THE IMPACT OF EXPLOITING GRAZERS (SCARIDAE) ON THE DYNAMICS OF CARIBBEAN CORAL REEFS

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Abstract. Coral reefs provide a number of ecosystem services including coastal defense from storms, the generation of building materials, and fisheries. It is increasingly clear that the management of reef resources requires an ecosystem approach in which extractive activities are weighed against the needs of the ecosystem and its functions rather than solely those of the fishery. Here, I use a spatially explicit simulation model of a Caribbean coral reef to examine the ecosystem requirements for grazing which is primarily conducted by parrotfishes (Scaridae). The model allows the impact of fishing grazers to be assessed in the wider context of other ecosystem processes including coral–algal competition, hurricanes, and mass extinction of the herbivorous urchin *Diadema antillarum*. Using a new analytical model of scarid grazing, it is estimated that parrotfishes can only maintain between 10% and 30% of a structurally complex forereef in a grazed state. Predictions from this grazing model were then incorporated into a broader simulation model of the ecosystem. Simulations predict that scarid grazing is unable to maintain high levels of coral cover ($\geq$30%) when severe hurricanes occur on a decadal basis, such as occurs in parts of the northern Caribbean. However, reefs can withstand such intense disturbance when grazing is undertaken by both scarids and the urchin *Diadema*. Scarid grazing is predicted to allow recovery from hurricanes when their incidence falls to 20 years or less (e.g., most of Central and South America). Sensitivity analyses revealed that scarid grazing had the most acute impact on model behavior, and depletion led to the emergence of a stable, algal-dominated community state. Under conditions of heavy grazer depletion, coral cover was predicted to decline rapidly from an initial level of 30% to less than 1% within 40 years, even when hurricane frequency was low at 60 years. Depleted grazers caused a population bottleneck in juvenile corals in which algal overgrowth caused elevated levels of postsettlement mortality and resulted in a bimodal distribution of coral sizes. Several new hypotheses were generated including a region-wide change in the spatial heterogeneity of coral reefs following extinction of *Diadema*. The management of parrotfishes on Caribbean reefs is usually approached implicitly through no-take marine reserves. The model predicts that depletion of grazers in nonreserve areas can severely limit coral accretion. Other studies have shown that low coral accretion can reduce the structural complexity and therefore quality of the reef habitat for many organisms. A speculative yet rational inference from the model is that failure to manage scarid populations outside reserves will have a profoundly negative impact on the functioning of the reserve system and status of non-reserve reefs.

Key words: biodiversity; coral reefs; ecosystem-based management; ecosystem function; grazing; marine reserve networks; reef fish.

INTRODUCTION

Coral reefs are among the most diverse ecosystems on Earth and at least 100 million people have either economic or cultural dependencies on their resources (Bryant et al. 1998, Cesar 2000, Whittingham et al. 2003). A combination of overpopulation, poverty, and changing climate threaten extensive areas of coral habitat, its biodiversity, and the viability of its commercial resources (Wilkinson 2002, Hughes et al. 2003, Hoegh-Guldberg 2004). Improved management of reef resources is essential if the functions and ecosystem services of coral reefs are to be sustained throughout an increasingly stressful physical environment, driven primarily by global changes in sea temperature and carbonate chemistry (Buddemeier et al. 2004).

The management of reef resources is often sought through a combination of fisheries regulations and marine reserves (Polunin and Roberts 1996). Most marine reserves have at least two goals; to help sustain fisheries and conserve marine biodiversity (Agardy 1994, Holland and Brazee 1996, Halpern 2003). In principle, fisheries may benefit if the reserve acts as a source of larvae to exploited areas or if adult fish move directly beyond reserve boundaries (spillover), thereby maintaining a local fishery around the reserve (DeMartini 1993, Palumbi 2001). Biodiversity conservation is usually sought by protecting an adequate area and number of habitats for a range of species, which is

typically achieved through a systematic approach to habitat and species representation (McNeill 1994, Ward et al. 1999, Possingham et al. 2000, Sala et al. 2002, Beger et al. 2003).

To date, much research has focused on the efficacy of marine reserves for fisheries management (see reviews by Roberts 1993, Hall 1998, Dayton et al. 2000, Russ 2002). Recent studies have extended this perspective to consider the compatibility of reserve designs for conserving both fisheries and marine biodiversity (Hastings and Botsford 2003). However, the use of reserves for managing nonfishery ecosystem services has received little explicit consideration. In the case of coral reefs, many ecosystem services, such as coastal defense from hurricanes, the generation of building materials, and the generation of revenue from tourism are underpinned by the corals themselves (Done et al. 1996, McManus 1997, Moberg and Folke 1999). Therefore, the wider aim of managing multiple ecosystem services requires a broad, ecosystem-level approach that encompasses fish, corals, and the processes that maintain them. Not only is an ecosystem-level approach more inclusive, but it is likely to increase the long-term sustainability of core services such as fisheries. Indeed, many fisheries management agencies are actively switching towards an ecosystem-based approach to fisheries (reviewed in Browman and Stergiou 2004) in which the multiple needs of the fishery, ecosystem, and human society are considered simultaneously (Food and Agriculture Organization of the United Nations 2003).

An ecosystem approach to management is particularly appropriate for coral reefs because ecosystem services, fishing, and habitat quality are intimately related. A healthy coral community contributes to the bioconstruction of a structurally complex habitat. A complex habitat, referred to as having high rugosity, provides refugia and food resources for many marine organisms and their prey (Hixon and Beets 1993). Rugosity is positively correlated to the density of many fish species (Luckhurst and Luckhurst 1978, Roberts and Ormond 1987, van Rooij et al. 1996) and may mediate density-dependent competition and predator–prey interactions (Carr et al. 2002). High rugosity may also facilitate higher alpha diversity at small scales (McCormick 1994). A decline in coral production may allow processes of bioerosion (Hutchings 1986) to exceed bioconstruction, resulting in a gradual flattening of the reef structure and fall in rugosity (Scoffin et al. 1980, Glynn 1997). Reef degradation will have direct negative consequences for coral-associated species (Jones et al. 2004) and indirect, delayed consequences for those taxa with a more general association with reef structure (McCormick 1994). Although habitat quality is by no means the only factor influencing reef organisms (see Caley et al. 1996), a well-maintained reef habitat will underpin multiple ecosystem functions and help achieve the goals of biodiversity conservation and high fisheries yield.

Of the processes influencing the structure of reef habitats, grazing is potentially one of the easiest to manage through restrictions to the level of fishing of grazing organisms (Roberts 1995, Rakitin and Kramer 1996). Extremes of grazing intensity have been shown to influence coral–algal interactions and the cover of living coral (Hatcher and Larkum 1983, Carpenter 1986, Lewis 1986, Morrison 1988, McClanahan 1992, Hughes 1994, Steneck 1994, Jompa and McCook 2002). For example, the Caribbean-wide mass mortality of the urchin, *Diadema antillarum* in 1983 (Lessios et al. 1984), may have contributed significantly to the lack of coral recovery at many sites in Jamaica that were impacted by hurricanes, coral disease, and long-term overfishing (Hughes 1994, Aronson and Precht 2000). Indeed, the paucity of *D. antillarum* persists in most of the Caribbean (Kramer 2003) leaving parrotfishes (Scaridae) as the dominant grazer in most areas (Carpenter 1986, Steneck 1994).

While many experimental studies have documented profound impacts of parrotfish *exclusion* on Caribbean reefs (Carpenter 1986, Lewis 1986, Morrison 1988, McClanahan et al. 2003), the impact of fishing, which leads to grazer depletion rather than exclusion, has not been quantified. Moreover, with the continued scarcity of *Diadema* and recent evidence suggesting that scarid grazing is spatially limited (Williams et al. 2001), it is not clear whether modern-day Caribbean reefs receive sufficient grazing to maintain essential ecosystem services such as net coral accretion. Here, I use two models to explore the impact of fishing parrotfishes on coral dynamics. The first model simulates ecosystem processes (Fig. 1) and by manipulating the incidence of hurricanes, it highlights Caribbean-wide variation in reef dynamics and their implication for marine reserves and ecosystem-based management. A second model quantifies the impact on grazing of depleting parrotfish biomass. Outcomes from this model are used to parameterize the simulation model and represent the impact of fishing parrotfishes.

In this era of a functionally obsolete urchin and dependency on vertebrate grazing, this study tests the following hypotheses:

H_1) An unfished community of parrotfishes provides adequate grazing to maintain net reef accretion (in the absence of acute disturbance events and *Diadema antillarum*).

H_2) Regional variation in hurricane frequency impacts the trajectory of Caribbean reefs.

H_3) Depleting the biomass of parrotfishes (grazing) has a disproportionately large impact on coral dynamics (compared to expected variation in other parameters).

H_4) Depleting the biomass of parrotfishes (grazing) can precipitate shifts in community state from coral-rich to macroalgal-dominated ecosystems.

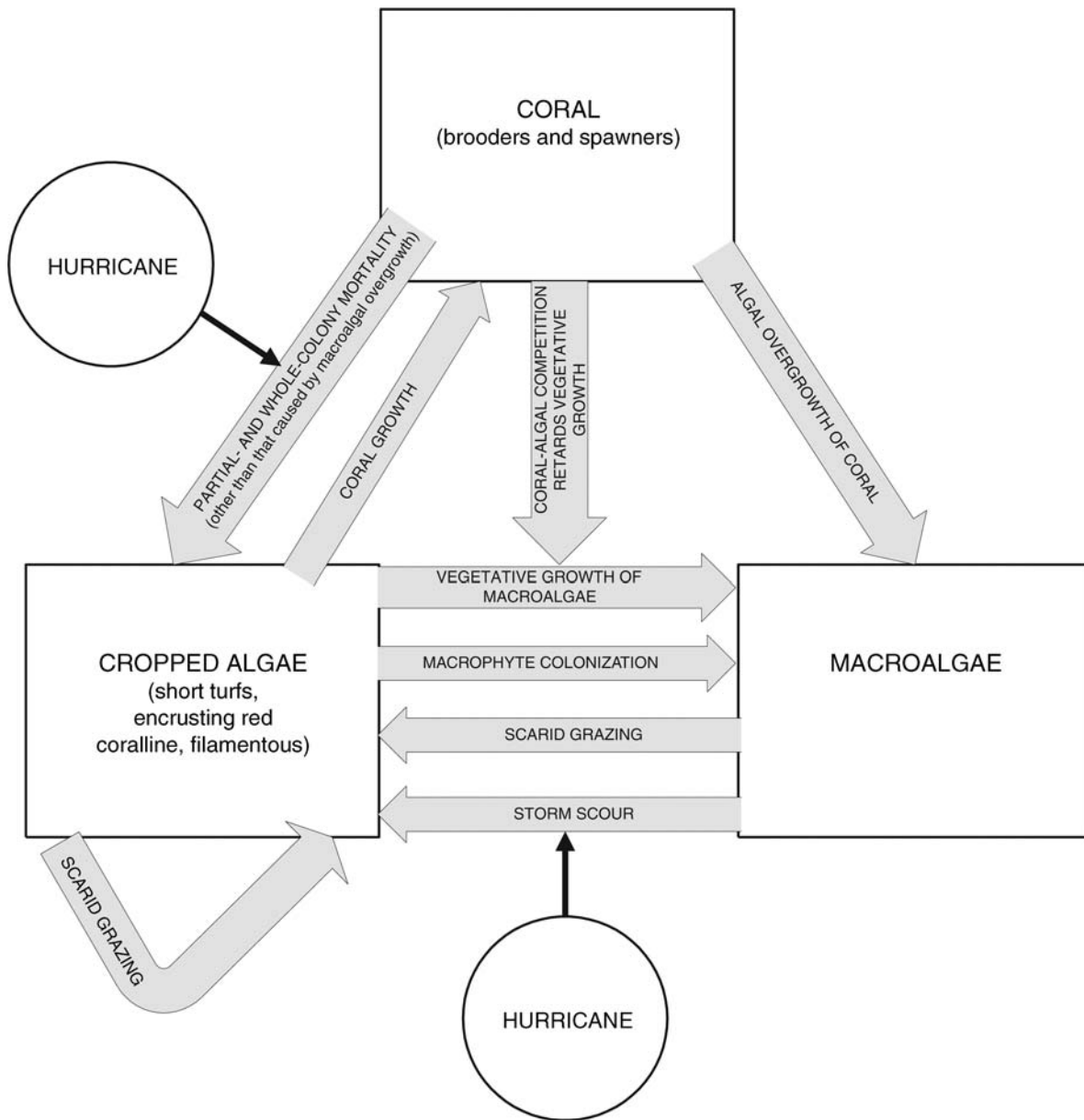Given current concerns over the impact of climate change (Hoegh-Guldberg 2004) and epidemics of coral

