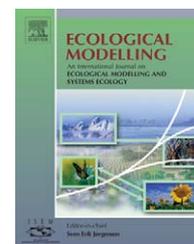


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Revisiting the catastrophic die-off of the urchin *Diadema antillarum* on Caribbean coral reefs: Fresh insights on resilience from a simulation model

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ABSTRACT

In 1983, the dominant urchin of Caribbean coral reefs (*Diadema antillarum*) experienced massive disease-induced mortality and its functional extinction persists to this day. Concurrently, reports of coral disease, coral bleaching and nutrification began to appear and many Caribbean reefs have deteriorated in the last two decades. Here, we describe a spatial simulation model of physical and ecological processes occurring on a dominant Caribbean reef habitat, often referred to as *Montastraea* reef. The model uses a square lattice to simulate the dynamics of two types of hard coral (a brooder and spawner), cropped algal substrata and macroalgae. Grazing occurs independently by *Diadema* and parrotfishes and influences the competitive interactions between corals and macroalgae. Four important types of disturbance are simulated: loss of the urchin *Diadema*, hurricanes, fishing of parrotfishes and nutrification. We use the model to revisit the impact of losing the keystone herbivore, *Diadema*. The urchin imparted great resilience to Caribbean reefs in the face of severe disturbances including: high hurricane frequencies (once per decade), overfishing of scarids and a range of nutrification levels, including a doubling of the vertical growth rate, vegetative growth rate and colonisation rate of macroalgae. Parrotfishes are able to compensate for the loss of this urchin under a limited range of physical and ecological conditions. When not exploited, parrotfishes allow coral to persist at least at equilibrium levels when hurricane frequencies drop to around once every 20 years (e.g. those found in Central America). However, coral cover declined under decadal hurricane frequencies which may partly explain observations in regions of intense hurricane activity such as Florida. Parrotfish grazing is sufficiently intense to mitigate nutrification impacts providing that the cover of corals is not heavily depleted by other processes such as hurricanes and disease. Indeed, the cover of living coral exhibits a strong interaction with both grazing and nutrification in determining the survival of coral recruits. Reefs of higher coral cover have greater

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resilience for a given level of nutrification or grazing and therefore management efforts that arrest declines in coral cover will build greater natural resilience in the system. The model provides a strong case for conserving parrotfishes because reef decline is predicted to be inevitable when urchins are scarce and fishing of grazers is intense (e.g. to the levels seen in Jamaica). Lastly, the model provides a new perspective on the bottom-up versus top-down debate of macroalgal blooms in Jamaica. Nutrification impacts are predicted to be most important when urchins are scarce and parrotfishes are relatively lightly exploited. Therefore, a full understanding of the impact of nutrification will only occur if no-take marine reserves permit scarid biomass to reach unexploited levels. Under these conditions, coral cover is only predicted to increase if nutrification levels are low.

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1. Introduction

Several recent articles have documented unprecedented declines in the health of coral reefs, most notably in the Caribbean (Connell, 1997; Wilkinson, 2002; Gardner et al., 2003; Pandolfi et al., 2003). The causes of reef degradation range from local point-sources of pollution to global rises in sea temperature and centuries of overfishing (see reviews by Knowlton, 2001; Hughes et al., 2003). An unhealthy reef usually has few large fish, little living coral, and is dominated by fleshy macroalgae which tend to support detrital trophic pathways rather than grazer-based systems which underpin fisheries (Carpenter, 1990a). Not only are macroalgal dominated states undesirable in terms of offering limited ecosystem services (Moberg and Folke, 1999), but they may represent a stable equilibrium (Knowlton, 1992; Hughes, 1994). If the latter hypothesis is correct, then reversals to a healthy, coral-dominated state may be unlikely.

The severity of reef decline in the Caribbean may be partly attributable to the region's relatively low species richness (Bellwood et al., 2004). For example, the Caribbean has only 28% the number of fish species and 14% the number of coral species found on the Great Barrier Reef (Bellwood et al., 2004). Thus, many of the ecological processes on Caribbean reefs are undertaken by a relatively small group of species and the potential for functional redundancy is limited. Perhaps the most striking example of limited redundancy occurs in the grazing community. Grazing is undoubtedly one of the key processes underpinning the resilience of coral reefs to disturbance (Bellwood et al., 2004). Several species of macroalgae compete with corals (de Ruyter van Steveninck et al., 1988; Jompa and McCook, 2002) and pre-empt space for coral settlement. Thus, by controlling the cover of macroalgae, grazers influence the replenishment rate, growth and fecundity of coral colonies. All three of these processes contribute to resilience, which in this context, refers to the ability of a coral reef to recover from perturbations (drops in coral cover) so that relatively high levels of living coral cover are maintained.

Grazers can be divided into three principal functional categories (Steneck, 1988); scrapers (urchins and parrotfishes), denuders (acanthurids, some pomacentrids and blennies) and non-denuders (pomacentrids) which maintain algal 'gardens'. Some scrapers can actively remove macroalgae (Bruggemann et al., 1994c), whereas scrapers and denuders help prevent macrophytes emerging from a grazed algal turf (Steneck, 1988). However, both the scraper and denuder functions are under-

taken by only a few species. Scraping is mainly conducted by three species of urchins and six species of parrotfish.

The urchin *Diadema antillarum* was one of the most important grazers on Caribbean reefs (Carpenter, 1986) and could attain extremely high densities in shallow water, occasionally in excess of 70 m^{-2} (Sammarco, 1982a). In January 1983, mass mortalities of this urchin were noted in Punta Galeta near the Atlantic entrance of the Panama Canal (Lessios et al., 1984). Within 13 months, mass mortalities had spread around the entire Caribbean and tropical Western Atlantic, an area of 3.5 million km^2 (Lessios, 1988a). Mortality rates ranged from 85% to 100% with a median of $\sim 99\%$ (Lessios, 1988a). To date, several reports have documented localised, partial recovery of *Diadema* (Edmunds and Carpenter, 2001; Miller et al., 2003) but their density remains low throughout much of the Caribbean, and particularly so on mid-depth forereefs. For example, synthesizing recent reef surveys throughout the region, Kramer (2003) found that urchins were absent in half of all sites sampled and the mean density was only 0.023 m^{-2} (maximum reported anywhere of only 0.2 m^{-2}).

Although several other species of urchin are found at relatively low densities on Caribbean reefs (e.g. *Echinometra viridis*), none appeared to show a compensatory increase once *D. antillarum* became functionally extinct (Hughes et al., 1987; Lessios, 1988a,b; Morrison, 1988). In contrast, several studies reported compensatory increases in the grazing rate of fishes (Morrison, 1988; Carpenter, 1990b; Steneck, 1994) and even increases in the density of juvenile parrotfishes (Carpenter, 1990b). Although fish may have been dominant grazers in some parts of the Caribbean even before the urchin die-off (Hay, 1984), fish are now the predominant grazers on almost all Caribbean reefs. In the continued absence of *Diadema*, we can ask whether reef fish have the capacity to fulfil the role vacated by this formerly widespread urchin. Specifically, to what extent has the die-off of urchins influenced the grazing capacity of Caribbean reefs and how will this influence the dynamics of coral populations?

Any analysis of the role of grazing should also consider the bottom-up processes governing the productivity of the algal community. While algal blooms are well documented in parts of the Caribbean (notably Jamaica, Hughes, 1994), the causality has been disputed (Hughes et al., 1999a; Lapointe, 1999). The problem in many areas is that rising coastal development and intense fishing have simultaneously increased the concentrations of nutrients available for macrophytes and reduced the density and sizes of grazing organisms. Consequently, algal blooms are favoured because of a strengthening of bottom-up

processes (nitrification) and a weakening of top-down processes (grazing).

Here, we present a spatial model of Caribbean forereefs and explore the impact of losing *Diadema*. We compare the impact of urchin die-off under conditions where fish are actively harvested versus protected. Thus, our results highlight how fishing can exacerbate the reduction in grazing that resulted from urchin mortality. To provide general insight into the impacts of nitrification versus grazer depletion on reefs, we add three scenarios of nitrification (giving a total of four scenarios). Specifically we ask the questions:

- (1) How did the dynamics of Caribbean reefs change after urchins become functionally extinct?
- (2) What are the relative effects of urchin loss, overfishing of grazing fishes, nitrification and reef state on the resilience (initial recovery) of coral reefs?
- (3) Are reefs more vulnerable to hurricane disturbance now that urchins are depleted?
- (4) To what extent can grazing fishes (primarily parrotfishes) compensate for the loss of urchin grazing?
- (5) What are the implications of the results for managing coral reef resilience?

2. Methods

2.1. Scope of model

The model was parameterised for mid-depth (5–15 m) forereefs of the *Montastraea annularis* zone (Geister, 1977) which typically have the highest biomass and diversity of reef organisms (Mumby, unpublished data). Populations of large, branching corals have been severely reduced in much of the Caribbean by white band disease (Aronson and Precht, 2001; for a model of such dynamics see, Lirman, 2003). We therefore modelled stylised massive growth forms of coral and included their recruitment, growth, fecundity and reproduction. The model is a square lattice of 2500 cells, each of which approximates 0.25 m² of reef, and can be occupied by a mixture of living and dead substrata (see Table 1). At this cell size, the lattice represents a minimum area of only 25 m × 25 m, which is clearly at odds with the size of individual reefs which may span kilometres or tens of kilometres. The gulf in scale was

bridged by using a torus (which has continuous boundaries), and by representing several modelled processes, such as hurricane disturbance, using their mean behaviour at reef scales rather than attempting to segregate the reef into sub-reefs of heavy and light disturbance (which would be difficult to parameterise meaningfully). It is assumed that sedimentation levels are low and algal production is high as is typical of seaward forereefs in either offshore, arid, or coastal areas with little terrigenous run-off. The model uses discrete time intervals of 6 months. This paper explores single reef dynamics but metapopulation behaviour is considered elsewhere (Mumby and Dytham, 2006).

