

A model-based approach to determine the long-term effects of multiple interacting stressors on coral reefs

JULIE C. BLACKWOOD,^{1,4} ALAN HASTINGS,² AND PETER J. MUMBY³

¹*Department of Mathematics University of California, Davis, California 95816 USA*

²*Department of Environmental Science and Policy, University of California, Davis, California 95816 USA*

³*School of Biological Sciences, Goddard Building, University of Queensland, St Lucia Campus, Brisbane, Queensland 4072 Australia*

Abstract. The interaction between multiple stressors on Caribbean coral reefs, namely, fishing effort and hurricane impacts, is a key element in the future sustainability of reefs. We develop an analytic model of coral–algal interactions and explicitly consider grazing by herbivorous reef fish. Further, we consider changes in structural complexity, or rugosity, in addition to the direct impacts of hurricanes, which are implemented as stochastic jump processes. The model simulations consider various levels of fishing effort corresponding to several hurricane frequencies and impact levels dependent on geographic location. We focus on relatively short time scales so we do not explicitly include changes in ocean temperature, chemistry, or sea level rise. The general features of our approach would, however, apply to these other stressors and to the management of other systems in the face of multiple stressors. It is determined that the appropriate management policy, either local reef restoration or fisheries management, greatly depends on hurricane frequency and impact level. For sufficiently low hurricane impact and macroalgal growth rate, our results indicate that regions with lower-frequency hurricanes require stricter fishing regulations, whereas management in regions with higher-frequency hurricanes might be less concerned with enhancing grazing and instead consider whether local-scale restorative activities to increase vertical structure are cost-effective.

Key words: coral reefs; fishery management; hurricane impacts; macroalgae; model; reef stressors.

INTRODUCTION

Coral reefs provide many important ecosystem services, including coastal defense from hurricanes and fisheries, as well as promote tourism (e.g., Peterson and Lubchenco 1997). However, coral reefs are under constant threat from many stressors that include both anthropogenic disturbances such as overharvesting of herbivorous reef fish and natural disturbances such as disease outbreaks, hurricanes, and coral bleaching (Bythell et al. 2000, Hoegh-Guldberg et al. 2007) on relatively short time scales. Consequently, particularly in the species-poor Caribbean, coral reefs are widely thought to exhibit at least two stable states, one with healthy levels of coral cover and the other with coral depletion usually corresponding to high levels of macroalgae (Knowlton 1992, Bellwood et al. 2004), although demonstrating the existence of such stable equilibria empirically is extremely difficult (Petraitis and Dudgeon 2004). To date, evidence for the existence of alternate states on Caribbean reefs stems only from a complex

mechanistic simulation model, for which all parameters were derived from field observations (Mumby et al. 2007b). The model predictions were tested against a time series of observations from Jamaica and found to be robust against a wide range of parameter tweaking.

Alternate states arise because of positive feedbacks that either reinforce or disrupt coral population trajectories (Mumby and Steneck 2008). An important driver of such trajectories is the recruitment of corals, which can be impeded by macroalgal pre-emption of space and competition (Lee 2006, Mumby et al. 2007a, Arnold et al. 2010). Feedbacks occur because of interactions between the cover of living coral and grazing intensity (Mumby 2006). For example, an increase in coral will intensify the grazing on non-coral hard substrata and reduce the cover of macroalgae (Williams et al. 2001). The resulting loss of macroalgae relieves the competition on coral recruitment and leads to higher coral cover, which then reinforces the rise of grazing intensity. Coral depletion is often viewed as undesirable, posing limitations to the ecosystem services provided by corals and thus preservation of coral reef ecosystems is essential to maintain such services.

We recognize that there are many other stressors that will apply to coral systems on longer time scales including changes in ocean chemistry and temperature as well as potential changes in sea level (Kleypas and Langdon 2007). We have chosen not to explicitly include these in our current investigation both because they will

Manuscript received 15 November 2010; revised 28 February 2011; accepted 18 March 2011. Corresponding Editor: N. T. Hobbs.

⁴Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, Michigan 48109 USA and Center for the Study of Complex Systems, University of Michigan, Ann Arbor, Michigan 48109 USA.
E-mail: juliecb@umich.edu

occur on longer time scales, and also to keep our current investigation simpler.

A central and defining goal in preserving coral reef ecosystems is through maintaining their resilience, which, in the context of coral, is the ability to exhibit recovery trajectories after disturbance (Mumby and Steneck 2008). Furthermore, coral reefs are built by living corals and vary in their complexity. Maintaining this complexity is important as it affects several ecosystem services, including biodiversity and fisheries production. Consequently, a critical question in management of coral reef ecosystems is whether there is sufficient resilience to combat stressors such as overfishing and storm impacts to determine when and how phase shifts, or this switch from a state of high coral cover to a coral-depleted state, may be prevented or reversed. Moreover, phase shifts are likely to depend on interactions between multiple coral stressors but empirical evidence is often limited by data collected over a relatively short time frame. As noted by Hughes and Connell (1999), an analysis of the overall health of a reef by considering data taken over short period of time may merely reflect short-term impacts of recent disturbances and regional or spatial variability may affect such observations. Thus, there is a pressing need for studies of the long-term influence of reef stressors to determine recovery patterns from interacting stressors. The relationship between multiple interacting coral stressors and whether they behave synergistically or additively will have profound influence on management decisions (Hughes and Connell 1999).