FIG. 1. Processes included in the simulation model (arrows) that link the major functional categories of reef organisms (boxes). Urchin grazing is not shown, and hurricanes are depicted as external sources of acute disturbance.

disease (Harvell et al. 1999), the model is also used to generate testable hypotheses for the response of reefs to various intensities and frequencies of disturbance.

METHODS

Two models were developed in this study. The first was a simulation model of ecosystem processes occurring on Caribbean forereefs (Fig. 1). Whilst this model included the net impact of grazers on algal communities, a second model was developed to estimate the impact of depleting the total biomass of parrotfishes on grazing. The latter model was sensitive to the species, sex, and

size frequency distribution of scarids. The scope of the simulation model is described in the next section, but the majority of parameters are justified in the Appendix. Details of the grazing models are presented here because of their novelty and importance to the study.

Scope of simulation model

I focus on Caribbean coral reefs because their low functional diversity simplifies the challenge of modeling their dynamics. The model was parameterized for mid-depth (5–15 m) forereefs of the *Montastraea annularis* zone (Geister 1977) which typically have the highest

TABLE 1. Contents of individual cells (0.25 m^2) within the model.

Substratum	Code	Examples	Range (cm^2)
Brooding coral†	BC	*Porites astreoides*	$1 \leq BC \leq 2500$
Spawning coral†	SC	*Siderastrea siderea*	$1 \leq SC \leq 2500$
Cropped algae, 0–6 mo	A_6	Filamentous, coralline red algae, and short turfs	$0 \leq A_6 \leq 2500$
Cropped algae, 6–12 mo	A_{12}	Filamentous, coralline red algae, and short turfs	$0 \leq A_{12} \leq 2500$
Macroalgae, 0–6 mo	M_6	*Dictyota pulchella*, *Lobophora variegata*	$0 \leq M_6 \leq 2500$
Macroalgae, 6+ mo	M_{12}	*Dictyota pulchella*, *Lobophora variegata*	$0 \leq M_{12} \leq 2500$
Ungrazable substratum‡	U	Sand	$U = 0$ or $U = 2500$

Note: All substrata are represented as area (cm^2).
† Up to three individuals per cell.
‡ Fills entire cell if present.

biomass and diversity of reef organisms (Mumby, *unpublished data*). Since white band disease has depleted populations of large, branching corals (Aronson and Precht 2001), I modeled stylized massive growth forms of coral and included their recruitment, growth, fecundity, and reproduction (either broadcast spawning of gametes or internal development of brooded planulae that disperse locally). The model is a square lattice of 2500 cells, each of which approximates 0.25 m^2 of reef, and can be occupied by a mixture of living and dead substrata (Table 1, Fig. 2). At this cell size, the lattice represents a minimum area of only 25 m by 25 m, which is clearly at odds with the size of individual reefs which may span kilometers or tens of kilometers. The gulf in scale was bridged by using a torus (which has continuous boundaries), and by representing several modeled processes, such as hurricane disturbance, using their mean behavior at reef scales rather than attempting to segregate the reef into sub-reefs of heavy and light disturbance. For example, reefs in the direct path of a hurricane may experience 50–100% whole-colony mortality, whereas mortality at the whole-reef scale may be nearer to 30% (Bythell et al. 1993). Subdividing the reef (torus) to capture small-scale variation in impacts would be both computationally challenging and difficult to parameterize meaningfully. It is assumed that sedimentation levels are low and that algal production is high as is typical of seaward forereefs in either offshore, arid, or coastal areas with little terrigeneous runoff. The model uses discrete time intervals of six months, which are appropriate for coral growth rates and commensurate with empirical studies on algal patch dynamics (de Ruyter van Steveninck and Breeman 1987). Simulations used either a single reef or four reefs connected in a circular, stepping-stone manner such that coral larvae are both retained in a local reef and transported in a unidirectional current to the next reef downstream (Fig. 2). Coding was accomplished using Matlab (The Mathworks, Natick, Massachusetts, USA) and each reef was represented separately using an 11-layer matrix where each layer represented the cover of a single size category of algae (layers 1–4), the number of coral colonies in a cell and cover of sand (layer 5), or the size of an individual coral colony (layers 6–11, divided equally

among brooders and spawners). Individual cells are updated on a 6-monthly basis and in a random sequence.

Although this is a simulation model, several of the parameters, such as coral growth rate, 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 connectivity scenarios rather than other internal parameters.

One parameter, the probability that corals of a given size are overgrown by macroalgae, was fitted by comparing model simulations to a twenty year time series of coral dynamics from Jamaica (Hughes 1994). Details of this parameterization are given in the Appendix, but the overall goodness-of-fit between model and empirical data is compelling (Fig. 3); the model behaves like a reef even when the overgrowth parameter is manipulated.

Modeling the process of grazing on Caribbean forereefs

Grazing of parrotfishes (scarids) in the simulation model.—Parrotfish (Scaridae) are usually the most significant fish grazer on Caribbean reefs (Carpenter 1986, Steneck 1994). Species differ in their preferred food and substratum requirements and feed almost continuously during the day (Randall 1961, 1967, Hanley 1984, Bruggemann et al. 1994*a*, *b*, *c*, 1996, Steneck 1994, van Rooij et al. 1995*b*, Overholtzer and Motta 1999). There is, therefore, a problem of scale; most observations of parrotfish grazing occur on a scale of seconds to minutes whereas the model has a discrete time scale of six months, largely because of the paucity of data on algal patch dynamics at finer temporal scales (see Appendix). 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 colonization, recruitment rate, and growth) and algal removal (principally grazing). The simulation model
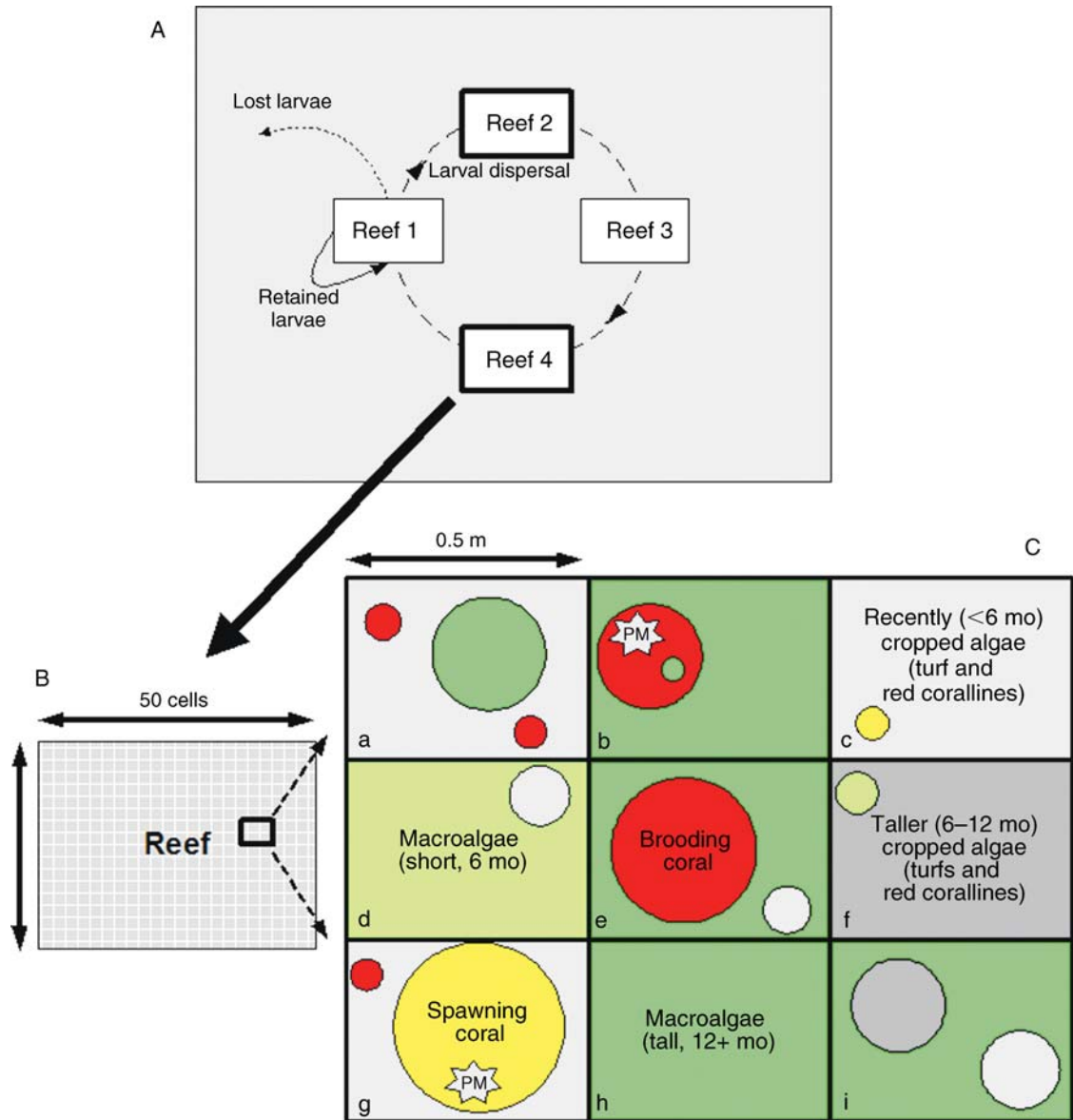
Fig. 2. (A) Implementation of simulation model including four reefs separated by ocean in a unidirectional stepping-stone approach. Reefs with a bold outline are reserves in which parrotfish grazing is maintained at high levels (30% of reef effectively grazed per iteration). (B) Individual reefs have a grid of 2500 cells whose typical composition is illustrated in detail in panel (C). Two types of coral (yellow, spawning; red, brooding) are shown with patches of partial-colony mortality (PM) that are initially colonized by cropped algae (gray; b, g) and later by macroalgae (green; b). Recently dead corals are shown in cells d, e, and i, and their shading denotes the age class (<6 mo vs. 6–12 mo) of cropped algae.