Although this is a simulation model, several of the parameters, such as partial mortality rates of corals, are entered as constants rather than allowed to vary probabilistically. While this would be inappropriate if the model were used to predict the full range of potential reef states, this approach avoids unnecessary variation from relatively well-established parameters and is consistent with other models of reef processes (McClanahan, 1995; Langmead and Sheppard, 2004). In other words, outcomes of the model focus on the impact of different grazing levels, hurricane frequencies and nitrification rather than other internal parameters. Parameters of the model are listed in Table 2 although several are elaborated below. Further empirical justification for parameters is given elsewhere (Mumby and Dytham, 2006; Mumby, 2006).

This model differs from other recent models of coral reefs in several respects. McClanahan (1992, 1995) modelled processes occurring on reefs in the Indian Ocean which, unlike Caribbean systems, have abundant urchin populations. The models took an energy-based approach and, though not spatially explicit, revealed the impact of various fishery strategies on ecosystem production. Hughes and Tanner (2000) used Leslie matrix models to explore the dynamics of several species of coral in Jamaica, which have been heavily impacted by fishing and loss of *Diadema*. While such models do not have a mechanistic basis, they were based on an unusually long time series of data. Langmead and Sheppard (2004) simulated patch disturbances of various sizes and examined their impact on the community structure of Caribbean corals. While their use of a cellular automaton is conceptually similar to that embraced here, their model did not include grazing, algal dynamics, nitrification, or hurricane events.

Table 1 – Contents of individual cells (0.25 m²) within the model

| Substratum | Constraints | Range (cm ²) |
|---|----------------------------------|----------------------------|
| Brooding coral (e.g. <i>Porites astreoides</i>), BC | Up to three individuals per cell | 1 ≤ BC ≤ 2500 |
| Spawning coral (e.g. <i>Siderastrea siderea</i>), SC | | 1 ≤ SC ≤ 2500 |
| Cropped algae [filamentous, coralline red algae and short turfs (<5 mm height)], 0–6 months, A ₆ | | 0 ≤ A ₆ ≤ 2500 |
| Cropped algae, 6–12 months, A ₁₂ | | 0 ≤ A ₁₂ ≤ 2500 |
| Macroalgae (e.g. <i>Dictyota pulchella</i> , <i>Lobophora variegata</i>), 0–6 months, M ₆ | | 0 ≤ M ₆ ≤ 2500 |
| Macroalgae, >6 months, M ₁₂ | | 0 ≤ M ₁₂ ≤ 2500 |
| Ungrazeable substratum (e.g. sand), U | Fills entire cell if present | U = 0 or 2500 |
| All substrata represented as area (cm ²). | | |

Table 2 – Parameterisation of simulation model

| Parameter | Details | Key references |
|---|---|--|
| Coral recruitment | Corals recruit to cropped algae, A_6 and A_{12} , because algal turfs are not heavily sediment-laden. Recruit at size 1 cm^2 . Recruitment rate of brooders and spawners (respectively): 1 and 0.1 per 0.25 m^2 of cropped algae per time interval | Rate adjusted for rugosity (~ 2) and cover of cropped algae at Glovers Reef (Mumby, unpublished data) |
| Coral growth | Coral size is quantified as the cross-sectional, basal area of a hemispherical colony (cm^2). BC have a lateral extension rate of 0.8 cm year^{-1} and SC grow faster at 0.1 cm year^{-1} (based on median rates for <i>Porites astreoides</i> , <i>P. porites</i> , <i>Siderastrea siderea</i> , <i>Montastraea annularis</i> , <i>Colpophyllia natans</i> and <i>Agaricia agaricites</i>) | Maguire and Porter (1977), Highsmith et al. (1983), Huston (1985), Chornesky and Peters (1987), Van Moorsel (1988) |
| Coral reproduction | Excluded, assume constant rate of coral recruitment from outside reef (i.e. no stock-recruitment dynamics) | |
| Colonisation of cropped algae | Turf algae arises (i) when macroalgae is grazed and (ii) after all coral mortality events except those due to macroalgal overgrowth (see coral-algal competition below). | Jompa and McCook (2002) |
| Colonisation of macroalgae | Macroalgae become established when cropped algae is not grazed for 12 mo. | Mumby (unpublished data), Jompa and McCook (2002) |
| Macroalgal growth | Macroalgae spread vegetatively over cropped algae. The probability that macroalgae will encroach onto the algal turf within a cell, $P_{A \rightarrow M}$, is given by (1) where $M_{4 \text{ cells}}$ is the percent cover of macroalgae within the von Neumann (4-cell) neighbourhood $P_{A \rightarrow M} = M_{4 \text{ cells}} \quad (1)$ | de Ruyter van Steveninck and Breeman (1987) |
| Competition between corals | If corals fill the cell (2500 cm^2), the larger coral overtops smaller corals (chosen at random if more than one smaller coral share the cell). If corals have equal size, the winner is chosen at random Corals always overgrow cropped algae | Lang and Chornesky (1990) |
| Competition between corals and cropped algae | | Jompa and McCook (2002) |
| Competition between corals and macroalgae 1: effect of macroalgae on corals | The probability that a coral is overgrown (extirpated) by macroalgae, $P_{C \rightarrow M}$, is calculated from Eqs. (2a) and (2b) where x is either BC or SC, λ is the exponent, 0.0012 (derived by fitting various exponents and intercepts to Fig. 1), M_{12} is expressed as a proportion of the area of the cell covered with macroalgae $P_{C \rightarrow M} = P_{\text{size}} \times M_{12} \quad (2a)$ $P_{\text{size}} = 0.83 \exp(-\lambda x) \quad (2b)$ | Tanner (1995), Jompa and McCook (2002) |
| Competition between corals and macroalgae 2: effect of corals on macroalgae | The vegetative growth rate of macroalgae, $P_{A \rightarrow M}$, is reduced by 25% when at least 50% of the local von Neumann neighbourhood includes coral proportion of coral, $C = \frac{BC + SC}{2500} \quad (3a)$ $P_{A \rightarrow M} = 0.75 \times M_{4 \text{ cells}}, \quad \text{if } C \geq 0.5 \quad (3b)$ $P_{A \rightarrow M} = M_{4 \text{ cells}}, \quad \text{if } C < 0.5 \quad (3c)$ | de Ruyter van Steveninck et al. (1988), Jompa and McCook (2002) |

Table 2 – (Continued)

| Parameter | Details | Key references |
|--|--|---|
| Grazing by fishes and impact of fishing | Grazing is spatially constrained. An unfished community of parrotfishes grazes a maximum of 30% of the seabed per 6-month time interval. Grazers do not discriminate between cropped algae and macroalgae. During a given time interval, cells are visited in a random order. All turf and macroalgae are consumed (and converted to A_6) until the constraint is reached (30%). Grazing does not eliminate coral recruits. Grazing is constrained to 10% in heavily fished systems | Williams and Polunin (2000), Williams et al. (2001), Mumby (2006) |
| <i>Diadema antillarum</i> | Urchin grazing is implemented in the same fashion as herbivorous fish. Up to 40% of the seabed can be grazed under normal conditions. Urchins and fish can graze the same areas | Carpenter (1984, 1988) |
| Partial-colony mortality of corals | Only applied to mature colonies (>250 cm ²) at an incidence of 5% per time interval. Partial mortality reduces the coral's base area size by 15 cm ² | Bythell et al. (1993), Mumby (unpublished data) |
| Whole-colony mortality of corals | Incidence of mortality in pubescent corals (60–250 cm ²), 2% per time interval (~4% per annum). Halved to 1% (2% pa) for mature colonies (>250 cm ²). These levels of mortality occur in addition to macroalgal overgrowth. | Bythell et al. (1993) |
| Hurricane impact on pubescent and mature corals (>60 cm ²): whole-colony mortality | Whole-colony mortality of larger corals is represented using a quadratic function (4) where x is the cross-sectional basal area of colony. Small colonies avoid dislodgement due to 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 $P_{hur} = -0.0000003x^2 + 0.0007 + 0.0551$ (4) | Bythell et al. (1993), Massel and Done (1993) |
| Hurricane impact on mature corals (>250 cm ²): partial-colony mortality | The extent of partial mortality, M_{hur} , is modelled using a Gaussian distribution with mean of 0.46 and standard deviation of 0.20. Each value of M_{hur} represents the percentage of original colony tissue that is lost due to the hurricane. If $M_{hur} \leq 0$, there is no mortality. If $M_{hur} \geq 1$, the entire colony is lost (though this is a rare event) | Mumby (unpublished data from Hurricane Mitch) |
| Hurricane impact on juvenile corals (1–60 cm ²) | Scouring by sand during a hurricane may cause 80% whole-colony mortality in juvenile corals | Mumby (1999) |
| Hurricane impact on macroalgae | Hurricanes reduce the cover of macroalgae to 10% of its pre-hurricane level | Mumby (unpublished data) |
| Hurricane frequency | Hurricanes were simulated using a binomial model which when implemented in discrete time approximates a poisson random distribution. Maximum long-term incidence of severe hurricanes ~10 years in Florida and 20 years in Mesoamerica | Trembl et al. (1997), Gardner et al. (2005) |

2.2. Algal overgrowth of coral

Macroalgae such as *Lobophora variegata* and *Dictyota* spp. are able to overgrow coral recruits (Bak and Engel, 1979; Sammarco, 1980; de Ruyter van Steveninck and Bak, 1986), and small corals of several years in age (RPM Bak, pers. comm.). Whether fleshy macroalgae cause rapid whole-colony mortality of larger colonies is unclear although they can cause extensive partial-colony mortality (Hughes and Tanner, 2000) which may then be followed by whole-colony mortality arising from further algal overgrowth. Little else is known about the degree to which algal overgrowth leads to whole-colony mortality in corals. We therefore had to quantify this parameter statistically by comparing model simulations to those of published field data. Since this was the only parameter fitted in this manner, we could generate model simulations for various putative coral–algal overgrowth relationships and identify that which best fitted the data of Hughes (1994) from Jamaica. It

follows from published evidence (cited above) that the probability of coral mortality within a 6-month period (one iteration) is negatively associated with increasing coral size. We created twenty putative negative exponential relationships and, using least squares, selected that which best fitted empirical data (Fig. 1; Table 2).