Grazing of algae by parrotfish, the primary grazer of Caribbean coral reefs, is important in suppressing algal overgrowth of corals and management of parrotfish exploitation is therefore likely to play a role in coral resilience. In our previous work, we developed a model of coral–algae interactions (Mumby et al. 2007b) that indicates hysteresis, supporting the existence of alternative stable states of high coral cover and coral depletion. This was then extended to explicitly include parrotfish dynamics and their mortality from fishing effort (Blackwood et al. 2010). We determined the short-term effects of fishing effort at different stages of reef recovery following an impact to investigate when and how it is possible to reverse a phase shift from a coral-depleted state via reductions in fishing effort. In particular, we considered coral recovery when habitat quality is still intact (e.g., following a bleaching event that did little damage to complexity) and when reef structure is relatively flat following an acute disturbance (such as a hurricane). Importantly, we used ideas from hysteresis to develop a simple model of ecosystem-based management by determining how fisheries management fits into the wider ecosystem impact. However, the two scenarios considered were looked at separately but they actually occur sequentially but on different time scales, which leads to much more complex models.

While our earlier work emphasized the short-term impacts of fishing regulations following a disturbance, in this paper we extend these studies to determine the effects of fishing effort coupled with slow changes in structural complexity on coral resilience. Following this analysis, we extend our model by introducing a second coral stressor, hurricane impacts, which we allow to have direct effects on reef structure. The time dynamics of the system are computed over a long time scale (100 years) and both hurricane impacts, which are stochastically implemented, and exploitation of parrotfish are included. Importantly, we introduce a model that allows us to analyze the effects of successive hurricanes coupled with exploitation of grazers on recovery. Furthermore, we consider various hurricane frequencies that are relevant to different geographic locations as well as several levels of damage to structural complexity, which is impacted by the storm itself in addition to the dominant coral species. By considering short-term dynamics of coral–algae interactions explicitly coupled with consequences from fishing effort and storm impacts, we provide a theoretical approach to predict recovery patterns and provide insight into necessary measures to be taken in management.

METHODS

Deterministic model: rugosity as a slow-changing parameter

Our previous work analyzed a model of coral–algae interactions assuming that parrotfish growth was limited by coral or algal abundance depending on the state of recovery from disturbances (Blackwood et al. 2010). The model explicitly considered parrotfish mortality as a result of fishing effort in order to develop management recommendations to promote coral recovery in the face of disturbance. This model assumes that a given area of available seabed is completely covered by macroalgae (M), algal turfs (T), and coral (C) so that $M + T + C = 1$, implying that

$$\frac{dT}{dt} = -\frac{dM}{dt} - \frac{dC}{dt}$$

and therefore we only need to explicitly consider the differential equations for macroalgae and coral. Further, the model assumes that parrotfish (P) abundance can be described by logistic growth with a time-varying carrying capacity and a constant rate of mortality from fishing effort (f). The model is now given by

$$\frac{dM}{dt} = aMC - \frac{g(P)M}{M+T} + \gamma MT \quad (1)$$

$$\frac{dC}{dt} = rTC - dC - aMC \quad (2)$$

$$\frac{dP}{dt} = sP \left(1 - \frac{P}{\beta K(C)} \right) - fP \quad (3)$$

where parrotfish abundance (P) have an intrinsic rate of growth s and the carrying capacity is a function of coral cover and is given by $\beta \times K(C)$ where β is the maximum carrying capacity and $0 < K(C) \leq 1$ limits carrying capacity. Thus, we model numerical responses of parrotfish as changes in habitat conditions through a time-varying carrying capacity. It is assumed that corals have a natural mortality rate of d and recruit to and overgrow turf at rate r . Coral are also overgrown by macroalgae at rate a and macroalgae spreads vegetatively over turf at rate γ . Parrotfish graze algae at rate $g(P)$ without distinguishing between algal types, and $g(P)$ is assumed to be directly proportional to parrotfish abundance relative to its maximum carrying capacity with the maximum grazing rate assumed to be 1 for simplicity (i.e., $g(P) = \alpha(P/\beta)$ where $\alpha = 1$ and β is the maximum carrying capacity). Parameters are given in Table 1 and are appropriate when parrotfish species in the genus *Sparisoma* dominate the community, such as in Belize. Further details as well as a sensitivity analysis to these parameters (resulting in minimal qualitative changes) can be found in Blackwood et al. (2010).

Using this model as a basis, we further generalize the limitations of habitat conditions on parrotfish growth. Previously, we considered two distinct stages of coral recovery. In the first, it was assumed that a reef suffered an acute disturbance such as a hurricane resulting in a relatively flat system (Woodley et al. 1981, Rogers et al. 1982). In such situations parrotfish lack adequate refugia and are likely to respond positively to increases in coral cover (and therefore habitat provides the greatest limitation on parrotfish; Emslie et al. 2008). Second, we assumed coral mortality from events such as bleaching or disease that remove living coral tissue but leave the reef structure intact (Brown and Suharsono 1990, Edmunds 1991). Here, it was assumed that parrotfish abundance is increased with greater food (algae) availability (i.e., food limitation provides the greatest limitation on parrotfish; Mumby 2006).

In this paper, we refine our model of coral–algae interactions to simultaneously consider the effects of changes in habitat quality and food limitation on parrotfish abundance to determine the long-term effects of multiple coral stressors. We assume that the resource effects on carrying capacity are multiplicative so that parrotfish cannot survive solely on one resource (i.e., habitat or food) allowing for severe food limitation. For the first part of our analysis, we regard habitat quality, R , as a parameter subject to slow changes allowing us to obtain a better sense of the consequences of variation in rugosity and fishing effort. Thus, R is assumed to be quantifiable and representative of in situ rugosity, a measure of reef complexity that may be increased slowly (on the order of decades to centuries, depending on geographic location) by reef-building corals. Specifically, the index for rugosity is measured using the “chain and tape” method, which provides the ratio between the length of a chain between two points and

the length of the chain when draped over a reef surface. Note that the structure is perfectly flat when $R = 1$. Although we do not include coral cover directly in carrying capacity, we note that R is subject to increases with coral cover and decreases by hurricane impacts and when bioerosion exceeds coral growth (e.g., in a coral-depleted state).