required 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. Williams et al. (2001) artificially increased coral cover in 5 × 5 m plots and observed a corresponding decrease in macroalgae whilst cropped substrata were maintained at an equilibrial 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 the model so to adapt their results to the habitat modeled here, and partially test the generality of their conclusions, a simple comparison was performed. First, I compared the rugosity between their site (Ambergris Caye, rugosity = 1.2) and that of Long Cay (LC), Glovers Reef, which better represents the reefs being modeled (rugosity = 1.98). The area grazed was then adjusted for the differences in surface area (rugosity, R) and parrotfish
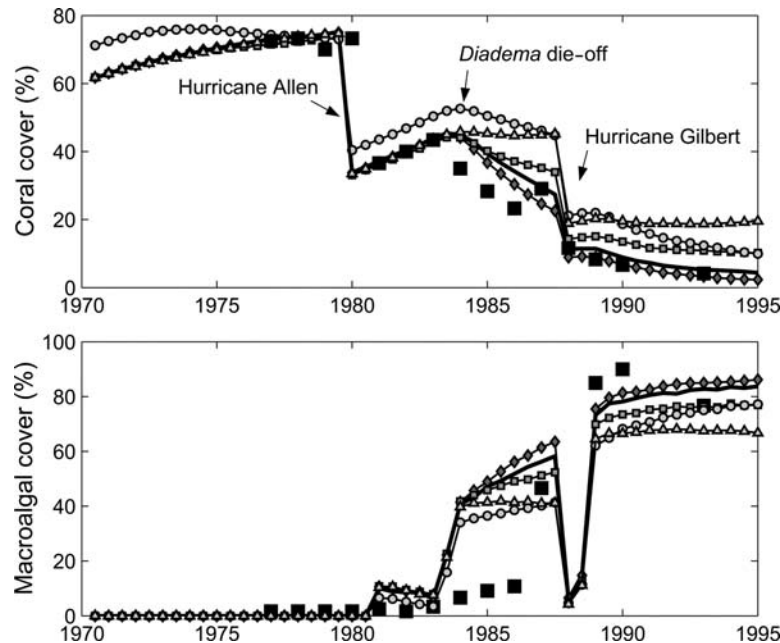
FIG. 3.   Refinement of the model predictions (heavy line) using empirical data (solid squares) for the decline in reefs in Discovery Bay (Jamaica), at a depth of 10 m between 1975 and 1993 (Hughes 1994). Each of the other lines represents a different putative relationship between the risk of algal–coral overgrowth and size of coral colony. That of the heavy line was used in subsequent model simulations.

biomass, B ($\sim$270 g/25 m^2 and 220 g/25 m^2 at Ambergris Caye and Long Cay in 1998, respectively) using Eq. 1, suggesting a drop in the grazable percentage from $\sim$60% of the reef to 30% of *Montastraea* reefs. This estimate was then compared to the observed cover of cropped substratum at Long Cay in the summer of 1998 when the reef was in good health (42% coral cover) since it had not been severely disturbed since 1978 (i.e., as close to equilibrial conditions as is likely to be found in Belize). Since the cover of cropped substrata was 31% in July 1998, which closely fitted the prediction (30%), grazing was constrained to a maximum of 30% of the substratum:

Percentage of reef grazed$_{LC}$

$$= \left[\left(\frac{B_{LC}}{B_W}\right)\left(\frac{R_W}{R_{LC}}\right) \times 63 \right] \quad (1)$$

where W denotes the Williams et al. study in a lower-rugosity habitat in which the percentage area grazed was 63%.

The approach described here to quantify scarid grazing in unexploited systems makes two implicit assumptions. First, 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 (Fig. 4) 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), and has

clear water and relatively high inorganic nutrient concentrations (McClanahan et al. 2004), possibly resulting from upwelling near the atoll. 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 patch would be regrazed sufficiently often to prevent macroalgal escape). The degree to which scarids can fully compensate for a change in algal colonization space is not fully understood. 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, a positive numerical response in parrotfish biomass at Long Cay has been documented in the four 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 ca 30% despite a drastic decline in coral cover from 42% to ca 18% in five years. This result seems to be representative of *Montastraea* reefs in Belize since a 300 km wide survey of cropped algae at 16 reefs recorded a mean cover of 28% (Mumby, *unpublished data*). These surveys were undertaken in June 2002, nearly four years after Hurricane Mitch had widespread impacts on the cover of corals and macroalgae (Kramer et al. 2000). Given that the dominant scarid in Belize (*Sparisoma viride*) grows quickly, potentially reaching a length of 250 mm between the hurricane impact and
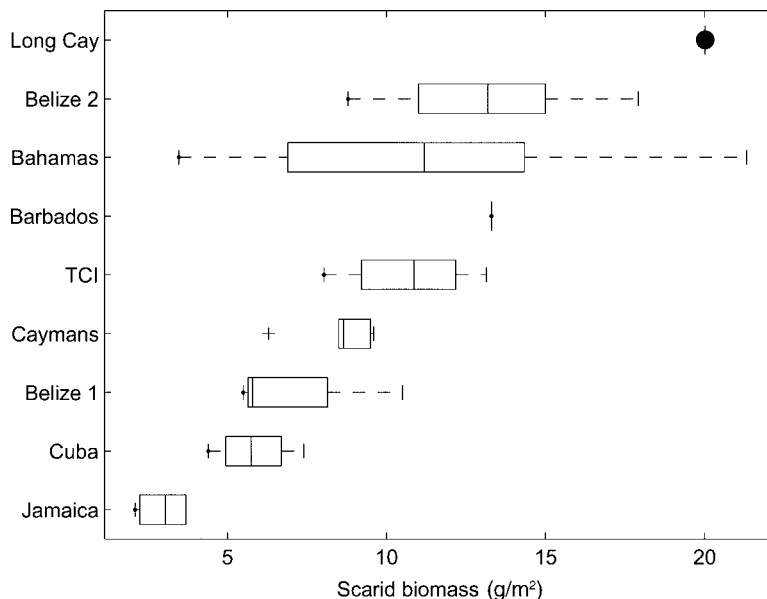
FIG. 4. Comparison of scarid biomass at several sites around the Caribbean. The depth of all sites falls between 8 and 12 m and small individuals (<12 cm standard length) are ignored. Data for Jamaica, Cuba, Cayman Islands, Barbados, and Belize 1 (relatively low-relief reefs) are derived from Williams and Polunin (2000). Data for Belize 2, Bahamas, the Turks and Caicos Islands (TCI), and Long Cay are derived from Mumby (*unpublished data*). Parameters shown are the median (vertical line), interquartile range (box), and absolute range (dotted lines).

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 around 30% of a *Montastraea* reef in a grazed state even allowing for increases in grazing rate and numerical responses to increased food availability.

Cells are grazed in a random order and all cropped algae and macroalgae are converted to (or remain in) the initial cropped algal state until the spatial constraint is reached (e.g., 30% of the total reef area). Once the threshold algal cover is reached, no further algae are grazed during the time step. Grazing does not eliminate coral recruits (Birkeland 1977). Parrotfishes do not discriminate between cropped algae and macroalgae which is consistent with field observations of bites taken by adult parrotfishes in which the ratio of bites on macroalgae (chiefly *Dictyota* spp.) to cropped algae was 1:1.05 (Mumby, *unpublished data*).

Effects of fishing parrotfishes on grazing (second model of the study).—The grazing behavior of parrotfishes varies among species, by size and by life phase (Bruggemann et al. 1994*a*, *b*, *c*, 1996). However, most accounts of scarid abundance provide total biomass rather than a detailed breakdown of community composition. A new model of grazing was created to estimate the relationship between total scarid biomass and total grazing intensity. This model is entirely unrelated to the simulation model and estimates scarid grazing intensity in area grazed per unit time (rather

than the net impact of grazing on the algal community which is used in the simulation model).

The model adapts the work of Bruggemann (1995) on two genera of parrotfishes in Bonaire (*Sparisoma viride* and *Scarus vetula*) by extending it to multiple scarid species, using data from Belize (based on 20-min observations of grazing intensity, $n = 18$ per species; Mumby, *unpublished data*). The model assumes that allometric relationships between FL and both bite rate and mouth size can be extrapolated within genera, and is formulated as follows:

Bite rate, r, of *Scarus* spp. =
$$W_{Sc}\{[1088 - (17.12 \, FL)] - \text{species offset}\} \qquad (2a)$$

Bite rate, r, of *Sparisoma* spp. =
$$W_{Sp}\{[3329 - (33 \, FL)] - \text{species offset}\}. \qquad (2b)$$

Bite rate, r (h^{-1}), is calculated as a function of species (s), length (l), and life phase (p) using (2a or 2b) where FL is the fork length (cm), W is a weighting factor for life phase such that values for the genus *Scarus* (W_{Sc}) are 0.85 for TP and 1 for IP and juveniles and those for *Sparisoma* (W_{Sp}) are 0.80 for TP, 1 for IP, and 0.84 for juveniles. Species-level offsets in the genus *Scarus* are 0 for *Sc. vetula*, 1196 for *Sc. taeniopterus*, and 1714 for *Sc. iserti*. Offsets in the genus *Sparisoma* are 260 for *Sp. aurofrenatum*, 142 for *Sp. rubripinne*, 264 for *Sp. chrysopterum*, and 56 for *Sp. viride*.
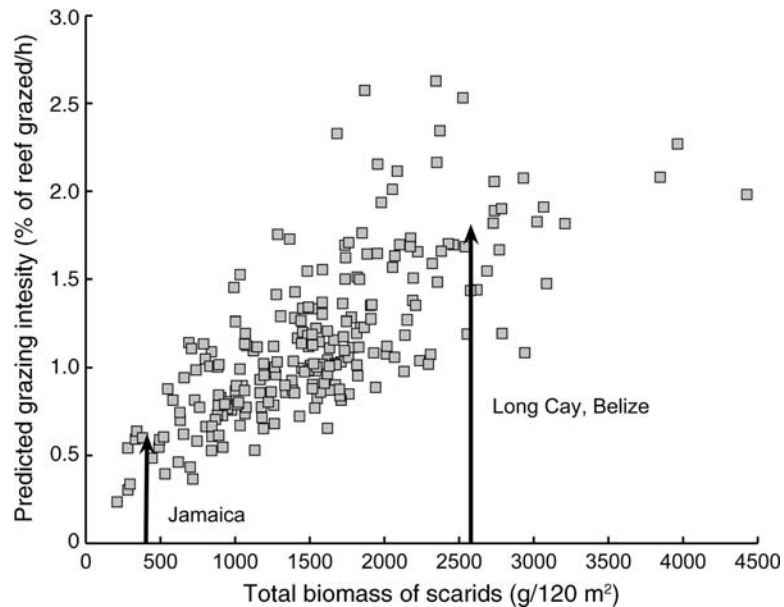
Fig. 5. Modeled grazing intensity of a parrotfish community as a function of its total biomass. The model is sensitive to scarid species, length, and life phase. All data were acquired from Belize and plotted per transect, providing a wide range of biomasses. Mean biomass of parrotfish from Jamaica was derived from Williams and Polunin (2000).