2.3. Grazing of reef fishes

Parrotfish (Scaridae) are usually the most significant fish grazer on Caribbean reefs (Carpenter, 1986; Steneck, 1994). Several studies have examined the grazing behaviour of Caribbean parrotfishes, many of which have taken place since the die-off of urchins (Randall, 1961, 1967; Hanley, 1984; Bruggemann et al., 1994a,b,c, 1996; Steneck, 1994; van Rooij et al., 1995; Overholtzer and Motta, 1999). Species differ in their preferred food and substratum requirements and feed almost continuously during the day. There is, therefore, a problem

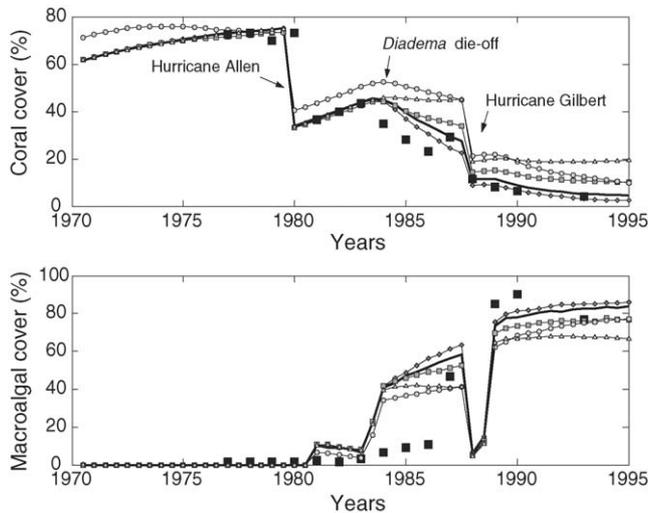


Fig. 1 – Refinement of the model predictions (line) using empirical data (■) for the decline in reefs in Discovery Bay (Jamaica), at a depth of 10 m between 1975 and 1993 (Hughes, 1994). Each line represents a different putative relationship between the risk of algal–coral overgrowth and size of coral colony. That of the solid line was used in subsequent model simulations. The upper panel represents coral cover and lower panel macroalgal cover.

of scale; most observations of parrotfish grazing occur on a scale of seconds to minutes whereas the model has a discrete time scale of 6 months. Moreover, observations of grazing rate do not predict algal cover directly because cover is the outcome of a dynamic balance between algal production (area for colonisation, recruitment rate and growth) and algal removal (principally grazing). The model actually requires an estimate of the net impact of grazing: the surface area of reef that is grazed sufficiently often that algae are maintained in a cropped state and prevented from escaping into a macroalgal canopy. To this end, we adapted the results of a study of grazing that was carried out on low rugosity forereefs at Ambergris Caye, Belize (Williams et al., 2001). Williams et al. artificially increased coral cover in 5 m × 5 m plots and observed a corresponding decrease in macroalgae while cropped substrata were maintained at an equilibrated level of 50% by the end of the 5-month treatment. The authors inferred that grazers were able to maintain up to 60% of the substratum in a cropped state.

The reefs studied by Williams et al. (2001) have a lower rugosity than that implied by our model so to adapt their results, and partially test the generality of their conclusions, we performed a simple comparison. Firstly, we compared the rugosity between their site (Ambergris Caye, rugosity = 1.2) and that of Long Cay, Glovers Reef which better represents the reefs being modelled (rugosity = 1.98). We next compared the total biomass of scarid fishes between sites and found the value from Ambergris Caye (~270 g 25 m⁻²) to slightly exceed that at Long Cay in 1998 (220 g 25 m⁻²). The biomass of parrotfish at Ambergris is unusually high for a rugosity of 1.2 (Mumby and Wabnitz, 2002) but this may reflect high proximity to

more rugose reefs in deeper water at Ambergris Caye. We then adjusted the area grazed for the differences in surface area (rugosity, R) and parrotfish biomass (B) using Eq. (5) and concluded that the total cover of cropped substratum would fall from ~60% to 30% (assuming that algal production is a linear function of substratum availability). We then compared this estimate to the observed cover of cropped substratum at Long Cay (LC) in the summer of 1998. At this point, the reef was in good health (42% coral cover) as it had not been severely disturbed since 1978 or earlier (i.e. as close to equilibrated conditions as is likely to be found in Belize). The cover of cropped substrata was 31% in July 1998 which closely fits the predicted cover of cropped substrata (30%) and we therefore decided to constrain grazing to a maximum of around 30% of the substratum.

$$\text{Percentage of reef grazed}_{LC} = \left[\left(\frac{B_{LC}}{B_W} \right) \left(\frac{R_W}{R_{LC}} \right) \times 63 \right] \quad (5)$$

W denotes the Williams et al. (2001) study in which the percentage area grazed was 63%.

The approach described here to quantify scarid grazing in healthy, unexploited systems, makes two implicit assumptions. Firstly, that the biomass of scarids at Long Cay is representative of unexploited *Montastraea* reefs. In fact, the biomass of scarids at this site is among the highest reported anywhere in the Caribbean (Mumby, 2006) and is likely to approach maximal levels for the region. The high biomass of parrotfishes is probably underpinned by relatively high primary production: the forereef at Long Cay faces the wider Caribbean (high fetch), has clear water and relatively high inorganic nutrient concentrations (McClanahan et al., 2004), possibly resulting from upwelling near the atoll. However, a second assumption of the model is that the entire scarid community can maintain the efficiency of its grazing even if coral cover declines and algae occupy a larger surface area of the reef, which would otherwise tend to reduce grazing efficiency (i.e. it is less likely that a given spot would be regrazed sufficiently often to prevent macroalgal escape). The degree to which scarids can fully compensate for a change in algal colonisation space is not yet quantified. However, a number of studies have reported substantial increases in grazing rate after an increase in algal production (Carpenter, 1985; Steneck, 1994; Russ and McCook, 1999; Diaz-Pulido and McCook, 2003). Furthermore, one of us (PJM) has documented a numerical response in parrotfish at Long Cay in the 4 years since the reefs were struck by Hurricane Mitch in 1998 (Mumby et al., 2005). Importantly, the total cover of grazed substratum has remained at approximately 30% despite a drastic decline in coral cover from 42% to 18% in 5 years. This result seems to be representative of *Montastraea* reefs in Belize since a 300 km wide survey of cropped substratum at 16 reefs recorded a mean cover of 28% (Mumby, unpublished data). These surveys were undertaken in June 2002, nearly 4 years after Hurricane Mitch had widespread impacts on the cover of corals and macroalgae. Given that the dominant scarid in Belize (*Sparisoma viride*) grows quickly, potentially reaching a length of 250 mm between the hurricane impact and sampling in 2002 (Choat et al., 2003), these results may incorporate a numerical response by parrotfishes to the change in benthic

community structure. In short, it seems fair to assume that parrotfishes can maintain only around 30% of a *Montastraea* reef in a grazed state even allowing for increases in grazing rate and numerical responses to increased food availability.

Although parrotfish will avoid very large macroalgal phaeophytes such as *Turbinaria* spp. and *Sargassum* spp., these are uncommon on the forereef. Mumby (unpublished data) recorded several thousands of bites by adult parrotfish and found a ratio of 1:1.05 for bites on macroalgae (chiefly *Dictyota* spp.) to cropped algae, respectively. Cells are grazed in a random order and all cropped and macroalgae are consumed (regrazed in the case of cropped algae) and converted to the initial cropped algal state until the spatial constraint is reached (e.g. 30% of the total reef area or 1,875,000 cm²). Once the threshold algal cover is reached, no further algae are grazed during the time step and grazing does not eliminate coral recruits (Birkeland, 1977).