Carrying capacity may now be described as a function of algal abundance ($M + T$) and habitat quality (R) so that parrotfish growth becomes

$$\frac{dP}{dt} = sP \left(1 - \frac{P}{\beta K(M + T, R)} \right) - fP$$

where

$$K(M + T, R) = \frac{(c_1 R + c_2)}{K_{\max}} \left(\frac{\delta(M + T)}{1 + \nu(M + T)} \right)$$

(see Table 1 for parameter values). We assume the relationship with rugosity is linear and that the response to algal cover follows a saturating function. This formulation now allows food availability to increase carrying capacity to a particular level before it no longer improves parrotfish growth whereas rugosity can continue to increase and potentially have larger impacts on parrotfish abundance. In particular, the difference in parrotfish density from high-quality (high rugosity) habitat to low-quality (low rugosity) habitat is much larger than the short-term effects of food abundance at high-quality habitat that is captured in our parameterization (see Appendix A). Additionally, this accounts for severe food limitation and low rugosity leading to small (or negative) growth rates. Further, $K(M + T, R)$ is normalized by K_{\max} so that the function simply provides limitation to the maximum carrying capacity, β (i.e., $K(M + T, R) \leq 1$). To determine the value of K_{\max} , we note that according to Alvarez-Filip et al. (2009), a perfectly flat reef structure is given by $R = 1$ and rugosity rarely is above $R = 3$ (which requires *Acropora* branching corals) so we limit rugosity to a maximum value of 3. Further, we assume that the carrying capacity will attain its maximum value ($K(M + T, R) = 1$) if and only if rugosity is at a maximum ($R = 3$) and there is high algal cover ($M + T = 1$) so there are adequate refugia and an abundance of food availability. We note that if such high algal abundance is obtained, bioerosion will begin to exceed coral growth that is captured in the following sections. Thus, although the maximum carrying capacity is unattainable it provides an upper limit on parrotfish abundance. Then with our parameterization $K_{\max} \approx 17.745$.

Nondimensionalization

The model we have developed has a number of parameters and at least some of our investigations are numerical. Thus, as a first step we nondimensionalize to reduce the number of parameters and to provide guidance into the relative importance of the different

TABLE 1. Parameter values and definitions.

Parameter	Value	Definition
s	0.49	Growth rate (yr^{-1}) of parrotfish, estimated using FishBase (Froese and Paul 2011).
a^\dagger	0.1	Rate (yr^{-1}) that macroalgae directly overgrow coral; such limited overgrowth was shown in Lirman (2001).
γ^\dagger	0.8, 1.6	Rate (yr^{-1}) that macroalgae spread vegetatively over algal turfs (Mumby et al. 2005). Value is different for each simulation section.
r^\dagger	1	Rate (yr^{-1}) of coral recruitment to algal turfs; coral always overgrow algal turfs (Jompa and McCook 2002).
d^\dagger	0.44	Natural coral mortality; accounts for 2–4% per year (Bythell et al. 1993), and predation account for 30% per year (Box and Mumby 2007). The remaining mortality results from coral disease or tissue damage following bleaching.
β	variable	Maximum carrying capacity. Value depends on location but is eliminated from model by nondimensionalization.
c_1, c_2	−3.21, 3.65	Determines the relationship between reef complexity and parrotfish carrying capacity; see Appendix A for details.
δ, ν	4.557, 0.9877	Determine the relationship between food availability and parrotfish carrying capacity; see Appendix A for details.
m_H	0.8	Mortality of macroalgae following a hurricane impact, following Mumby (2006).
h_G^*, h_E^*	0.03, 0.01	Growth and erosion of reef complexity, respectively; chosen so that complexity changes on slower time scale than coral–algal dynamics.

\dagger The parameters for the original model are those used in Mumby et al. (2007a), which were based on the parameterization used for the corresponding simulation model (Mumby et al. 2007a), and $\gamma = 0.8$ is the parameter used in that model. Also, these are the parameter values prior to nondimensionalization; for the nondimensional model, each of these parameters is divided by s . Parameter values are appropriately scaled with the dimensions of proportion of patch per year.

time scales inherent in the model. This step is important in identifying what the parameter combinations that control the dynamics are (Petersen and Hastings 2001). We now recall that our grazing function is given by

$$g(P) = \alpha \frac{P}{\beta}$$

where α is the maximum grazing rate (assumed to be one), and β is the maximum carrying capacity of parrotfish. Thus, we nondimensionalize parrotfish density so that we can consider abundance relative to carrying capacity by letting $(P/\beta) = \tilde{P}$ so that \tilde{P} is parrotfish abundance relative to maximum carrying capacity. Then,

$$\frac{d\tilde{P}}{dt} = s\tilde{P} \left(1 - \frac{\tilde{P}}{K(M+T,R)} \right) - f\tilde{P}.$$

With our nondimensionalization, the grazing function becomes $g(P) = g(\tilde{P}\beta) = \alpha\tilde{P}$ and the carrying capacity of parrotfish is now bounded between zero and 1. Furthermore, we nondimensionalize time by defining $\tau = t \times s$ and our model becomes

$$\frac{dM}{d\tau} = \hat{a}MC - \frac{\hat{a}\tilde{P}M}{M+T} + \hat{\gamma}MT \tag{4}$$

$$\frac{dC}{d\tau} = \hat{r}TC - \hat{d}C - \hat{a}MC \tag{5}$$

$$\frac{d\tilde{P}}{d\tau} = \tilde{P} \left(1 - \frac{\tilde{P}}{K(M+T,R)} \right) - \hat{f}\tilde{P} \tag{6}$$

where the hats denote the nondimensional forms of the parameters (e.g., $\hat{a} = a/s, \hat{f} = f/s$) and the grazing function is now given by $\hat{g}(P) = \hat{\alpha}\tilde{P}$. We note that this particular

nondimensionalization of time allows us to view fishing effort relative to the growth rate of parrotfish (\hat{f}). Therefore, the nondimensional \hat{f} is bounded above by 1, since if $\hat{f} > 1$, or $f > s$, fishing effort exceeds the growth rate of parrotfish and the parrotfish population will be driven to extinction. This can be seen by considering the equation for parrotfish as $P \rightarrow 0$. Neglecting higher order terms, if $\hat{f} > 1$, then

$$\frac{d\tilde{P}}{d\tau} = \tilde{P} - \hat{f}\tilde{P} < 0.$$

Hereafter, we drop the hats and redefine $P := \tilde{P}$ for simplicity.