Allometric scaling between FL and bite size, m (in square centimeters) is modeled as

$$m = M \times 0.001(\text{FL})^2 \qquad (3)$$

where M is a constant that takes the value 4.013 in *Scarus* and 5.839 in *Sparisoma*. Derivations of Eqs. 2 and 3 can be found in Bruggemann (1995).

Total grazing intensity (TG) is then

$$\text{TG} = \sum_{s=1}^{S} \sum_{l=1}^{F_s} \sum_{p=1}^{\text{NP}} r_{s,l,p} m_{s,l,p} \qquad (4)$$

where S is the number of species, F_s is the number of size categories for species s, and NP is the number of phases. Eqs. 3 and 4 are then combined to convert bite rate to the percentage of the reef (two-dimensional area) grazed per hour, G:

$$G = \left(\frac{\text{TG}}{10\,000}\right)\left(\frac{1}{\text{ta}}\right) \qquad (5)$$

where ta is the area of a sampling unit (in square meters) which, in this case, was 120 m^2.

A final level of the model apportioned G into four food types (algal turfs, encrusting corallines, macroalgae, and coral), but these more detailed results are not reported here.

Some of the most intensively fished reefs in the Caribbean are found in Jamaica (Pandolfi et al. 2003). Williams and Polunin (2000) presented data on the total biomass of scarids in Jamaica and the scarid grazing model was used to scale their observations of biomass to the expected grazing intensity of scarid communities in

Jamaica. Grazing levels from Jamaica could then be used to represent the impact of severe scarid exploitation on the net grazing activity of parrotfishes in the simulation model. Using data on the full community structure of scarids on 24 *Montastraea* reefs in Belize and Mexico, the grazing model was used to relate total biomass to total grazing intensity (Fig. 5, $r = 0.75$, $P < 0.0001$). Grazing intensity at the simulation model calibration site of Long Cay was approximately three times (1.61 vs. 0.58) greater than that in Jamaica so the net grazing impact of heavily fished scarid communities was rescaled linearly to one-third that of Long Cay (i.e., 10% of the reef could be maintained in a cropped state per time interval of the model). As a final check, the total combined biomass of scarids and acanthurids were compared between Jamaica and Long Cay and also resulted in a ratio of 1:3 (3.9/11.3 g/m^2). Many sites in the Caribbean for which scarid biomass data are available lie between these two extremes (Fig. 4) and intermediate levels of fishing were simulated by setting the grazing constraint at 20% of the reef surface area.

Grazing of Diadema antillarum *in simulation model.*— 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 1982, Hay and Taylor 1985, Foster 1987, Morrison 1988). *Diadema* is an efficient grazer of algal communities and may regraze the substratum more frequently than herbivorous fish (Carpenter 1986). The grazing of *D. antillarum* was modeled using data from the U.S. 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 mass·m^{-2}·d^{-1}. The relative importance of urchin grazing (G_{ur}) and fish grazing (G_{par}) can be estimated by assuming that the higher rate of algal removal included both grazers whereas the lower rate only comprised fishes:

$$G_{ur} = \left[\left(\frac{PR_{all}}{PR_{par}} \right) G_{par} \right] - G_{par}. \tag{6}$$

If grazing fishes are able to graze 30% of the reef efficiently (G_{par}), then Eq. 6 predicts the grazing component attributable to urchins as ~40%, where production for all grazers, $PR_{all} = 3.74$ and that of parrotfishes, $PR_{par} = 1.58$.

Urchin and parrotfish grazing were modeled independently in a spatially random manner such that the consumption of algae overlapped in space. If *Diadema* and scarids used to compete for food, the model could, in principle, have overestimated urchin grazing because the scaling relationship was based on recent scarid studies where grazing was not hindered by urchin competitors (i.e., G_{par} 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. First, 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 individual/m^2 (Bak and van Eys 1975, Bauer 1980, Hunte et al. 1986), the exception being some reefs in Belize, although densities as high as 4 individuals/m^2 were reported (Hay 1984). Second, urchins are very effective grazers even at low densities (Levitan 1988*a*). Recent experiments in the Bahamas have found that *Diadema* densities of only 1 individual/ m^2 can maintain small experimental patch reefs in a cropped algal state (Craig Dahlgren, *personal communication*). Such efficient grazing is not surprising given that the foraging range of this urchin is approximately 0.5 m^2 to 4 m^2, is regrazed every 3–6 d, and may be maintained for more than a year (Carpenter 1984).

Reef scenarios used for simulations and sensitivity analysis

Unless otherwise specified, scenarios assume that the total cover of coral is relatively high (30%) at the beginning of simulations and evenly divided among brooders and spawners, that macroalgae begin with 20% cover, that 10% of the reef is set aside as ungrazable substratum (sand), and the remainder is cropped algae. Thus, each scenario investigates the impact of grazers, connectivity, or disturbance on what may be "healthy" reefs offering high-quality habitat. Coral sizes are selected at random until the required starting cover is reached (though an alternative strategy is used in the sensitivity analysis). Marine reserve networks comprise four reefs connected in a circle of alternate reserves and nonreserves (Fig. 2). The only direct impact of reserves is that grazing fishes are fully protected. Since the reefs have no fixed dimensions, no assumptions are made about the total area set aside as reserves; rather, I

investigate how coral reefs respond when their level of grazing, and that of their main source reef, is manipulated. The core response variables are (1) coral cover in percentage units which includes both spawners and brooders, (2) change in total coral cover after 10 years, measured in absolute units of percentage of cover so that a drop in cover from 30% to 25% would be recorded as −5%, and (3) survival of recruits, representing the survival of an entire cohort between the size of recruitment (0.8 cm^2) and reaching puberty (60 cm^2).

Sensitivity analyses were carried out using the percentage of total coral cover after 20 years as a response variable. Initial runs used standard parameterization (Appendix, Table 2) with 15% cover of both brooders and spawners, a stock-recruitment relationship for connectivity and no hurricanes. For both non-depleted and heavily depleted levels of grazing, each parameter was adjusted to both its lowest and highest plausible level (Table 2) and 10 simulations undertaken for each. Those parameters whose range was either not applicable or unknown were subjected to a 10% change on either side of the standard value.

Although densities of *Diadema antillarum* have increased in a few areas and in shallow water (Edmunds and Carpenter 2001, Miller et al. 2003), their density remains low throughout much of the Caribbean, and particularly so on mid-depth forereefs. 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 individuals/ m^2 (maximum reported anywhere of only 0.2 individuals/ m^2). While a return of urchins to premortality levels may benefit reef resilience, it would be unsafe to assume that urchins will make a substantial recovery at large scales and that outbreaks of disease are not repeated. In light of this, urchins were excluded from most scenarios.

RESULTS

H_1: An unfished community of parrotfishes provides adequate grazing to maintain net reef accretion (in the absence of acute disturbance events and Diadema antillarum)

The total cover of living coral always increased when grazing was carried out by an unexploited community of parrotfishes (Fig. 6). Brooders exhibited an increase in cover when their initial abundance was low (2.5% cover) but the cover of spawners only increased once the total cover of living coral exceeded approximately 15% (Fig. 6). Recruit survival was positively related to coral cover and reached an asymptote at the highest covers simulated (40–50%).

H_2: Regional variation in hurricane frequency may impact the trajectory of Caribbean reefs

In the absence of *Diadema antillarum*, coral cover showed a net decline when reefs were disturbed by hurricanes on a decadal basis (Fig. 7). Halving the hurricane frequency to 20 years, which is representative

TABLE 2. Sensitivity of model parameters.

Parameter	Parameter value		
	Standard	Minimum	Maximum
Standard parameterization			
Parameters entered as constants			
Growth rate of brooders (cm/yr)†	0.8	0.6	1.0
Growth rate of spawners (cm/yr)†	0.9	0.7	1.1
Retention coefficient	0.25	0.23	0.27
Dispersal coefficient	0.1	0.092	0.108
Initialize population with largest 15% of coral size categories (cm^2)	1–2500	1720	2463
Puberty size (cm^2)‡	60	49	165
Size of full maturation (cm^2)‡	250	239	355
Macroalgal growth reduction (%) by corals§	25	22.5	35
Macroalgal overgrowth of coral, λ	−0.0012	−0.00108	−0.001
Partial-colony mortality rate (adults) ‖	0.05	0	0.1
Size of partial-colony mortality event (cm^2) ¶	15	3	60
Whole-colony annual mortality rate (pubescent corals) ‖	0.04	0	0.07
Whole-colony annual mortality rate (adult corals)‖	0.02	0	0.07
Parameters under experimental manipulation			
Hurricane frequency			
Every 60 yr			
Every 40 yr			
Every 20 yr			
Every 10 yr			
Four-reef metapopulation, hurricanes every 40 yr			
Retention 0.25, dispersal 0.10			
Retention 0.10, dispersal 0.25			

Notes: The response variable is total coral cover after 20 years of simulations in the absence of hurricanes and where the initial cover of brooding and spawning corals is 15%. Ten simulations were carried out for both the minimum and maximum parameter value, and the results were combined and compared to the standard parameterization.

† Sources: Huston (1985), Chornesky and Peters (1987), Van Moorsel (1988).
‡ Source: Soong (1991).
§ Sources: de Ruyter van Steveninck et al. (1988), Jompa and McCook (2002).
‖ Source: Bythell et al. (1993).

of parts of Central America, allowed coral cover to fluctuate around an equilibrial level of approximately 30%. Further reductions in hurricane frequency, to levels found in South America (e.g., 40–60 years), permitted rapid reef growth. The dynamics of coral cover were insensitive to changes in hurricane frequency once their incidence fell below 40 years (Fig. 7). The presence of *D. antillarum* enabled reefs to withstand a decadal incidence of hurricanes and reduced the variation among trajectories for different hurricane frequencies (i.e., trajectories for hurricanes at 10 year and 40 year intervals became less divergent). Covers of brooding and spawning corals began at 15% (ratio 1:1) and typically shifted to a ratio of 5:1 by the end of a 50-year simulation (range 4.9:1 to 7:1). In other words, brooders gradually displaced spawners.

H_3: *Depleting the biomass of parrotfishes (grazing) has a disproportionately large impact on coral dynamics (compared to expected variation in other parameters)*

The results of a sensitivity analysis, using percentage of total coral cover after 20 years as the response variable, are given in Table 2.

Grazing level.—Reducing the efficacy of parrotfish grazing from 30% to 10% of the reef led to fundamen-tally different reef communities. Under high grazing, coral cover increased from an initial level of 30% to approximately 65%. Conversely, cover decreased to approximately 7% when grazers were heavily depleted (Table 2). The divergent response of reefs to grazer depletion was preserved for all ranges of variables such that coral cover always increased under high grazing and always decreased under low grazing.

Parameters used as constants.—Manipulating the range of individual parameters had a limited impact of only a few percent cover units on the outcome of simulations (Table 2). The most sensitive parameter was whole-colony mortality rate of adult colonies but even the most severe chronic levels (7% per year) failed to overturn the general positive trajectory of increasing coral cover under high grazing (Table 2).

Parameters under experimental control (except grazing).—Well-grazed coral reefs were able to withstand hurricane frequencies of ≤20 years (Fig. 7). However, reducing grazing levels to those associated with over-fished reefs always resulted in coral decline and less than 5% cover within 30 years (Fig. 8). The rate of coral decline was greater under more frequent dis-turbance but still reached 1% within 40 years of minimal hurricane frequency (60 years). Changing the

TABLE 2. Extended.