2.4. Grazing of *D. antillarum*

The role of urchin grazing on Caribbean reefs has received a wealth of research (Ogden et al., 1973; Carpenter, 1981, 1984; Hay, 1981, 1984; Sammarco, 1982b; Hay and Taylor, 1985; Foster, 1987; Morrison, 1988). *Diadema* is an efficient grazer of algal communities and may regrazed the substratum more frequently than herbivorous fish (Carpenter, 1986). This urchin possesses enormous ecological plasticity in its response to food availability such that it may reduce its body size in response to food or density limitation (Levitan, 1989, 1991; Karlson and Levitan, 1990) and drastically increase its size when food resources are plentiful and population densities are low (Levitan, 1988). After the region-wide mass mortality of *Diadema*, many studies reported considerable increases in the standing crop and/or cover of fleshy macroalgae (Hughes et al., 1985; de Ruyter van Steveninck and Bak, 1986; Liddell and Ohlhorst, 1986; Carpenter, 1990a). While these observations may imply that urchins were more important than fishes in controlling macroalgae, several authors noted the potentially confounding issue that some of the most heavily studied reefs had also been heavily fished (Ogden et al., 1973; Sammarco, 1980; Hay, 1984). Fishing not only releases urchins from their fish predators (McClanahan and Kurtis, 1991) but also reduces the density of scarids (Roberts, 1995), thus reinforcing a negative correlation between the two taxa. Although urchins and scarids compete in the Indo-Pacific (McClanahan, 1992), the degree to which they competed for food in the species-poor Caribbean remains enigmatic, particularly where fishes were not heavily exploited (Lessios, 1988a).

The grazing of *D. antillarum* was modelled using data from the US Virgin Islands. After the die-off of *Diadema*, Carpenter (1988) found that the biomass of algae removed dropped by more than half from 3.74 to 1.58 g dry wt m⁻² day⁻¹. We can estimate the relative importance of urchin and fish grazing if we assume that the higher rate of algal removal included both grazers whereas the lower rate only comprised fishes. If grazing fishes are able to graze 30% of the reef efficiently (G_{parrot}), then Eq. (6) predicts the grazing component attributable to urchins as ~40%, where production for all grazers, $P_{\text{all}} = 3.74$

and that of parrotfishes, $P_{\text{parrot}} = 1.58$.

Percentage of reef grazed by urchins, G_{urchins}

$$= \left[\left(\frac{P_{\text{all}}}{P_{\text{parrot}}} \right) G_{\text{parrot}} \right] - G_{\text{parrot}} \quad (6)$$

Urchin and parrotfish grazing were modelled independently in a spatially random manner such that the consumption of algae overlapped in space. If *Diadema* and scarids used to compete for food, we could, in principle, have over-estimated urchin grazing because the scaling relationship was based on recent scarid studies where grazing was not hindered by urchin competitors (e.g. G_{parrot} may have been 20% instead of 30%). However, it seems more likely that an effective urchin grazing of 40% of the reef is an underestimate. Firstly, prior to the mass mortality, densities of urchins at a depth of 5–10 m on relatively unfished reefs were usually reported to exceed 1 m⁻² (the exception being some reefs in Belize although densities as high as 4 m⁻² were reported, Hay, 1984). For example, Bauer (1980) reported *Diadema* densities of 9.1 m⁻² at depth of 7.6 m in Cozumel, Hunte et al. (1986) found densities of 9 m⁻² in Barbados, and Bak and van Eys (1975) reported densities of 8.5 m⁻² in Bonaire and Curaçao. Secondly, urchins are very effective grazers even at low densities (Levitan, 1988). Recent experiments in the Bahamas have found that *Diadema* densities of only 1 m⁻² can maintain small experimental patch reefs in a cropped algal state (Craig Dahlgren, pers. comm.). Such efficient grazing is not surprising given that the foraging range of this urchin is ~0.5–4 m², is re-grazed every 3–6 days, and may be maintained for more than a year (Carpenter, 1984). At high urchin densities (>16 m⁻²), *Diadema* may be able to exclude macroalgae from entire reefs but to the detriment of coral recruitment (Sammarco, 1980). We do not attempt to model such explosions of urchin populations but discuss their implications later.

2.5. Effects of nutrification

The direct effects of elevated nutrient levels on algal productivity are mixed and dependent on the type of nutrient, background levels of nutrients at the site and the algal species. Taking several studies from Florida as examples, Smith et al. (2004) recorded significant effects of nutrification on the calcareous green alga *Halimeda tuna*: in some habitats, nutrification led to a doubling in the production of new segments and 25% increase in the growth rate of such segments. In contrast, Delgado and Lapointe (1994) found that rising nitrogen and phosphorus concentrations did not influence the productivity of the common, branching phaeophyte, *Dictyota cervicornis*. Similarly, Miller et al. (1999) concluded that experimental increases in nutrient concentration had no significant effects on the cover of Caribbean macroalgae whereas levels of grazing did.

Given the mixed evidence for nutrient impacts on algae, we embraced some of the more striking published results and therefore, the simulation is likely to over-estimate actual impacts of nutrification. We created four scenarios of algal growth (Table 3) in which the first was the standard model described above.

Table 3 – Nutrifcation experiments that enhanced the competitive ability of macroalgae from scenarios 1 to 4

| Scenario | Vertical growth rate ^a | Vegetative growth rate ^b | Colonisation rate |
|----------|-----------------------------------|---|--------------------|
| 1 | 12 Months | $\propto M_4 \text{ cells}$ (Eq. (1)) | 12 Months |
| 2 | Doubled (6 months) | $\propto M_4 \text{ cells}$ (Eq. (1)) | 12 Months |
| 3 | Doubled (6 months) | Doubled [$\propto (M_4 \text{ cells}/2)$] | 12 Months |
| 4 | Doubles (6 months) | Doubled [$\propto (M_4 \text{ cells}/2)$] | Doubled (6 months) |

For further clarification of scenario 1, see text.

^a Time taken for macroalgae to reach adequate size and begin coral overgrowth.

^b Lateral growth of established canopies and includes competitive effects of corals on macroalgal growth rate.

2.6. Scenarios simulated

To get a general insight into the effects of losing urchins on reef communities, we assessed gross changes in coral cover for a 50-year period in which hurricanes occurred at various intervals (on average, once per decade, 20, 40 and 60 years). We assumed that total coral cover was initially high (30%) and was equally dominated by brooding and spawning corals. Four levels of grazing were simulated (Table 4) to represent the loss of urchins and exploitation of parrotfishes. To quantify the putative grazing intensity of heavily overfished scarids, we scaled the grazing intensity to the biomass of parrotfishes in Jamaica (Williams and Polunin, 2000). The biomass of parrotfishes in Jamaica was approximately one-third that of Long Cay (Belize) and we therefore used a grazing intensity of 10% for overfished scarids. Additional simulations explored the impact of fishing scarids for reefs of various states (coral cover).

The effects of grazing, nutrifcation, initial reef state and coral growth rate on the survival of coral recruits were compared formally by simulating dynamics in the absence of acute disturbance (hurricanes). The survival of an entire cohort of recruits to adolescent size (60 cm²) was quantified after a period of 20 years and used as the response variable. The levels of predictor variables (grazing, initial reef state, etc.) represented expected ranges rather than exceptional extremes. For simplicity, simulations that manipulated coral growth rate applied the same rate to both brooding and spawning corals.

On initialisation, corals are usually sampled at random from the full size distribution and located randomly in space. The influence of initial size distribution is examined elsewhere (Mumby and Dytham, 2006) but we include here a consideration of the influence of spatial pattern in the coral community. Sources of acute coral mortality such as hurricanes are notoriously patchy in space (Done, 1992) and therefore the distribution of older, larger corals reflects the integrated

impact of many disturbances. It seemed appropriate to create size-dependent aggregation as a positively correlated phenomenon with increasing colony size. Each coral is either distributed randomly or in a spatially aggregated manner. Corals were first divided into five size categories, which from the smallest were juveniles (cross-sectional basal area <60 cm²), pubescent (61–250 cm²), small-sized mature (251–500 cm²), medium-sized mature (501–1000 cm²) and large-sized mature (>1001 cm²). Juvenile corals were distributed at random. For all other size categories, a proportion N_C of colonies were distributed (seeded) randomly across the reef (typically 1%). Each remaining colony in each size category was then randomly assigned a seed and located by randomly sampling a normal distribution where the mean (m) and standard deviation (S.D.) represent the distance (in cells) from the seed. The values of m and S.D. ($m/S.D.$) were, from pubescent to large-sized mature: 10/10, 5/10, 5/4 and 5/3. These parameters are not based on empirical data but created highly patterned data. All simulations assigned 10% of the seabed to ungrazed substratum (e.g. sand).

2.7. Statistical analyses

The impact of nutrifcation, urchin grazing, parrotfish grazing, initial reef state and coral growth rate on the survival of coral recruits was modelled statistically using a quasibinomial generalized linear model (GLM) with logit link (Pinheiro and Bates, 2000). Applying a statistical model to the simulation output allowed us to examine interactions among variables across a wider range of levels than was originally simulated. A quasi-binomial model was favoured over a binomial model because the data were over-dispersed (the estimated dispersion was higher than expected for binomial GLM). One advantage of this method over ANOVA in that data are treated as numeric variables (rather than categories) and that the large number

Table 4 – Grazing scenarios simulated

| Status of <i>Diadema</i> | Status of Scaridae | Proportion of reef grazed by <i>Diadema</i> , d (%) | Proportion of reef grazed by Scaridae, s (%) | Total proportion of reef grazed to cropped state per 6-month iteration (%) |
|--------------------------|--------------------|---|--|--|
| Present | Not exploited | 40 | 30 | 58 |
| Present | Heavily exploited | 40 | 10 | 46 |
| Absent | Not exploited | 0 | 30 | 30 |
| Absent | Heavily exploited | 0 | 10 | 10 |

Note that urchins and scarids may regrazed the same areas and therefore the total area grazed is not simply the sum of both grazers. Total area grazed = $[d + s] - [ds]$.

of zeros are not problematic. Preliminary screening of model predictions suggested that some variables (e.g. parrotfish grazing) may have quadratic behaviour and quadratic terms were therefore included in the GLM. Terms were added until the addition of new terms did not alter the model (analysis of variance using approximate *F*-test). We do not give the full GLM structure because it is highly complex (84 terms) and since there are many interactions, the coefficients cannot be interpreted directly. Moreover, the GLM was not used to test hypotheses because the data arise from simulation. Rather, we used the statistical model to examine the interactions among factors on the predicted response (survival rate). The resulting interaction plots were one-dimensional and isolated the contribution of one variable on the response when all other variables were held constant.