Analysis of habitat quality and parrotfish exploitation

We now provide an analysis of the equilibrium structure for all relationships between rugosity R and fishing effort f (Fig. 1) and details are provided in Appendix B. The coral-dominated and coral-depleted equilibria in terms of coral cover (C), macroalgae (M), and parrotfish abundance (P) are $(C^*, M^*, P^*) = ([r-d]/r, 0, [1-f]K[M^*+T^*, R])$ and $(C^*, M^*, P^*) = (0, 1, 0)$, respectively. We note that, for all feasible values of f and R , these equilibria exist (recalling that turf algae $T^* = 1 - C^* - M^*$) Fig. 2 demonstrates the stability of these equilibria in each qualitatively different region in Fig. 1 by displaying bifurcation diagrams of C^* vs. f for a fixed value of R . Note that we do not need to include the upper branch of the nontrivial equilibrium, as it can easily be shown that if $C^* > (r-d)/r$, then $M^* < 0$, which requires a negative initial value of M and is therefore biologically irrelevant.

Figs. 1 and 2 demonstrate that regions with low habitat quality (e.g., following an acute disturbance causing major damage to structure) demonstrate little

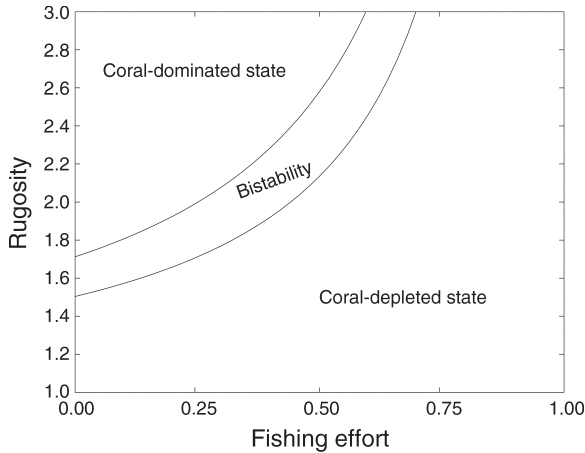


FIG. 1. Bifurcation diagram of rugosity (R) vs. fishing effort (f) where f is the nondimensional fishing effort relative to parrotfish intrinsic growth rate (r). The region labeled “coral-dominated state” represents all values of R and f where $C^* = (r - d)r$ is the only stable equilibrium (C^* is coral cover at equilibrium; d is the natural coral mortality rate). In the “coral-depleted” region, $C^* = 0$ is the only stable equilibrium and, in the “bistability” region, coral cover may become depleted or recover depending on initial conditions.

resilience even when fishing effort is kept as a minimum. On the contrary, states with high habitat quality demonstrate more resilience to disturbance and implementation of fishing regulations may promote coral recovery and increase resilience. In other words, when habitat quality is low, there exist few initial states that

will ultimately end in high coral cover and conversely, when habitat quality is high there are many initial states that will arrive at high coral cover. Importantly, this analysis provides a representation of how slow changes in rugosity may affect dynamics on the time scale of coral–algae interactions.

Changes in rugosity with time

The above analysis considers the dynamics when rugosity is held constant but we now extend this analysis further to account for slow changes in rugosity that occur inter-hurricane, a result of production from reef-building corals and bioerosion. Therefore, we now provide a formulation of changes in rugosity with time. Model development is constrained by the lack of available data on the underlying processes governing these changes. Thus, we implement the simplest phenomenological model that exhibits appropriate behavior on the boundaries. Specifically,

$$\frac{dR}{dt} = h_G C(3 - R) - h_E(1 - C)(R - 1)$$

which has the properties that rugosity is bounded below by 1 and above by 3. Increases in rugosity result from production by existing living corals at a rate h_G ; if rugosity is low, coral recruitment will have a faster impact on rugosity than coral recruitment when rugosity is already at a high level. Furthermore, bioerosion may exceed growth if coral cover is low at a rate h_E . The equilibrium value for a fixed value of coral cover is given by the following:

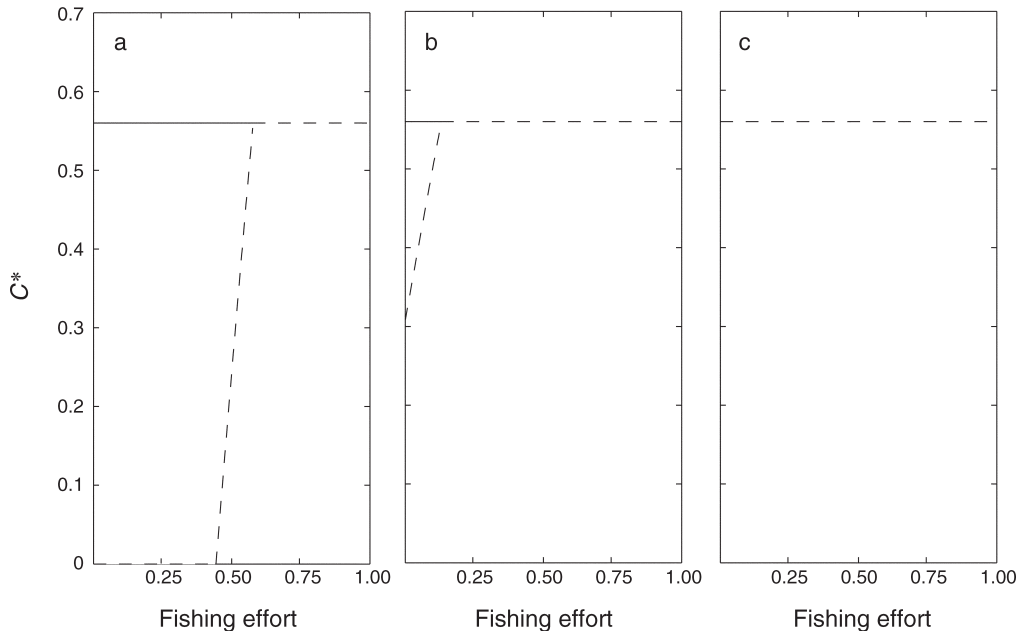


FIG. 2. Bifurcations diagrams of equilibrium value of coral cover vs. fishing effort relative to parrotfish growth rate (f) for different values of rugosity (R) to demonstrate the implications of Fig. 1: (a) $R = 2.4$, (b) $R = 1.6$, (c) $R = 1.2$. Solid lines are stable equilibria, and dashed lines are unstable equilibria. Notice that the existence of the nontrivial unstable equilibrium (corresponding to coexistence of coral and macroalgae) indicates regions of bistability.

$$R^* = \frac{h_E(C - 1) - 3h_G C}{h_E(C - 1) - h_G C}.$$

We use the parameter values $h_G = 0.03$ and $h_E = 0.01$ so changes in rugosity occur over a longer timescale (order of decades to centuries) than coral–algae interactions. These are plausible parameter values but as data availability increases these values can be made more precise; for our purposes, however, they capture the desired properties of rugosity. Given constant high coral cover ($C \approx 0.56$) an equilibrium value of rugosity of 2.58 will be approached and given a constant low coral cover ($C = 0.01$) the equilibrium value 1.06 will be approached. Again, we nondimensionalize time by setting $\tau = s \times t$ to view dynamics on the time scale relative to parrotfish growth.

Stochastic hurricane implementation

Hurricane impacts are implemented as jump processes so that their occurrences are stochastic and impacts are instantaneous. Jump processes were perhaps first implemented in financial models, in particular by Merton (1971), and are also used in population genetics to describe rare mutations (e.g., Champagnat and Lambert 2007). We assume that in the presence of a jump caused by a hurricane or violent storm with similar effects, the impact to coral cover depends on the time since last impact (where the proportion of coral cover affected is denoted by F , see Appendix C for parameterization), macroalgae is always reduced by a constant proportion (m_H) to a low level and turf immediately recolonizes empty space left from disturbed coral and macroalgae. This assumption is reasonable and has been observed following hurricanes; for example, immediately following Hurricanes Frances and Jeane temporary relief was provided from macroalgae (Lapointe et al. 2006). Although we assume there are no direct impacts on parrotfish abundance, indirect effects will occur as a result of changes in their carrying capacity. Thus, we redefine our model as a set of stochastic differential equations:

$$dC = g_C(C, M, P, R, \tau)d\tau - C(F + \sigma\varepsilon)dq$$

$$dM = g_M(C, M, P, R, \tau)d\tau - Mm_H dq$$

$$dP = g_P(C, M, P, R, \tau)d\tau$$

$$dR = g_R(C, M, P, R, \tau)d\tau - R(G - 1 + \sigma\varepsilon)dq$$

where the growth functions are

$$g_C(C, M, P, R, \tau) = rTC - dC - aMC$$

$$g_M(C, M, P, R, \tau) = aMC - \frac{\alpha PM}{M + T} + \gamma MT$$

$$g_P(C, M, P, R, \tau) = P \left(1 - \frac{P}{K(M + T, R)} \right) - fP$$

$$g_R(C, M, P, R, \tau) = h_1 C(3 - R) - h_2(1 - C)(R - 1)$$

and q is a Poisson jump process with jump rate λ such that $dq = 0$ with probability $1 - \lambda d\tau$ and $dq = 1$ with probability $\lambda d\tau$. Here, G is the expected proportion of rugosity affected by hurricane impacts (varies for each simulation). We note that coral-depauperate reefs would suffer relatively lightly from hurricane damage, though large colonies of *Montastraea* and *Diploria* routinely disappear during hurricane events, which reduces complexity, albeit slowly (P. J. Mumby, *personal observation*). The term $C(F + \sigma\varepsilon)dq$ is an impulse function that results in a jump from C to $C(F + \sigma\varepsilon)$ if $dq = 1$ with standard deviation $\sigma > 0$ (and thus ε is a random variable following the standard normal distribution) to account for variability in impact to coral and rugosity. We note that this inherently accounts for variability in the effects to algal cover since $M + T = 1 - C$. Further, we assume hurricane impacts only have negative effects on coral cover and the damage level cannot exceed 100%, so in the following analysis in the case that $F + \sigma\varepsilon < 0$, we simply set $F + \sigma\varepsilon = 0$ and if $F + \sigma\varepsilon > 1$, we set $F + \sigma\varepsilon = 1$. We analogously constrain the impacts to rugosity. Further, we assume that recovery trajectories from hurricanes immediately resume to pre-hurricane rates. To determine the expected next occurrence of a hurricane, our simulations utilize the fact that Poisson processes have an exponential waiting time between events. We implement this distribution for simplicity but caution that this does not account for seasonality and local changes in hurricane frequency; managers should therefore adapt their policies to local conditions.