High scarid grazing mean (SE)		Low scarid grazing mean	
Coral cover (%)	Absolute disparity (%)	Coral cover (%)	Absolute disparity (%)
65.8 (0.51)		7.0 (0.71)	
64.4 (4.07)	12.5 (0.49)	7.0 (0.22)	0.5 (0.12)
66.9 (0.14)	1.1 (0.14)	6.2 (0.45)	1.3 (0.30)
65.7 (0.18)	0.5 (0.07)	7.3 (0.15)	0.4 (0.12)
65.7 (0.20)	0.4 (0.13)	7.1 (0.18)	0.4 (0.13)
58.3 (0.70)	7.43 (0.70)	9.3 (0.32)	2.2 (0.32)
66.8 (0.51)	1.5 (0.35)	6.9 (0.20)	0.5 (0.11)
65.0 (0.26)	0.9 (0.18)	6.9 (0.22)	0.5 (0.15)
66.0 (0.20)	0.5 (0.13)	7.1 (0.19)	0.5 (0.09)
65.4 (0.31)	0.8 (0.19)	7.3 (0.99)	3.0 (0.23)
65.9 (0.31)	0.8 (0.15)	6.9 (0.15)	0.3 (0.07)
65.0 (0.53)	1.5 (0.32)	6.9 (0.16)	0.4 (0.09)
62.9 (2.49)	7.6 (0.96)	7.1 (0.20)	0.5 (0.13)
42.5 (12.33)	38.0 (7.54)	6.0 (1.81)	5.5 (0.35)
64.5 (3.71)	−1.3 (3.71)	5.9 (0.81)	−1.4 (0.81)
61.3 (3.82)	−4.5 (3.82)	4.2 (0.66)	−2.8 (0.66)
35.7 (7.53)	−30.1 (7.53)	4.3 (1.00)	−2.6 (1.00)
19.9 (5.51)	−45.8 (5.51)	1.1 (0.48)	−5.9 (0.48)
62.8 (3.9)	−2.9 (3.9)	6.4 (0.75)	−0.6 (0.75)
59.8 (5.65)	−5.9 (5.65)	3.7 (0.20)	−3.2 (0.20)

connectivity scenario from a stock–recruitment relationship to full open recruitment had a limited impact on trajectories of coral cover (Fig. 8). Similarly, reversing the importance of retention and dispersal in a four-reef metapopulation only changed final coral cover by 3%, whereas depleting grazers changed coral cover by 55% (Table 2).

In summary, depletion of grazers exerts a fundamental, overarching impact on the dynamics of Caribbean forereefs.
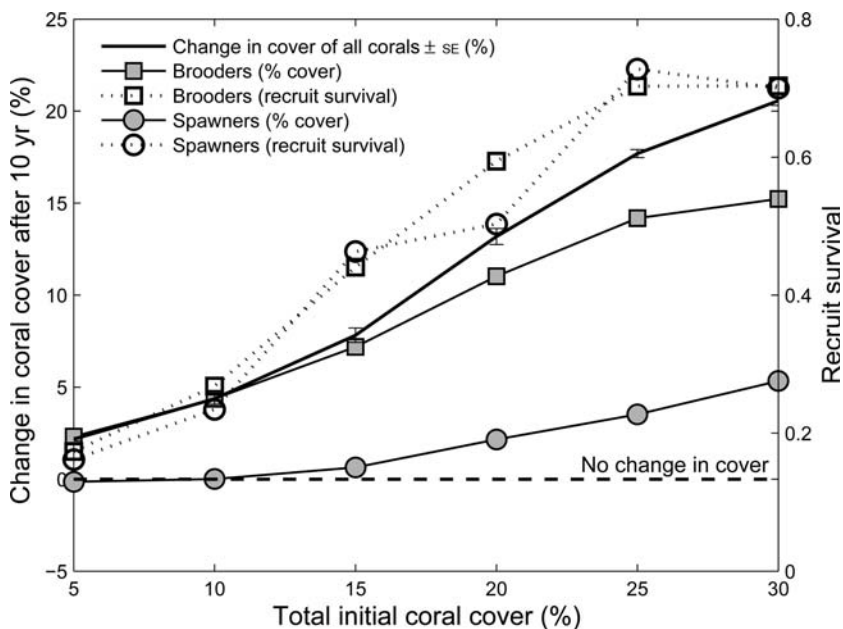

FIG. 6. Response of reefs to full scarid grazing as a function of initial starting conditions. A change in cover of +4% at an initial cover of 10% represents an increase in absolute cover from 10% to 14%. Recruit survival relates to a cohort reaching puberty size (60 cm²) on the 10th year of simulations. Coral recruitment was set to maximum levels regardless of stock size.
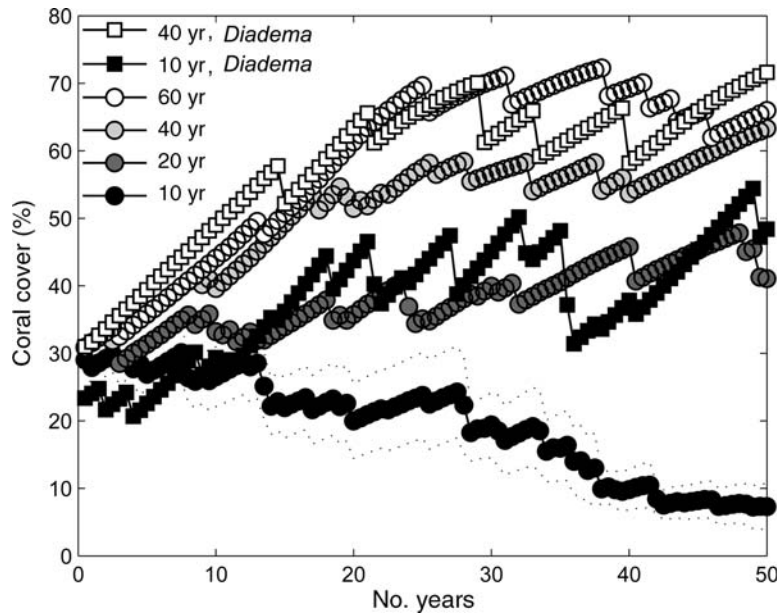
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FIG. 7. Response of reefs to increasing frequencies of hurricane disturbance. Circles denote high scarid grazing (30% of reef effectively grazed). Squares denote high scarid grazing and the urchin *Diadema antillarum*. To convey the scale of variation, standard errors ($n = 10$) are shown for the 10-yr hurricane trajectory. Coral recruitment was set to maximum levels regardless of stock size.

H_4: *Depleting the biomass of parrotfishes (grazing) can precipitate shifts in community state from coral-rich to macroalgal-dominated ecosystems*

The impact of depleting parrotfishes is plotted for a simple network of four reefs, two of which have full grazing (30% of reef) and two have partially depleted grazing (20% of reef) (Fig. 9). Reefs with full grazing

undertook a variety of trajectories, characterised by clear phases of growth between successive hurricanes. In contrast, coral cover declined steadily on reefs with partially depleted grazers, even though hurricanes occurred at the same frequency (40 years) as on reefs with full grazing (Fig. 9). Switching from retention-based systems (Fig. 9a) to dispersal-based systems (Fig.
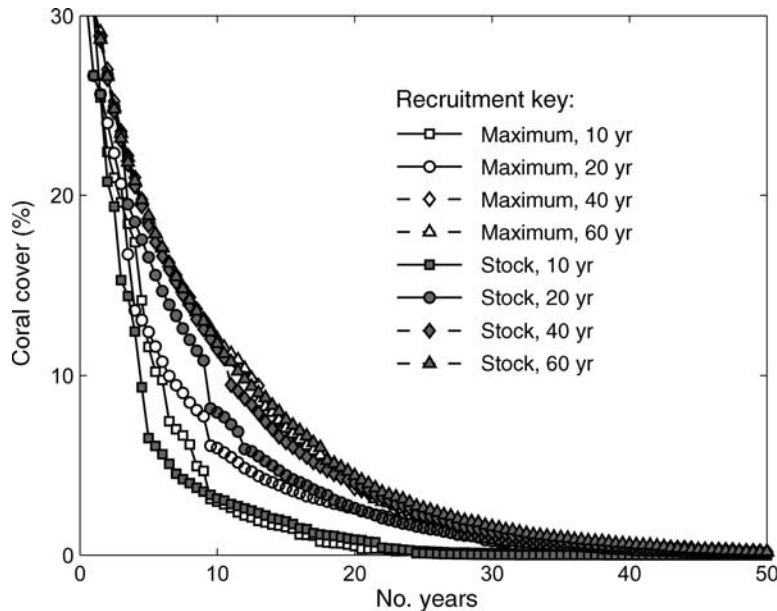

FIG. 8. Response of overfished reefs to various frequencies of hurricanes and two scenarios of connectivity (maximum vs. stock recruitment).
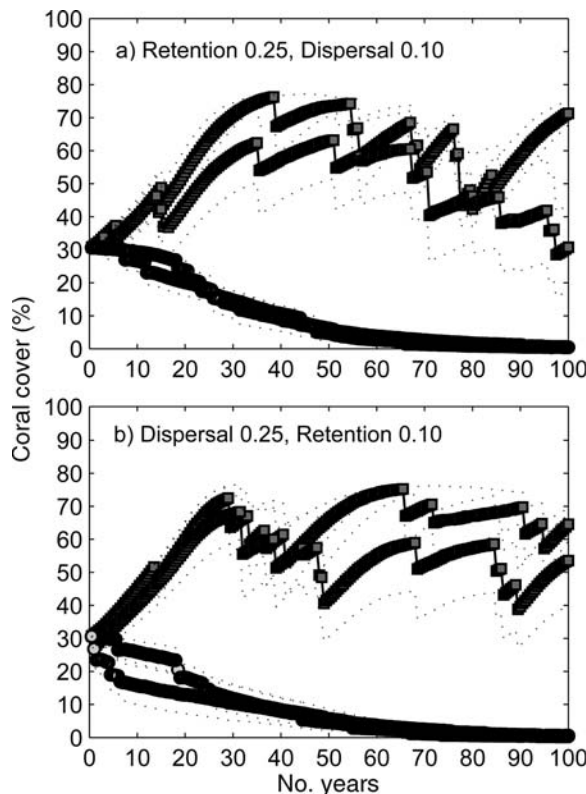
FIG. 9. Dynamics of a four-reef reserve network with contrasting connectivity scenarios. Larval supply is dominated by retention features in panel (a), whereas connectivity is greater in panel (b), which stresses dispersal among adjacent reefs. Grazers are not depleted in the two reserves (squares, two upper lines) but are partially depleted (grazing 20% of the reef per time interval) in nonreserves (circles, two lower lines). Hurricanes occur at an average interval of 40 yr. Dotted lines represent SE from 10 simulations.

9b) had no clear impact on the dynamics of the system; mean coral cover fluctuated between a lower limit of 30–40% and an upper limit of approximately 70%, depending on the time since disturbance.