3. Results

3.1. Effects of urchin, parrotfishes and nutrification on coral reef dynamics

The presence of *Diadema* permitted reefs to maintain high levels of coral cover even under the most severe hurricane fre-

quency of once per decade (Fig. 2a). Moreover, the presence of urchins compensated for heavy scarid exploitation and provided adequate grazing for coral cover to persist. The loss of *Diadema* strongly influenced the response of reefs to hurricane disturbance. Reefs with a healthy biomass of scarids were able to maintain coral cover providing that the periodicity of hurricanes was 20 years or greater (Fig. 2) whereas decadal incidences of hurricanes led to declining coral cover. In the absence of urchins, heavy exploitation of scarids resulted in declining coral cover even under the mildest disturbance regime simulated (Fig. 2).

The importance of urchin grazing was also seen when examining the decadal change in coral cover for each level of nutrification (Fig. 3). When urchins were present, coral cover increased under all but one of the scenarios plotted: severe nutrification when the reef was initially at a fairly unhealthy 10% coral cover (Fig. 3b). With both a healthy initial coral cover and urchin community, coral cover could increase despite heavy depletion of scarids and severe nutrification. Loss of the urchins left the system much more vulnerable to nutrification impacts. The degree to which a healthy scarid community could maintain a net increase in coral cover was highly sensitive to the initial condition of the reef and nutrification level. With a healthy 30% coral cover and no nutrification, scarids

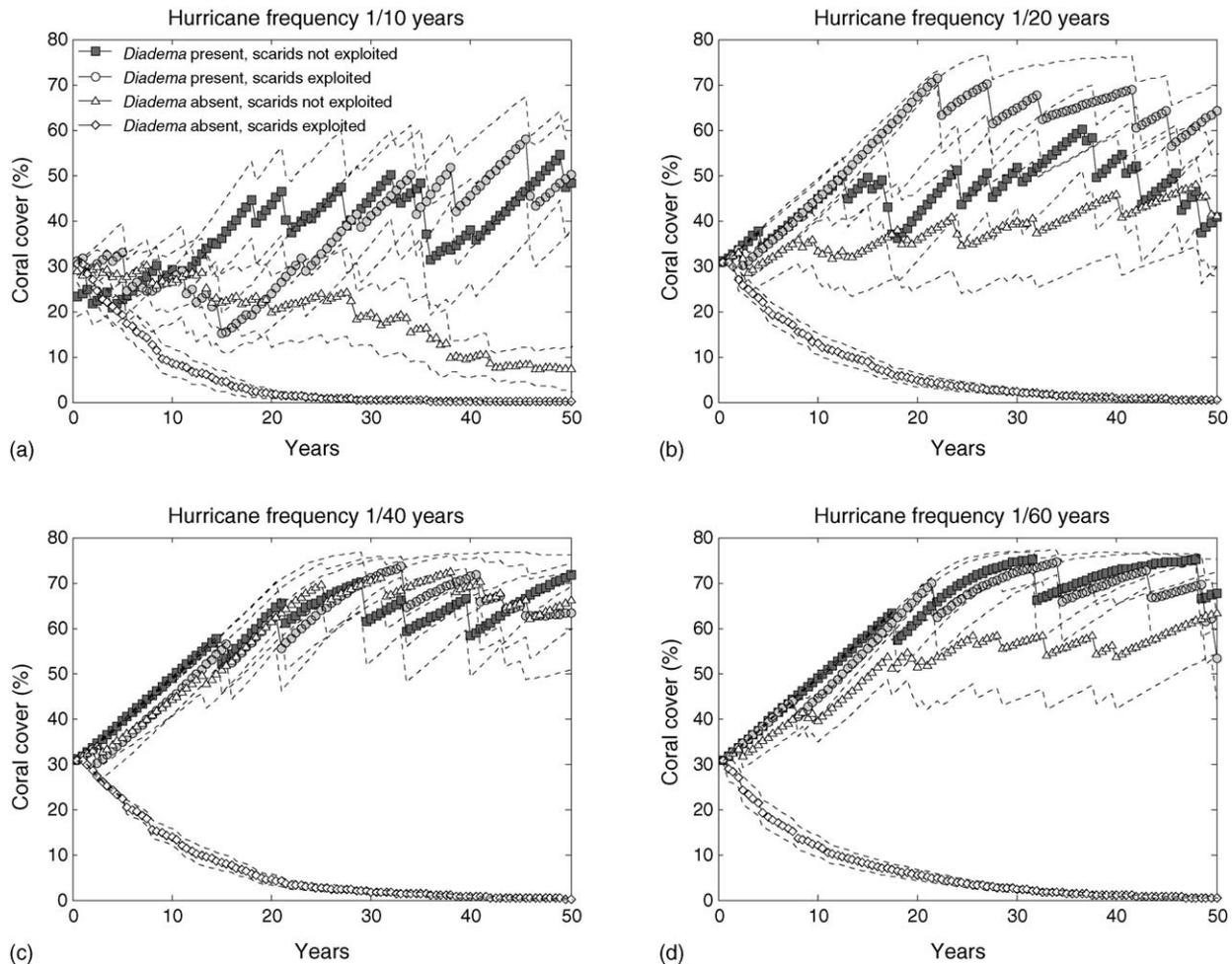


Fig. 2 – (a–d) Dynamics of coral communities over a 50-year period for four grazing scenarios and hurricane frequencies. Dotted lines denote standard errors around mean coral cover, based on at least 10 simulations.

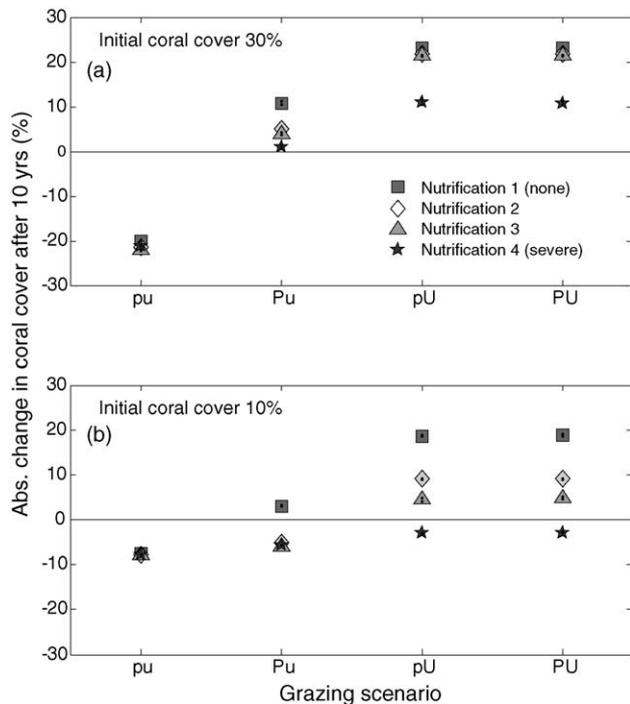


Fig. 3 – Influence of nutrification scenarios and the short-term recovery of coral cover from an initial cover of 30% (a) and 10% (b). Nutrification scenarios are explained in Table 2. No hurricanes occur in these scenarios. Depleted grazing is indicated using lower case where ‘p’ represents parrotfishes grazing 10% of the reef and ‘u’ represents no urchins. For example, PU denotes healthy parrotfishes and presence of urchins (see Table 3 for each scenario).

were able to fulfil the role vacated by urchins (Fig. 3a). However, reefs with lower coral cover were vulnerable to nutrification: at an initial 10% coral cover, reefs fell into decline in all scenarios of elevated nutrient effects (Fig. 3b). Moreover, depletion of scarids had a catastrophic impact on coral cover, with declines occurring across all levels of nutrification irrespective of initial coral cover.

Reef dynamics were also simulated for a 10-year period and the change in total coral cover plotted as a function of initial cover and scarid grazing (Fig. 4). Cover always declined when parrotfish were heavily exploited. At intermediate levels of grazer exploitation, cover only increased when the initial cover exceeded a threshold of ~30% (Fig. 4). At high levels of grazing, coral cover always increased even when the initial value was only 10%. Overall, the impact of increased grazing intensity was non-linear, particularly when coral cover was low: a given change in grazing had a disproportionately large impact on coral cover when grazing levels were high.

To highlight the influence of losing urchins on coral population dynamics, the size-frequency distributions of both coral forms were plotted at the beginning and end of a 15-year period during which no nutrification took place (Fig. 5). In the absence of urchins and with heavy exploitation of scarids, the coral community became bimodal, comprising recruits and larger, adult colonies. Few colonies moved beyond recruit size into puberty, creating a bottleneck in early ontogeny

(Fig. 5c and d). In contrast, high levels of grazing prevented formation of a bottleneck and led to a more natural distribution of size classes (Fig. 5a and b). Qualitatively similar results were obtained for other nutrification scenarios (not shown).