Simulations

We provide simulations for various circumstances dependent on dominant coral species and location (which affects hurricane frequency). Given limited data, we simulate three different levels of damage that are likely to be relevant to various situations. First, we assume a hurricane impact always has a high impact on reef structure and there is a 50% reduction in rugosity following a hurricane (i.e., rugosity of 3 will be reduced to rugosity of 2). Second, we consider hurricanes with a main source of damage being pruning out coral colonies. Thus we assume only a 5% reduction in rugosity. Third, we consider an intermediate case where a hurricane has the same proportional effect on rugosity as coral cover.

Additionally, we consider varying hurricane frequencies that depend on geographic location. The first frequency we consider is low frequency (one hurricane estimated every 30 years), most consistent with Bonaire. Second, we consider high frequency hurricanes (one hurricane every 9 years) most consistent with the Bahamas and finally intermediate hurricane frequencies (one hurricane every 15 years), most consistent with Belize (Edwards et al. 2010). Additionally, the initial conditions are set at high coral cover ($C_0 = 0.56$),

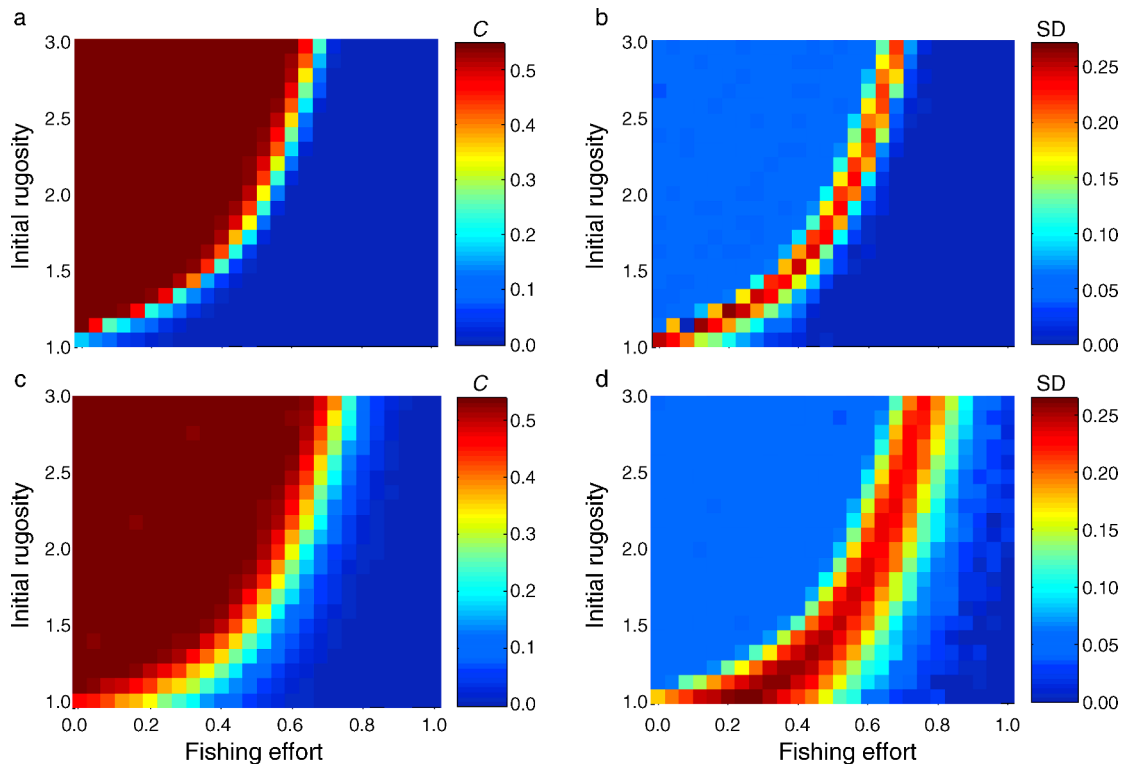


FIG. 3. Simulation results for coral cover, C . The horizontal axis is fishing effort level, and the vertical axis is the initial rugosity. Panels (a) and (c) display the mean final value of coral cover, and panels (b) and (d) show the standard deviation. All use intermediate damages to rugosity; panels (a) and (b) have low hurricane frequency (one every 30 years), and panels (c) and (d) have high hurricane frequency (one every 9 years). This demonstrates the increased variability along the transition between high and low coral cover as well as the increased resilience to fishing effort with higher hurricane frequencies.

macroalgae is low ($M_0 = 0.01$), and parrotfish is at the corresponding equilibrium value corresponding to no fishing effort so that we assume fishing effort begins at the beginning of the simulation period. Furthermore, for various levels of fishing effort f and initial rugosity level R_0 such that $0 \leq f \leq 1$ and $1 \leq R_0 \leq 3$, we simulate the dynamics for 100 years and provide 1000 realizations for each set of conditions under the assumption that the initial time was the time of last hurricane impact and standard deviation $\sigma = 0.05$ to account for variability in impacts. We note that for each simulation, we display the results for all levels of rugosity between 1 and 3, but when the hurricane impact is low the system is most likely to be dominated by massive corals, and thus the initial rugosity is likely to be much less than three.

In the following two sections we provide our simulation results under two different scenarios; in the first we assume that the growth rate of coral and macroalgae are similar, and in the second we demonstrate the effects of increasing rates of macroalgal growth.

RESULTS

In this section, we assume that coral and macroalgal growth rates are similar (with a ratio of 0.8). This is likely to occur when there are branching acroporids

(*Acropora cervicornis*) in the system. Branching corals grow at an order of magnitude faster than most massive corals, which currently dominate Caribbean reefs (Huston 1985). Branching corals are often much less common now principally because of outbreaks of white band disease in the past few decades (Bythell and Sheppard 1993); though there are signs of recovery in parts of the Caribbean (P. J. Mumby, *personal observation*).