Causes and symptoms of coral decline

Examination of temporal shifts in the relative size-frequency distribution of corals under different disturbance scenarios (Fig. 10) suggested that hurricanes and the overexploitation of grazers affect coral population dynamics differently. For a given level of coral cover, the size distribution of corals rapidly became bimodal under intense exploitation of grazers (Fig. 10). A population bottleneck occurred in juvenile size classes as demonstrated by examining the mean mortality rate (from 10 simulations) of a cohort of juvenile corals, passing from recruitment (size 0.8 cm^2) to puberty (60 cm^2) within 10 years of a healthy reef (30% coral cover) being simulated. Mortality rates rose from 0.28 in unfished systems (Fig. 6) to >0.99 in systems where grazers were heavily depleted.

A more even size distribution emerged where grazer levels were high but hurricanes occurred frequently (Fig. 10). In this case, juvenile and pubescent colonies occupied a higher proportion of the population and the main bottleneck occurred in the number of large colonies.

Impacts of the severity and frequency of coral mortality on coral cover

Coral cover tended to decline once the severity of disturbance (mortality rate) exceeded 50%, even when events occurred relatively rarely at once per decade (Fig. 11). Not surprisingly, frequent and severe disturbances led to progressively greater declines in coral cover from the initial 30%. At the lowest mortality rate simulated (10%), coral cover could only increase if events occurred on less than a biannual basis.

DISCUSSION

The dynamics of coral reefs are driven by processes acting over a wide range of spatial and temporal scales (Hatcher et al. 1987, Hatcher 1997, Karlson 1999). Such complexity precludes an experimental approach to studying the interactions of multiple disturbances such as the overfishing of grazers and hurricane frequency. Not surprisingly, much of our understanding of the impacts of grazer depletion stem from either small-scale caging studies where the process can be isolated (Lewis 1986, Morrison 1988) or case studies in which the circumstances of reef degradation have been observed (e.g., the decline of coral cover in Jamaica [Hughes 1994]). Here, I used a simulation model to integrate empirical studies across spatial and temporal scales and investigate the impact of managing grazers in the wider context of ecosystem dynamics. Outcomes of each hypothesis and objective could not have been predicted a priori simply by examining the parameterization.

Tests of hypotheses: the relative importance of scarid grazing and hurricanes after the die-off of Diadema antillarum

The empirical data presented here support the assertion of Williams et al. (2001) that scarids can only graze a fraction of the forereef surface intensively. Using a species-specific model of scarid grazing, I suggest that this fraction ranges from approximately 10% to 30%, depending on the depletion of scarid biomass. Incorporating spatially limited grazing into a simulation model of ecosystem processes illuminated the sensitivity of Caribbean forereefs to parrotfish exploitation and the impact of losing the urchin Diadema antillarum.

The impact of heavy exploitation of scarids dwarfed that of any other model parameter, suggesting that Caribbean reefs are highly sensitive to fishing of this functional group. Even intermediate levels of exploitation resulted in a steady decline of coral cover (~0.5% per year). Simulations suggest that grazer depletion causes a population bottleneck among juvenile corals
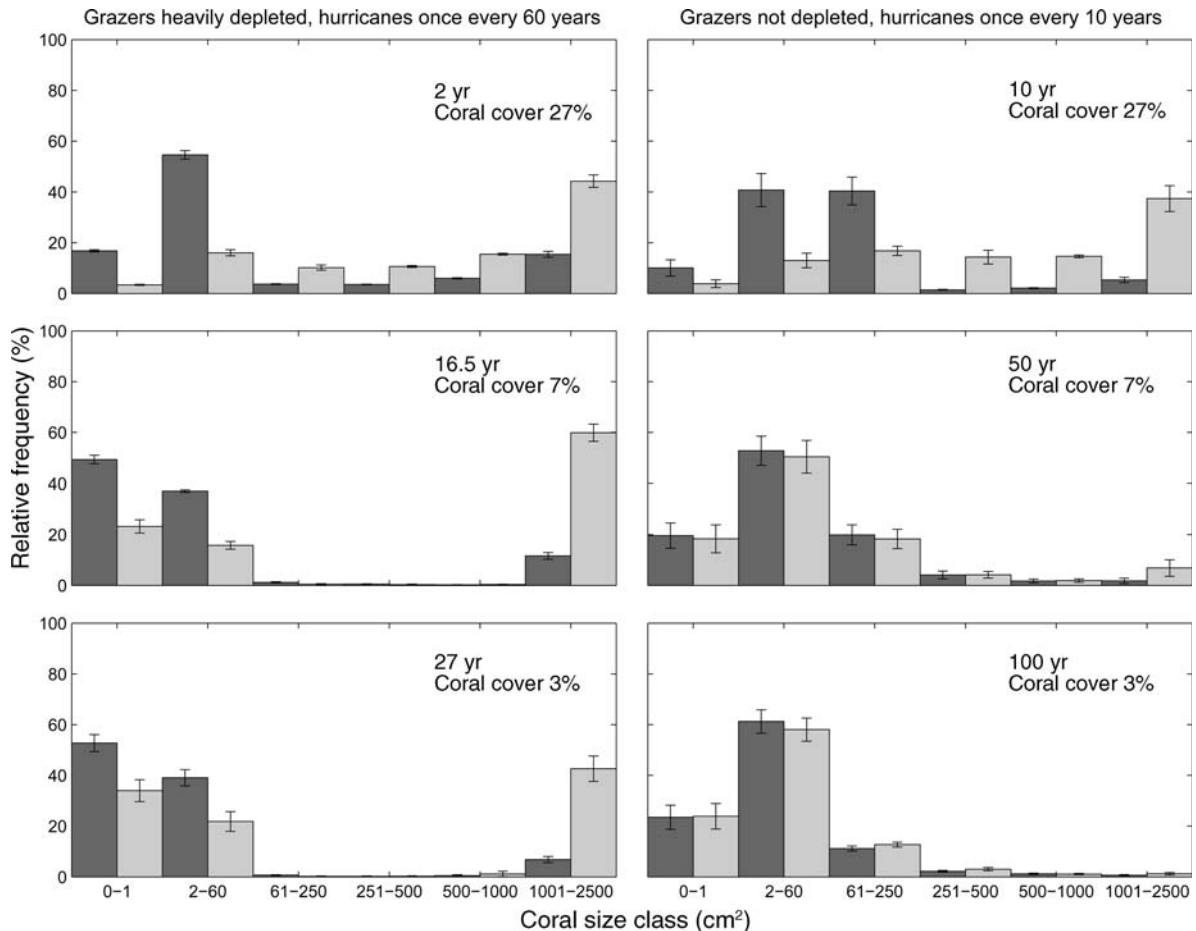
FIG. 10. Comparison of two disturbances on the size–frequency distribution of corals (mean ± SE, $n = 10$ simulations). Depletion of grazers is shown on the left, and intense hurricanes on the right. Total coral cover is identical in each row (comparison), although the time required to reach such cover differs between disturbances. All systems had maximum coral recruitment rates independent of stock size. Coral cover was initially 30%.

such that few reach the adult population. The size-specific mortality rate of juvenile corals was modeled as a linear function of macroalgal cover (Appendix). Thus, any process affecting the cover of macroalgae exerted an indirect influence on the survival of juvenile corals. Feedbacks emerged from the model which tended to drive the system towards either a coral-rich or coral-poor state. For example, a coral mortality event increases the colonization space for algae that then increases the number of possible feeding sites for fish and reduces the probability that any given patch of reef will be grazed. Reduced grazing intensity leads to an increase in macroalgal cover and therefore an increase in the mortality rate of juvenile corals. Mortality rates of coral will then continue to increase as coral cover falls and is replaced by macroalgae, thus reinforcing the decline. Space limitation compounds this mechanism because macroalgae prevent the settlement of new corals (Diaz-Pulido and McCook 2004) and therefore the overall level of replenishment. The reverse feedback is

also possible in which rising levels of coral cover concentrate grazing, reduce macroalgal cover, and reduce the mortality rate of juvenile corals (assuming that increases in coral cover are not detrimental to grazer densities).

Through its impact on macroalgal cover, the grazing intensity of parrotfish will determine whether a reef of given coral cover experiences positive or negative feedbacks (or potentially finds an unstable equilibrium, see Suding et al. [2004]). These emergent properties of the system arise because parrotfish grazing is spatially-constrained and unable to prevent a macroalgal bloom once coral cover falls below some threshold level. Had grazing not been subjected to spatial constraints then coral cover, macroalgal cover and the mortality rates of coral recruits would be less tightly coupled. For example, a reduction in coral cover might not result in additional macroalgae if parrotfish communities had a vast capacity to increase their total grazing in response to increased food availability (as is the case in urchins
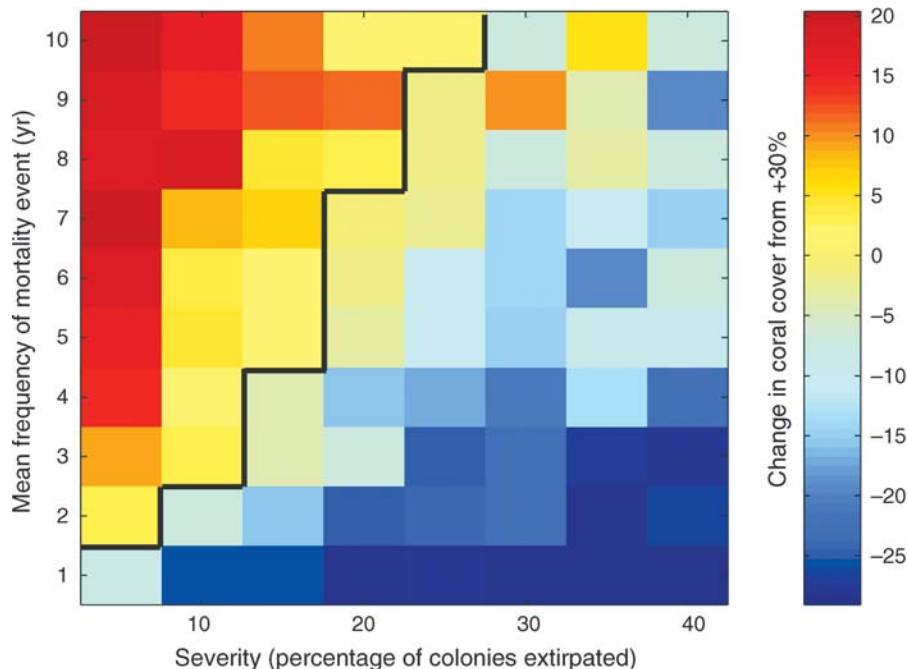
Fig. 11. The effect of whole-colony mortality rate and the frequency of mortality events on relatively "healthy" reefs. Coral cover is initially 30%, the grazing of parrotfishes is high (30% of the reef), and the probability of coral recruitment is set to maximum (1) irrespective of stock size. Absolute change in coral cover is presented after a 10-yr period, where maximum loss is 30%. The black line is an attempt to isolate increasing coral cover (left) from decreasing cover.

[Levitan 1988b]). The mechanisms described here support the hypothesis than coral reefs can occupy alternative stable community states (Knowlton 1992, Hughes 1994), and an analysis of thresholds and unstable equilibria is forthcoming.