3.2. Survival of coral recruits

The preceding section identified the formation of a bottleneck to coral population dynamics at recruit stages. We now explore the processes acting on recruit survival directly. The interaction plots derived from the statistical model reveal the separate and interactive impacts of each independent variable on recruit survival (Figs. 6–8). The first striking result was that recruit survival (hereafter referred to simply as survival) was always virtually zero when grazing was confined to parrotfishes that experience heavy exploitation (Fig. 6a). Secondly, for a given level of nutrification, survival was usually greater when urchins were present. The only exceptions to this rule were high (Fig. 6), in which case, the per capita survival slightly exceeded that under the equivalent urchin-rich scenario. The presence of *Diadema* allowed fair survival (>20%) in all but one scenario; when initial coral cover was low (10%) and nutrification was highest. Under this severe nutrification scenario, survival increased only once coral cover exceeded ~20% (Fig. 6). This result highlights a third generalisation: under adverse conditions of high nutrification and/or low grazing, survival is often positively and non-linearly related to initial coral cover (Figs. 6 and 7). When urchins were present, the main difference in nutrification impact occurred between scenarios 3 and 4 (Fig. 6), when the colonisation rate of macroalgae was doubled (Table 3).

When urchins were present, increasingly healthy levels of parrotfish grazing had little or no additional impact on

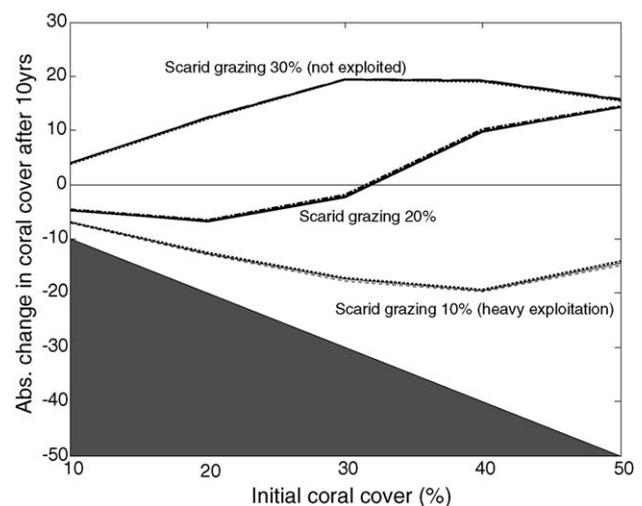


Fig. 4 – Net impact of scarid exploitation on reefs of various initial coral cover. An absolute change in coral cover is plotted after a 10-year period in which no hurricanes occurred. Black panel marks the maximum reduction in coral cover from initial levels, assuming 100% mortality. Standard errors are plotted using dotted lines.

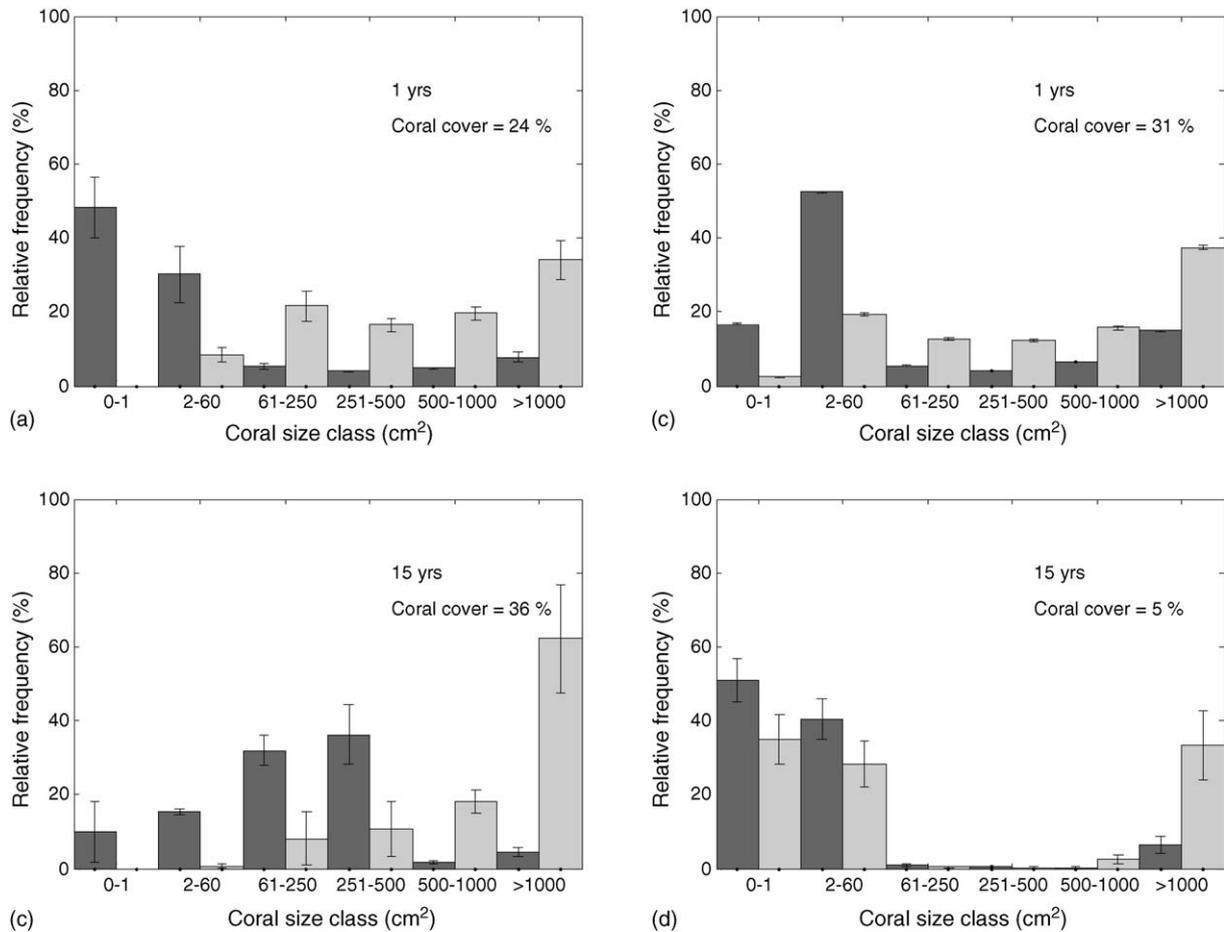


Fig. 5 – Relative size-frequency distributions of brooding (dark grey) and spawning (light grey) corals at the beginning and end of a 15-year period. Hurricanes occur on average once per decade. Grazing is high (*Diadema* plus scarids) in the lefthand panels (a and b) but low in the righthand panels (no *Diadema* and heavily exploited scarids; c and d). Size classes represent settlers (1 cm²), recruits (2–60 cm²), pubescent colonies (61–250 cm²) and various mature size classes (>250 cm²). Error bars denote standard errors based on 10 simulations.

survival. This phenomenon was clearly shown in two types of interaction plot. Firstly, the impact of nutrification in urchin-based simulations was virtually identical whether parrotfish grazing was set at healthy (30%) or overfished (10%; Fig. 6a and b). Secondly, under urchin-based simulations, parrotfish grazing levels could not be separated when survival was plotted against initial coral cover (Fig. 7).

When urchins were absent, survival was only possible across a wide range of coral cover if nutrification was absent (i.e. the standard scenario 1). Increasing levels of nutrification led to an interaction with coral cover such that survival increased markedly once cover exceeded 30% (Figs. 6b and 7a). Healthy communities of parrotfishes were only able to mitigate the most severe nutrification in relatively healthy reef environments, where cover exceeded 30%. Indeed, reefs with say 50% coral cover and a healthy parrotfish community were remarkably resistant and barely influenced by the absence of urchins, level of nutrification or coral growth rate (Fig. 8a).

Coral growth rate had a relatively weak effect on survival and only when urchins were present and nutrification occurred at all but highest levels (Fig. 8). Thus, the effect of

changing coral growth rate in urchin-depleted systems seems limited.

3.3. Influence of spatial structure within the coral community on coral dynamics

The model was found to be sensitive to initial spatial structure within the coral community. In general, enforcing size-dependent spatial aggregation led to slightly faster changes in coral cover, be they either positive or negative (e.g. difference in coral cover of 1–6% over 20 years, Fig. 9). However, the addition of spatial structure did not affect the conclusions reported above; the direction of reef response was similar for any given initial coral cover or grazing intensity (Fig. 9).