For each set of initial data and corresponding hurricane frequency and intensity, we provide plots of the mean ending values of coral cover and rugosity in addition to their standard deviation to provide a representation of the expected long-term impacts as well as a measure of their variability. The plots not shown in the paper as well as a table briefly summarizing of each of the results are provided in Appendix D. Our results indicate that for both coral cover and rugosity, there is a band of high variability along the transition between states of high coral cover and coral depletion (see Figs. 3 and 4). Thus, states lying within this band have more variability in whether the outcome is a favorable or unfavorable state. Furthermore, the width of this bands increases with increases in hurricane frequency (as can be seen in Appendix D), providing an indicator of the

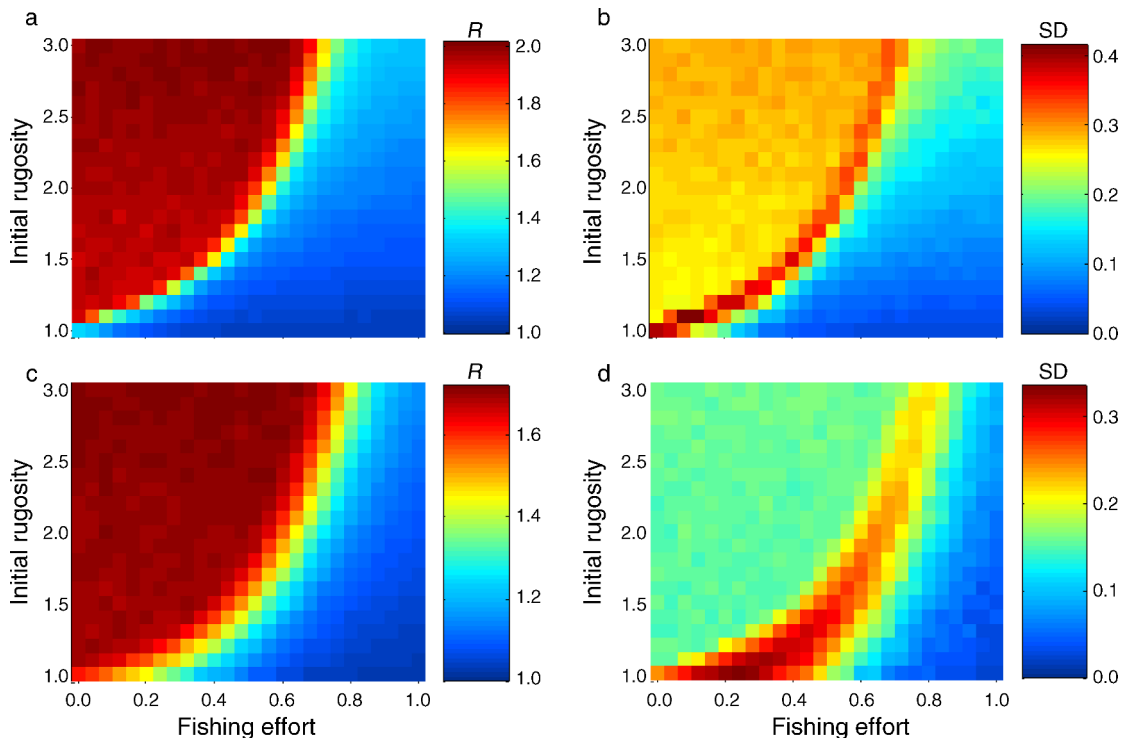


FIG. 4. The structure is the same as Fig. 3 except this figure corresponds to results for final rugosity, demonstrating that regions with high hurricane frequency have higher resilience to fishing effort but suffer greater damage to rugosity, demonstrating a need for consideration of local restorative interventions to build vertical relief for the coral.

expected level of uncertainty in these regions with respect to frequency of impacts.

Interestingly, our results also indicate that the higher the frequency of hurricane impacts, the more likely the system is to end in a state of high coral cover even for states predicted to end in a coral-depleted state according to Fig. 1. In other words, there is greater resilience to increases in fishing effort with higher frequency hurricanes (see Fig. 3). This results from increases in coral recruitment following a hurricane, as more space has been freed for coral colonization by the removal of macroalgae (Bythell et al. 2000, Renken et al. 2010). This is partly a result of our model formulation: there is, however, a trade-off between high coral cover and the corresponding level of rugosity. Although high hurricane frequencies result in a greater number of states (or a greater subset of initial conditions in our parameter space) with high coral cover, the structural complexity suffers increasing damage with higher impact levels (see Figs. 4 and 5). In turn, this reduces refugia for parrotfish and limits the ecosystem services provided by the corals, such as coastal hurricane defense (Sheppard et al. 2005). Thus, while there is greater flexibility in fishing regulations, to promote ecosystem services that are founded on a complex reef structure there is a need to determine whether management that provides vertical relief by promoting coral recruitment is cost effective. Moreover, the observed increased resilience to fishing

effort on reefs with high hurricane frequency declines as the level of hurricane damage increases, as can be observed in Appendix D.

To further demonstrate these results, Fig. 6 displays the time dynamics for hurricanes with intermediate

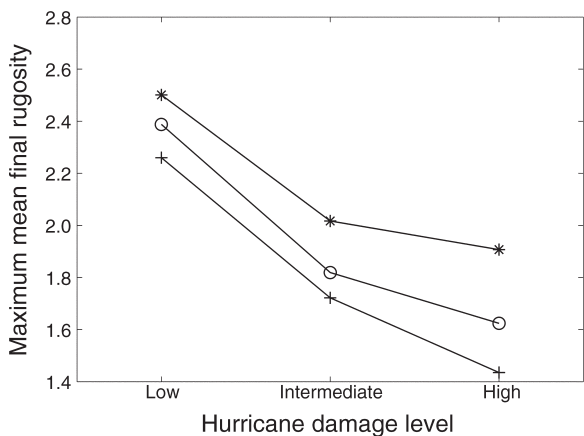


FIG. 5. Maximum mean level of final rugosity for all feasible initial levels of rugosity and fishing effort is plotted for each level of hurricane damage. Stars correspond to low frequency, circles correspond to intermediate, and crosses correspond to high hurricane frequency. This demonstrates the difference in impacts to rugosity between high and low damage as well as high and low hurricane frequencies.