Model simulations with hurricane frequencies of 10-, 20-, and 40-yr intervals were intended to illuminate differences in the long-term (multidecadal) dynamics of the northern Caribbean (e.g., the Florida Keys and the Bahamas), western Caribbean (e.g., Belize, Honduras), and southern Caribbean (e.g., the Netherlands Antilles), respectively (Gardner et al. 2005). Where *Diadema* remain functionally absent (Kramer 2003), it seems that hurricane activity will promote regional differences in the dynamics of coral reefs. Under exclusive grazing of fishes, the model predicts that coral cover will tend to decline on forereefs in Florida, fluctuate around an equilibrium in Belize and increase in the Netherlands Antilles. However, these "predictions" are best thought of as large-scale and long-term underlying dynamics with the following caveats. First, while the model integrates current understanding of reef ecology, empirical parameterization for the overgrowth of corals by macroalgae is lacking. Although the model was not unduly sensitive to this parameter, it may prove necessary in future to modify its parameterization beyond that embodied by the sensitivity analyses. Further empirical data are also required on processes of coral recruitment including the links between macro-

algal cover, the availability of preferred settlement substrata (e.g., the coralline *Titanoderma prototypum*), and larval supply (Mumby 1999b). Second, the parameterization for hurricanes was based on severe (category 5) events including Hurricane Hugo and Hurricane Mitch (Appendix). A more realistic, though stochastic, model would vary the intensity of hurricane events in addition to their incidence. Indeed, the model was not designed to predict the possible state space of future coral reefs as this would have required extensive stochasticity and obscured the more deterministic dynamics under investigation. Third, the trajectories of individual reefs are notoriously variable and influenced by other acute disturbances such as disease and extremes of temperature (Precht and Miller 2006), neither of which were modeled.

Generation of hypotheses

The outcomes of model simulations generate three, potentially testable hypotheses about the impacts of disturbance on Caribbean forereef communities. All three hypotheses assume that *D. antillarum* remain functionally extinct on the majority of reefs.

Hypothesis 1.—Spatial heterogeneity in coral cover will initially increase in areas where hurricanes occur with a decadal frequency (e.g., Florida). Heterogeneity will then decline as an increasing number of reefs are impacted by hurricanes but fail to recover. In contrast, spatial heterogeneity in reefs experiencing infrequent

hurricanes (<40-yr incidence) will be comparable to that before the loss of *Diadema*. Changes in spatial heterogeneity will be greater in more disturbed regions.

Hurricanes cause a heterogeneous seascape with reefs in various states of recovery (Connell 1978, Aronson and Precht 1995, Bythell et al. 2000). For a given disturbance regime, the spatial heterogeneity in coral cover will depend on the rate of recovery; faster rates of recovery will reduce the disparity among reefs and reduce heterogeneity. The model predicts that average recovery trajectories are slower in the absence of *Diadema*. Spatial heterogeneity will initially rise because the disparity between recently impacted and later successional reef states will no longer disappear swiftly through rapid recovery. In time, an increasing proportion of reefs will shift to the disturbed state and either remain in that state or experience slow rates of change. At this point, spatial heterogeneity will decline across the seascape. In contrast, average recovery trajectories are less severely impacted by the loss of *Diadema* where the frequency of hurricane disturbance is low (i.e., in parts of the southern Caribbean). This is because the recovery rate of an individual reef is positively related to its coral cover and infrequent hurricanes are unlikely to compound one another and heavily suppress coral cover. While loss of urchins may slow the recovery rate of individual reefs, the impact is weak when coral cover is high (note, for example, that scarid grazing permitted high rates of recruit survival when coral cover exceeded 25%; Fig. 6). In short, loss of the urchin *Diadema* will have a relatively weak impact on the spatial heterogeneity of coral cover in southern parts of the Caribbean. Testing this hypothesis will be challenging and require large-scale sampling of Holocene reefs (e.g., Aronson et al. 2004) and surveys of extant communities in which appropriate covariates, such as recruitment rates and incidences of acute mortality, are recorded (i.e., parameters measured by the Atlantic and Gulf Rapid Reef Assessment program [Kramer 2003]).

Hypothesis 2.—The size-frequency distribution of corals becomes bimodal when scarids are heavily exploited, but unimodal with relatively few large colonies when hurricanes are the chief limiting factor.

Recent surveys of the size–frequency distribution of corals in the Florida Keys revealed a unimodal distribution depauperate in large corals (Bak and Meesters 1999). While these data cannot be considered representative of hurricane-disturbed reefs, they provide partial support for the model predictions. Tests of the predictions concerning scarid depletion require new data from heavily-fished reefs.

Hypothesis 3.—The net response of reefs to the intensity and frequency of disturbance follows the pattern plotted in Fig. 11.

Model predictions were compared to Hughes' (1994) 20-yr data set of coral cover in Jamaica (Fig. 3). Further tests and refinements to the model can be carried out as the results of other long-term monitoring projects, such

as CARICOMP (Ogden et al. 1997), are published. Specifically, the predicted interaction of disturbance intensity and frequency (Fig. 11) provide a testable hypothesis. If the hypothesis is borne out in situ, then it will provide a basis for forecasting the impact of acute disturbances such as outbreaks of coral disease. For example, Croquer et al. (2003) found that an outbreak of white plague II affected 24% of colonies at their study sites in Venezuela. It does not necessarily follow that diseased or bleached colonies will experience whole-colony mortality (as implicitly modeled here), but if they did, mortality rates may reach 20–30% per event. At that level of severity, the model predicts that coral cover would decline once the frequency of mortality events exceeds once every five years.

On a related note, the model predicts that the 10-fold higher recruitment rate of brooding corals will lead to the displacement of spawning taxa. This outcome is not surprising, given that spawners' only competitive advantage was a higher growth rate (see Nee and May 1992). However, this result raises questions about the coexistence of brooders and spawners on Caribbean coral reefs. How have brooders and spawners coexisted during the Holocene, given a vast disparity in recruitment rates? It seems doubtful that the disparity in recruitment is a recent phenomenon, because numerous authors reported similar patterns before diseases depleted the abundance of *Acropora* spp. and the urchin *Diadema antillarum* (e.g., Bak and Engel 1979). Two possible and complementary mechanisms of coexistence are (1) the "storage effect," in which major recruitment events for spawners occur episodically when conditions are favorable (Edmunds 2002), and (2) that spawners have other competitive advantages over brooders. Brooding species may experience higher mortality rates during coral bleaching events (McField 1999) but the selectivity of other types of disturbance require consideration. Do hurricanes preferentially impact brooders? Are massive brooding colonies less effectively attached to the substratum than spawners with similar morphology? Do corals experience senescence and if so, are longevities affected by reproductive mode? Model simulations, together with new empirical research will help elucidate the plausibility of putative mechanisms for species coexistence.

Implications for the management of Caribbean reefs

The management of Caribbean parrotfishes is mostly approached implicitly through no-take marine reserves (specific policies banning scarid fishing are only known from Florida and Bermuda). By maintaining high levels of scarid grazing in reserves, the model implicitly assumed that the main impact on parrotfish density is fishing. However, scarid populations are influenced by primary production (van Rooij et al. 1995*a*), natural predation (Mumby et al. 2006), recruitment (Tolimieri et al. 1998), and rugosity (van Rooij et al. 1996, Mumby and Wabnitz 2002), which may also mediate predation

and recruitment success (see Hixon and Carr [1997] for an example). Predation is unlikely to constrain the biomass of the largest and most important grazers because growth rates are fairly high (Choat et al. 2003), large-bodied predators are scarce on most Caribbean reefs (Pandolfi et al. 2003), and larger scarids escape the risk of predation from predators such as grazers (Mumby et al. 2006). Recruitment rates are likely to be influenced by both larval supply and postsettlement mortality (Tolimieri 1998), which are partly determined by the size of the scarid metapopulation and quality of the reef habitat, respectively. If exploitation of scarids outside reserves depletes their biomass and grazing, the model predicts a dramatic reduction in coral production. Logically, this will result in declining rugosity as colonies destroyed by bioerosion and physical disturbance are not replaced (see Glynn 1997). By reducing the quality of habitat in exploited areas, this direct impact of fishing may reduce the metapopulation size of many taxa and the degree of spill in and spillover from the reserve (Sale et al. 2005). Thus, the model assumption that reserves protect scarid grazing becomes progressively less safe as coral cover declines in non-reserve areas. More importantly, a speculative yet rational inference from the model is that failure to manage scarid populations outside reserves will have a profoundly negative impact on the functioning of the reserve system and status of nonreserve reefs. Practical steps for scarid management will almost certainly involve gear restrictions, particularly on the use of fish traps which are highly selective for adult parrotfish (Rakitin and Kramer 1996).

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APPENDIX

Justification of model parameters (except grazing)

Algal growth and competition with coral.—Reef algae were divided into cropped algae and macroalgae (Table 1 in main text). Cropped substrata represent encrusting coralline red algae, fine filamentous algae (which is usually not visible by eye), and short algal turfs (<5 mm height). These were grouped into a single category because coral recruits are associated with all these classes under the low levels of sedimentation implied here. For example, of 2223 coral recruits (diameter, 5–20 mm) sampled on natural substrata in Belize (Mumby, *unpublished data*), 49% occurred on corallines and 44% on noncoralline cropped substrata (the remaining 7% were surrounded by sponges, colonial ascidians, or macroalgae).

If cropped algae are not grazed, spores of macroalgae (e.g., *Dictyota* spp. and *Lobophora variegata*) develop and form a canopy that prevents coral settlement. The recruitment of macroalgae through dispersal of fragments and germlings appears to be highly constrained in space over short time scales. In Curaçao, de Ruyter van Stevenick and Breeman (1987) observed very little colonization of *Lobophora* in plots located outside the main *Lobophora* stand (zero cover after 10 months, 3% cover after 12 months). Similarly, grazer-exclusion cages deployed on forereefs in Belize just after Hurricane Mitch scoured much of the algal canopy developed little (<10%) additional cover of macroalgae within five months (Mumby, *unpublished data*). In contrast, established canopies of macroalgae can spread laterally at a faster rate than their isolated emergence from cropped algae. When plots (25 × 30 cm) were cleared in a *Lobophora* mosaic, they were completely regrown within six months (one time step of the model), regardless of season (de Ruyter van Stevenick and Breeman 1987). I therefore modeled two forms of macroalgal growth. First, if cropped algae are not grazed for a period of one year, they become macroalgae. Second, established macroalgae spread vegetatively such that the probability that cropped algae in cell X will be overgrown by macroalgae ($P_{A \to M}$) within six months is given by Eq. A1 where M_{4c} is the proportion of all macroalgae within a von Newmann (four-cell) neighborhood of X. Where local coral cover is high ($\geq$50%), coral–algal competition reduces the rate of macroalgal growth by 25% (based on de Ruyter van Stevenick et al. 1988, Jompa and McCook 2002):

$$C \text{ (proportion of coral)} = \frac{(\text{BC} + \text{SC})}{2500} \qquad \text{(A1a)}$$

$$P_{A \to M} = 0.75 \times M_{4c} \quad \text{if } C \geq 0.5 \quad \text{(A1b)}$$

$$P_{A \to M} = M_{4c} \qquad \qquad \text{if } C < 0.5. \quad \text{(A1c)}$$

Macroalgae such as *Lobophora variegata* and *Dictyota* spp. are able to overgrow coral recruits (Bak and Engel 1979, Sammarco 1980, de Ruyter van Stevenick and Bak 1986), and small corals of several years in age (R. P. M. Bak, *personal communication*). 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. I 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, I generated model simulations for putative coral–algal overgrowth relationships and identify those that best fitted the data of Hughes from Jamaica (Hughes 1994). It follows from published evidence that the probability of coral mortality within a six-month period (one iteration) is negatively associated with increasing coral size. Twenty putative negative exponential relationships were tested and the one that minimized the sum of their squared deviations from each empirical data point was selected (Fig. 3).