4. Discussion

4.1. Importance of urchin and scarid grazing

The model predicts that the urchin, *D. antillarum*, imparted great resilience to Caribbean forereefs. In the presence of

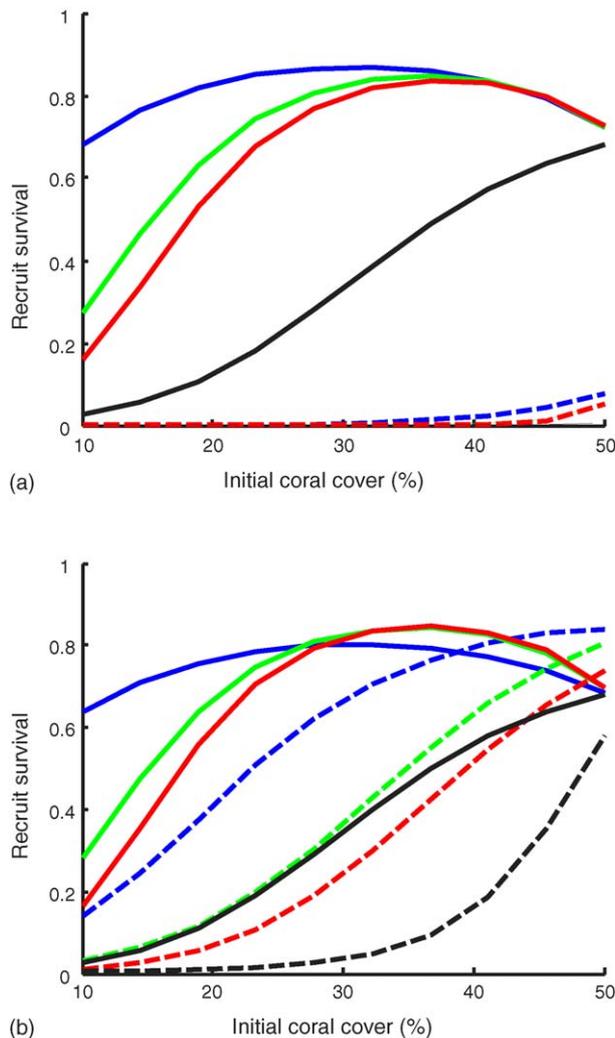


Fig. 6 – Interaction plot of grazing scenario against initial coral cover for the survival of coral recruits. Coral growth rate is held constant at 0.6 cm year^{-1} but parrotfish grazing is either heavily depleted (a) or unexploited (b). Nutrification scenarios are coloured in the order blue (none), green, red and black (severe, see Table 2). Solid lines denote urchins present, dotted lines denote urchins absent. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

this urchin, coral cover increased even under an intense regime of one severe hurricane per decade. Moreover, only extremely severe nutrification impacts, which represented doubling of the vertical growth rate, vegetative (horizontal) growth rate and colonisation rate of macroalgae, led to a decline in coral cover and even then, only on reefs whose initial coral cover was low. Therefore, for all but the most severe nutrification impact simulated, coral reefs were always predicted to recover after a hurricane; even when the hurricane reduced coral cover to low levels. This conclusion is borne out by the recovery trajectory of *Montastraea* reefs in Jamaica immediately after Hurricane Allen (Fig. 1 and

Hughes, 1994): scarids had been heavily depleted in this system but coral cover recovered until the die-off of *Diadema* in 1983.

Our conclusions concerning *Diadema* need to be considered in light of the model's inevitable ecological limitations. First of all, we did not model the shallow reef habitats where this urchin reaches its highest densities; our results represent forereef communities at a depth of $\sim 5\text{--}15 \text{ m}$. However, although densities of *Diadema* decline with increasing depth (de Ruyter van Steveninck and Bak, 1986), there is abundant evidence that densities of this urchin were ecologically significant in this habitat (Bauer, 1980; Carpenter, 1981; de Ruyter van Steveninck and Bak, 1986). Secondly, we expect that the representation of urchin grazing erred on the conservative side, potentially underestimating the capacity of urchins to graze algae (see Section 2). While a potential underestimate of urchin grazing has little impact on our conclusions, the effects of extremely intense urchin grazing warrant brief discussion. Urchin densities can explode when their principle fish predators are heavily depleted (McClanahan and Shafir, 1990) as was the case in Jamaica (Sammarco, 1980). When densities of urchin exceed $\sim 16 \text{ m}^{-2}$, they can significantly reduce the density of pre-visible coral recruits (Sammarco, 1980). Our scenario of heavy fish exploitation did not incorporate population explosions of urchins which may cause reduced coral survival. However, given that recruit survival was high under urchin grazing (60–80%), even a three-fold reduction in survival would be broadly equivalent to the resilient scenarios of healthy scarids (Fig. 6b), and therefore the implications of rising urchin density on coral cover seem limited in this habitat. Clearly, outbreaks of urchins are best avoided (Bellwood et al., 2004) and fisheries management strategies can help regulate urchin density by protecting urchin predators (McClanahan, 1995).

One emergent consequence of urchin grazing was a decline in the survival of coral recruits once initial coral cover exceeded levels of approximately 40%. Under these highly favourable conditions for coral recruitment and growth, space became limiting such that larger corals would virtually fill entire cells and exclude smaller corals, including recruits. While this exclusion reduced per capita survival rates, the absolute effect was moderate (typically a reduction from 0.80 to 0.65) and had no detectable impact on recovery. In short, reefs with such high levels of coral cover and grazing are highly resilient and insensitive to minor reductions to the per capita survival of recruits.

Scarid grazing is important in that it contributes to sediment production (Bruggemann et al., 1996) and grazes microhabitats that are inaccessible to urchins. The model suggests that coral dynamics are not regulated by algae once around 46% of the reef is grazed efficiently. In the absence of urchins, however, the fate of the reef was critically dependent on the level of scarid grazing. High levels of scarid grazing (grazing 30% of the reef) were able to compensate for the loss of urchin grazing under some, but not all, physical and ecological conditions. Coral cover declined under a regime of decadal hurricanes and when nutrification coincided with low coral cover.

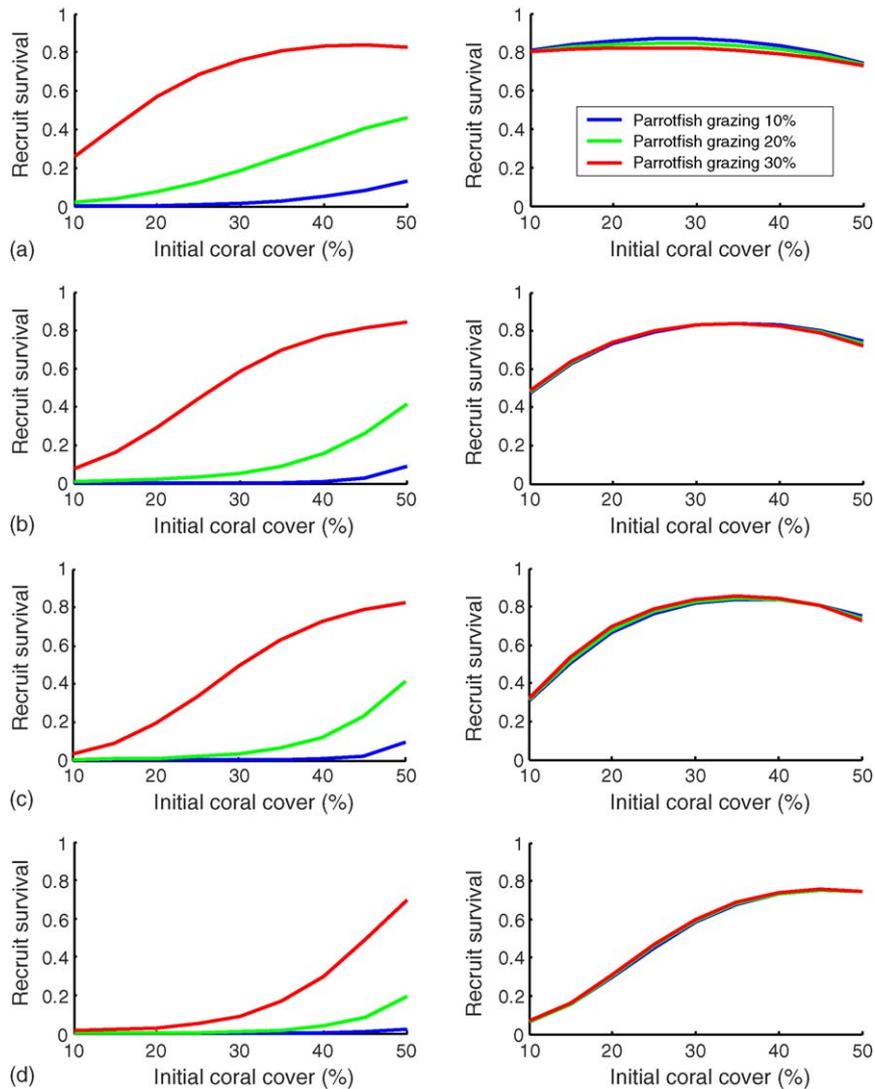


Fig. 7 – Interaction plot of nutrification level, grazing scenario and initial coral cover for the survival of coral recruits. Coral growth rate is held constant (at 0.6 cm year⁻¹) but parrotfish grazing is either heavily depleted (blue lines), moderately depleted (green lines) or unexploited (red lines). Panels are paired and denote the absence (left) and present (right) of urchins. Each pair of panels denote a nutrification scenario where (a) denotes scenario 1 (Table 2) and (d) denotes scenario 4 (severe, see Table 2).

4.2. Impact of nutrification on coral reefs

Outcomes of this study provide some additional perspective to the bottom-up versus top-down debate on rising levels of macroalgae on reefs in Jamaica (Lapointe, 1997, 1999; Hughes et al., 1999b). The lack of coral recovery after the die-off of urchins would be predicted from the intense exploitation of scarids, irrespective of the level of nutrification (at least, given the range of scenarios simulated here). Thus, any additive role of nutrification to coral reef decline would have been difficult to detect even if it had occurred. Equally, the ecological effects of nutrification may have been subtle during the presence of urchins because such intense grazing largely overwhelms the influence of nutrients. Nutrification impacts exerted their strongest influence on coral dynamics under relatively high levels of scarid grazing but in the absence of urchins. There-

fore, the ‘acid test’ for nutrification impacts may occur if no-take marine reserves permitted scarid populations to recover. At low levels of coral cover, such as those found today, the model provides a case for minimising levels of nutrification: under this scenario, coral cover only increased under the basic scenario of no nutrification.

