Skirving *et al.*, 2006), and the stochastic element includes hurricane trajectories. A key challenge for reef science is to identify and predict the deterministic variation in reef health and attempt to stratify management interventions accordingly.

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### **Supporting Information**

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Simulation model design and parameterization.

**Appendix S2.** Predicting Colony Dislodgement.

**Appendix S3.** Additional Results.

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