The probability that a coral is overgrown (extirpated) by macroalgae, $P_{C \to M}$, is calculated from Eq. A2 where x is the area of either BC or SC (Table 1), λ is the exponent, 0.0012 (derived by fitting various exponents and intercepts to Fig. 3), and M_{12} is expressed as a proportion of the area of the cell:

$$P_{C \to M} = P_{size} \times M_{12} \qquad \text{(A2a)}$$

$$P_{C \to M} = 0.83 \, \exp(-\lambda x). \qquad \text{(A2b)}$$

Corals and the connectivity among reefs.—Although it is becoming increasingly apparent that coral settlement and early postsettlement mortality is influenced by specific algal species (Harrington et al. 2004), there are insufficient data to parameterize these early processes. Rather, the model uses observed densities of coral recruits on natural substrata on relatively healthy

offshore reefs in Belize (Mumby 1999*a*) that had a high adult coral cover (~45%) and among the highest biomasses of grazing fishes reported in the Caribbean (Fig. 4). Corals recruit in the model at an initial size (diameter) of 1 cm. The observed density of brooding species (principally *Agaricia* spp. and *Porites* spp.) in the size range (0.5–1 cm) was 3.98 (~4) per 0.25 m^2 of quadrat placed horizontally on the seabed (*n* = 559 recruits). These corals would form one six-month cohort in the model, but the density had to be adjusted to the mean rugosity (structural complexity) of these reefs at 1.98 (~2). Thus, corals recruit into the model at a density of 2 individuals/0.25 m^2 (or one cell) of cropped algae. The density of recruits for spawning species was observed to be at least 10-fold lower than that of brooders at 0.31 individuals/0.25 m^2 of horizontal quadrat (see also Bak and Engel 1979, Rogers et al. 1984, Hughes 1985, Smith 1992, Mumby 1999*a*). When rescaled for model implementation, the density of spawner recruits was set at one-tenth (approximately 0.07–0.1) that of brooders.

For simplicity, corals were represented as hemispheres with a linear extension rate (sensu Maguire and Porter 1977). Reviewing published data of skeletal extension rates for the species *Porites astreoides*, *P. porites*, *Siderastrea siderea*, *Montastraea annularis*, *Colpophyllia natans,* and *Agaricia agaricites* (Huston 1985, Chornesky and Peters 1987, Van Moorsel 1988), a median growth rate was used of 8 mm/yr in brooders and 10 mm/yr in spawners, with a range of 6–11 mm/yr. Both the onset of maturity and reproductive output of corals are size dependent (Soong 1993). Puberty sizes and fecundities in Caribbean corals are well established (Szmant 1991, Soong and Lang 1992, Soong 1993). However, before the implementation of reproduction is described, it should be borne in mind that the processes between reproduction and subsequent settlement of new corals are almost entirely unknown (Mumby 1999*b*). Modeling these processes required a necessarily contrived framework of larval connectivity.

The efflux of larvae from a reef was quantified from the size-frequency distribution of both brooders (based on the species *Porites astreoides*) and spawners (based on the species, *Siderastrea siderea*). Both species reach puberty at a cross-sectional area of around 60 cm^2 and full maturity at around 250 cm^2 (Soong 1993). The fecundity of pubescent corals is approximately 25% that of fully mature colonies. These were then set as size-based parameters for puberty, maturation, and relative fecundity. The second stage, which is contrived, involves scaling total reproductive output to recruitment rates throughout the metacommunity. An arbitrary common currency of larvae was based on the fecundity of *Porites astreoides*, which has approximately two eggs per gonad, six gonads per polyp, and 18 polyps per cm^2 of coral (Szmant 1986). A linear stock–recruitment relationship was then established by assuming that the coral recruitment rates described earlier would only occur if the adult stock was relatively high and if larval supply was optimal. High adult stock was determined arbitrarily as a reef with at least 30% total coral cover (which is relatively healthy in the Caribbean; see Ginsburg 1994, Kramer 2003), comprising an even mix of species (15% cover each), a random allocation of coral sizes and random distribution over the reef. The mean total larval output of such a reef was simulated 100 times, varying the spatial configuration and size composition of corals. A proportion of larvae are retained by the reef (arbitrarily 5–25%) and a proportion dispersed to the nearest reef downstream (arbitrarily 2–10%). The remaining larvae are lost (Fig. 2). These values allow fivefold differences to be simulated in larval retention or dispersal. To create a linear stock–recruitment relationship under the assumption of optimal larval supply, I calculated critical values of total larval input (T_1) for various stock sizes (30–3% total coral cover, *C*) at maximum rates of larval retention and dispersal. The probability of coral recruitment to cropped algae, P_r, was then fitted linearly to these critical values so that

$$P_r = 1 \quad \text{where } C \geq 30\% \ (T_1 \approx 2.9 \times 10^9)$$
$$P_r = 0 \quad \text{where } C \geq 3\% \ (T_1 \approx 2.9 \times 10^7)$$
$$0 < P_r < 1 \quad \text{where } 3\% < C < 30\%.$$

Two alternative larval connectivity scenarios were included in the model. Stock size and recruitment could be decoupled by enforcing $P_r = 1$ irrespective of *C*, and recruitment could be stochastic by selecting P_r at random.

Coral–coral competition.—Coral–coral interactions often form intransitive networks in which competitive dominance reverses between species (Lang and Chornesky 1990). The importance of coral–coral interactions in structuring reef communities has been questioned (Van Woesik 2002), particularly on Caribbean reefs which often have lower coral cover than their Indo-Pacific counterparts. For example, Hughes and Jackson (1985) noted that coral–coral interactions accounted for less than 10% of all coral mortality events observed in Jamaica. Since their observations were made between 1977 and 1980, while macroalgae were relatively scarce on Jamaican reefs, it seems likely that coral–coral interactions are even less common today. However, simple competitive interactions were imposed if corals reached the maximum implied size of a cell (2500 cm^2). The larger coral would overtop smaller corals (chosen at random if >1 or if both corals had equal size). Corals were able to overgrow cropped algae (Birkeland 1977, McCook et al. 2001) and displace macroalgae (although the latter algae could overgrow and extirpate coral). The model tracked individual corals and reported the size–frequency distribution and cover of both reproductive modes.

Disturbance (other than overgrowth of small corals by macroalgae).—Bythell et al. (1993) studied the mortality of corals in St. Croix for a 26-month period during which

reefs were disturbed by Hurricane Hugo, the largest storm to affect the site for 60 years. Deriving data for a six-month period (one time step in the discrete-time model) with no hurricane, the proportion of adult colonies experiencing partial-colony mortality lay between approximately 0% and 3% for *Diploria strigosa*, 1.5% and 9% for *Porites astreoides*, and 3% and 10% for *Montastraea annularis*. An intermediate incidence of partial-colony mortality of 5% was applied to mature colonies in each time interval. Under these levels of chronic disturbance, individual partial-colony mortality events cause a reduction in colony size of 15 cm^2 cross-sectional area, which is the median value observed on *M. annularis* prior to Hurricane Mitch (Mumby, *unpublished data*).

The data of Bythell et al. (1993) were also used to estimate chronic whole-colony mortality rates (i.e., events caused by toppling, wave surge, and occasional diseases). For pubescent colonies, I used the mean chronic whole-colony mortality rate of *P. astreoides* colonies in the size range 50–200 cm^2, rescaled to six months (approximately 2%). Chronic whole-colony mortality rates were reduced in larger, mature colonies to 1% (~2% per annum) based on an observed frequency of 1.5% for *P. astreoides* (Bythell et al. 1993).

Hurricanes are an integral part of coral reef dynamics (Edmunds and Witman 1991, Rogers 1993, Bythell et al. 2000). Under partially sheltered conditions, such as those in which *Montastraea* reefs occur (Geister 1977), the probability of whole-colony mortality is a parabolic function of colony size (Massel and Done 1993). The maximum whole-colony mortality rate for intermediate-sized corals was set at 50%, following the observed impact of Hurricane Hugo on *Porites astreoides* on a heavily impacted forereef in St. Croix (77% reduction in tissue surface area of which ~75% was attributable to whole-colony mortality [Bythell et al. 1993]). A minimal whole-colony rate of 5% for larger colonies (>2000 cm^2) was estimated as half the reported overall mortality rate of *P. astreoides* colonies in the size class >200 cm^2 and assuming that mortality rate continued to decline with increasing size. The overall parabolic relationship of the probability of whole colony mortality, P_{hur}, was calculated from Eq. 3 where x is either BC or SC (the cross-sectional basal area of a coral colony):

$$P_{hur} = -0.0000003x^2 + 0.0007x + 0.05. \quad (A3)$$

Coral recruits suffer intense scouring and dislodgement during hurricanes and a mortality rate of 80% was recorded for coral recruits (2–20 mm diameter) after Hurricane Mitch, which struck Belize in 1998 (Mumby 1999a).

Hurricane-induced incidences of partial-colony mortality were derived from the impact of Hurricane Mitch on mature colonies of *Montastraea annularis* in Belize (Mumby, *unpublished data*). At least 90% of entire colonies experienced partial-colony mortality after the hurricane ($n = 90$). The mean reduction in living coral tissue, measured six months (one time step) after the hurricane was 46% of the colony (SD = 33%, $n = 13$) at one site and 50% of the colony (SD = 23%, $n = 17$) at a second site, separated by a distance of 3 km. Given that Mitch was a category 5 storm and that many hurricanes are less intense, the lower value was used in the model. Hurricanes remove up to 90% of macroalgae from the reef (Mumby, *unpublished data*, after Hurricane Mitch).

The frequency of hurricanes varies with latitude and longitude throughout the Caribbean and individual storm tracks are archived from the year 1851 (data *available online*).[2] The most frequently disturbed areas, such as the Florida Keys, experience events with an average incidence of approximately 10 years (Gardner et al. 2005). The average frequency of disturbance drops to around 20 years in Mesoamerica (western Caribbean) and 40–50 years in parts of the southern Caribbean such as the Netherlands Antilles. Hurricanes were simulated on a probabilistic basis such that their incidence on a single reef was unpredictable over ecological time.

Rugosity.—The dynamics of reef rugosity are not modeled explicitly, largely because the net impact of bioerosion cannot easily be generalized (C. Schoenberg, K. Holmes, and C. Perry, *personal communication*). However, it is reasonable to assume that sustained low levels of coral cover, particularly those resulting from recruitment failure (see *Results*), will lead to declining habitat rugosity because corals lost during storms are unlikely to be replaced. Indeed, decreases in habitat rugosity have been observed on scales of years when coral cover remains low (Moran 1986, Scott et al. 1988, Glynn 1997; T. P. Hughes, *personal communication*). I concede that the precise rate of rugosity decline will depend on local levels of physical disturbance and bioerosion, which show considerable variation among reefs (Perry 1998). Given these limitations, I only speculate upon the impact of declining rugosity when the model predicts sustained low levels of coral cover and little coral replenishment.

[2] ⟨http://hurricane.csc.noaa.gov⟩