4.3. Mechanistic behaviour of model

The overall trajectory of coral cover on modelled reefs depended on three factors: initial levels of coral cover, the physical environment (nutrient level, hurricane frequency) and grazing. One of the most interesting results was interaction of initial reef state and grazing on the trajectory of coral cover. In the absence of *Diadema*, exploitation of scarids was more likely to result in reef degradation when coral cover was

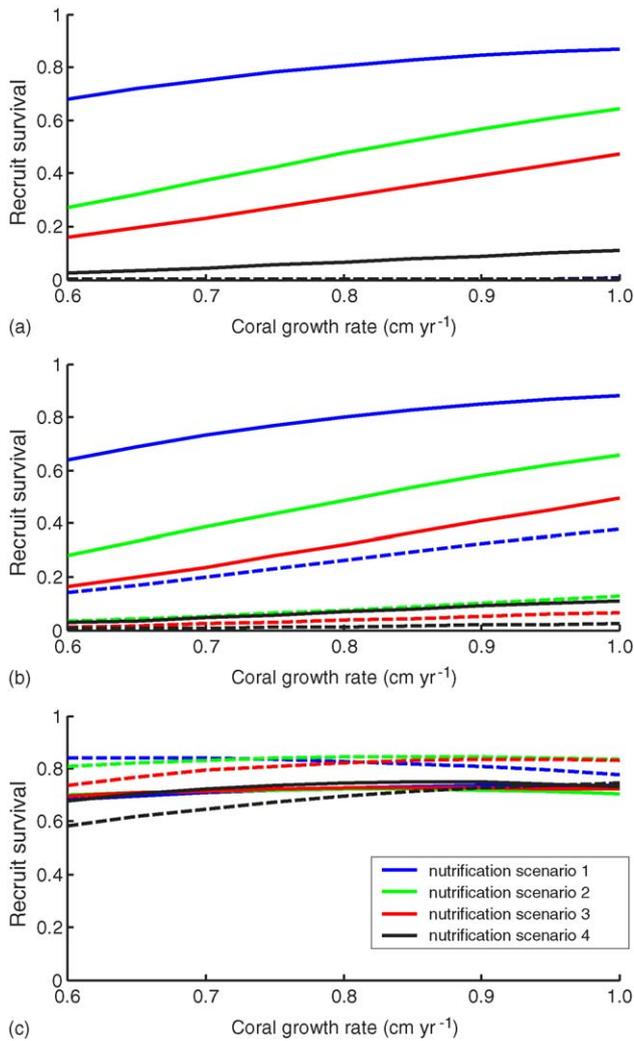


Fig. 8 – Interaction plot of grazing scenario against coral growth rate for the survival of coral recruits. Initial coral cover is held constant in each panel and is 10% (a and b) or 50% (c). Parrotfish grazing is depleted in (a) but unexploited in (b and c). Nutrification scenarios are coloured in the order blue (none), green, red and black (severe, see Table 2). Solid lines denote urchins present, dotted lines denote urchins absent. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

low. In other words, reefs with low coral cover had less resistance to grazer depletion. Several mechanisms underpin these interactions.

Firstly, the root cause of coral decline was a bottleneck in the number of juvenile corals reaching adulthood. With few corals joining the adult population, sources of chronic and acute mortality in adult colonies resulted in declining coral cover. The survival of coral recruits mirrored the trajectories of coral cover, exhibiting interactions between initial reef state and grazing; i.e. survival was poorest when both grazing and coral cover were low. Importantly, since rates of recruit survival were independent of initial conditions, the observed interaction of survival and coral cover was an

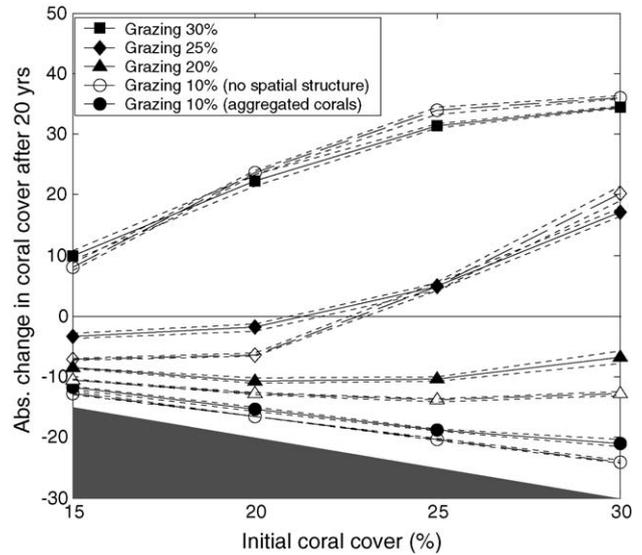


Fig. 9 – Influence of spatial aggregation in corals on sensitivity of reefs to scarid exploitation. An absolute change in coral cover is plotted after a 10-year period in which no hurricanes occurred. Open symbols denote results from standard model in which corals are distributed at random. Levels of scarid grazing are distinguished by symbol shape (see legend). Black panel marks the maximum reduction in coral cover from initial levels, assuming 100% mortality. Standard errors are plotted using dotted lines.

indirect, emergent property of the model. To understand the cause of such interactions, we must consider the dynamics of macroalgae which were the main source of mortality in coral recruits.

Most aspects of macroalgal dynamics were explicitly incorporated in the model such as consumption by grazers, the dependence of vegetative growth on local algal cover, the pre-emption of algal settlement space by corals and coral–algal competition. However, an important interaction developed between grazing and coral cover, the outcome of which drove either positive or negative feedbacks on macroalgal cover. For example, a coral mortality event increases the availability of colonisable space for algae. Grazers now forage over a larger area and this reduces the intensity of grazing because individual patches of reef will, on average, be grazed less often. Reductions in grazing intensity increase the probability that macroalgae will develop from ungrazed patches of cropped algae. In contrast, a rise in coral cover can be self-reinforcing because it reduces the foraging area available to grazers, thereby increasing the intensity of grazing and reducing the cover of macroalgae. The reduction in macroalgae has a beneficial affect on the survival of coral recruits which further reinforces rising coral cover. These coral–grazer interactions are important and explain much of the model behaviour. An equivalent interaction occurred between the level of nutrification and reef state; the impact of a given level of nutrification was worse when coral cover was low. Such similarities in interaction are not surprising given that nutrification reduces the efficacy of grazing on macroalgal cover and is

therefore functionally equivalent to depleting grazer biomass (see Szmant, 2002).

Interactions between corals, macroalgae and grazers also took place when the distribution of corals was aggregated. High levels of aggregation create local refugia where both algal cover and growth rate is reduced, thus constraining the rate of algal encroachment. Such refugia can enhance the survival of coral recruits (results not shown) and account for the modest increase in the rate of coral cover reported here for aggregated corals at appropriately high grazing intensities.

4.4. Implications of model outcomes for reef management

The existence of positive and negative feedbacks between coral cover and grazing have an important implication for reef management when grazing is confined to fishes. At certain levels of grazing, the fate of the reef is predicted to be partly dependent on its current state. In short, the resilience of a reef, or its ability to recover to a former state, may be disproportionately poor as its health declines. The clear implication is that arresting reef decline should be an immediate and high priority of management because natural restoration will become more difficult as coral cover declines.

A key management implication of this study is that parrotfish exploitation should be carefully controlled. The relationship between scarid grazing intensity and recruit survival was non-linear such that changes in grazing have a larger influence when grazing levels are high than when grazing levels are low. Therefore, minor levels of scarid depletion could have a disproportionately severe deleterious impact on coral cover and reef resilience. Given the continued scarcity of *Diadema* (Kramer, 2003), healthy scarid communities are predicted to be a pre-requisite for a resilient coral reef. However, the model suggests that even healthy scarid communities may not prevent the decline of coral cover where *Diadema* is functionally absent and the disturbance regime is intense. This scenario may apply to the shallow forereefs of Florida, which experience hurricanes on a decadal basis (Gardner et al., 2005) and coral cover has decreased (Dustan et al., 2001). Indeed, some of the healthiest reefs in Florida are now found in deep water, which experience a natural refuge from hurricane impacts (Peter Glynn, pers. comm.).

The relatively minor impact of coral growth rate was of interest in the context of global climate change. Rising concentrations of atmospheric carbon dioxide are changing the saturation state of calcium carbonate in the ocean with a putatively negative effect on coral growth rates (Kleypas et al., 1999). Here, we predict that small changes to growth rate may not have severe consequences to coral cover on ecological time scales and at low latitudes. However, other effects of changing saturation states, such as a shift towards more brittle carbonate skeletons, are yet to be evaluated or modelled and may have important consequences for reef rugosity and hurricane impacts.

Outcomes of the model clearly reveal the vulnerability of ecosystems whose functional composition lacks species diversity; loss of a single species can have catastrophic consequences on the ecosystem. The degree to which scarids compensate for the continued paucity of *Diadema* on Caribbean

reefs will depend on the level of fishing and the intensity of disturbance faced by corals. The latter dependency is particularly sobering given the plethora of disturbances affecting reefs such as outbreaks of white plague (Garzon-Ferreira et al., 2001), white band disease (Aronson and Precht, 2001) and coral bleaching (Lang et al., 1992), neither of which were included in the simulations here. We cannot assume that *Diadema* will experience a widespread recovery to pre-mortality levels in the near future, and therefore healthy scarid populations are a pre-requisite for reef resilience. In the meantime, management measures need to focus on mitigating the direct causes of coral mortality.

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