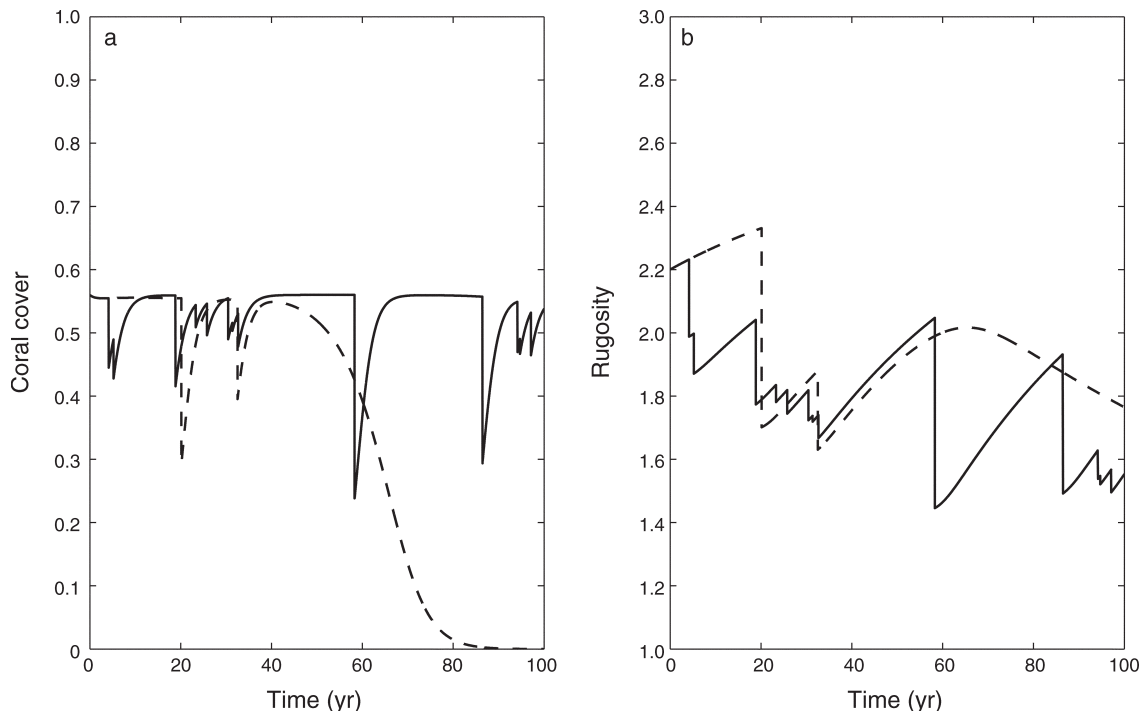


FIG. 6. Time dynamics for intermediate damage levels to rugosity following a hurricane impact: (a) coral cover and (b) rugosity values over time. The solid lines are at high hurricane frequency, and the dashed lines are at low frequency. For each, the initial value of rugosity is 2.2, and the fishing effort relative to parrotfish intrinsic growth rate is set at 0.58.

impact levels to rugosity, one with high frequency and the other with low frequency. Each has a relatively high level of fishing effort relative to the growth rate of parrotfish (0.58). With a low hurricane frequency, the state eventually approaches a coral-depleted state and rugosity only faces major declines once coral cover is low, since bioerosion exceeds growth. This indicates that a reduction in fishing effort could allow this system to regain resilience. Conversely, when the hurricane frequency is high this realization maintains high coral cover but rugosity faces severe damage as a consequence of the hurricane impact. Here, there is a greater need to determine whether it is cost effective to focus on vertical restoration efforts by using artificial reefs to build alternative reef habitat.

The effect of increasing macroalgal growth rates

The above results assume that the rate of vegetative spread of macroalgae over algal turfs (γ) and the rate of coral overgrowth of algal turfs (r) are similar. However, this implicitly assumes that coral growth is relatively high, which may result from the presence of branching corals and indicates that this particular system is not affected by disease. Currently, the most abundant corals are commonly massive genera such as *Montastraea*, *Diploria*, and *Colopophyllia*. Here, macroalgal growth rates can be approximately ten times faster than corals (increase in percentage cover units of 40% vs. 4% in corals; Mumby and Harborne 2010, Mumby 2009).

Thus we now determine how increasing the rate of macroalgal spread over algal turfs relative to the growth rate of coral affect our results.

We conduct identical simulations as the previous section, only here we increase the rate of macroalgal spread to 1.6, or a 100% increase. We note that for values much higher than this (>2), the number of states ending in coral cover is negligible. This could be a result of our assumption that the pre-hurricane rates are resumed following a hurricane, and therefore post-hurricane nutrient enrichment does not affect the rate γ (Andréfouët et al. 2002). In comparison to our above results, we still observe an increase in variability between the transition from regions ending in high coral cover vs. coral depletion. Moreover, the effect observed in the previous section that corresponds to greater resilience to fishing effort when hurricane frequency increases diminishes as macroalgal growth rates increase. In fact, even when hurricane damage is at an intermediate level these effects are no longer observed and instead, regions with low frequency hurricanes have greater resilience to fishing effort compared to high frequency hurricane regions (see Fig. 7 and the simulation results in Appendix D).

In general, our observations indicate that there is greater resilience to fishing effort for higher frequency hurricanes only when hurricane damage levels and the growth rate of macroalgae are sufficiently low.

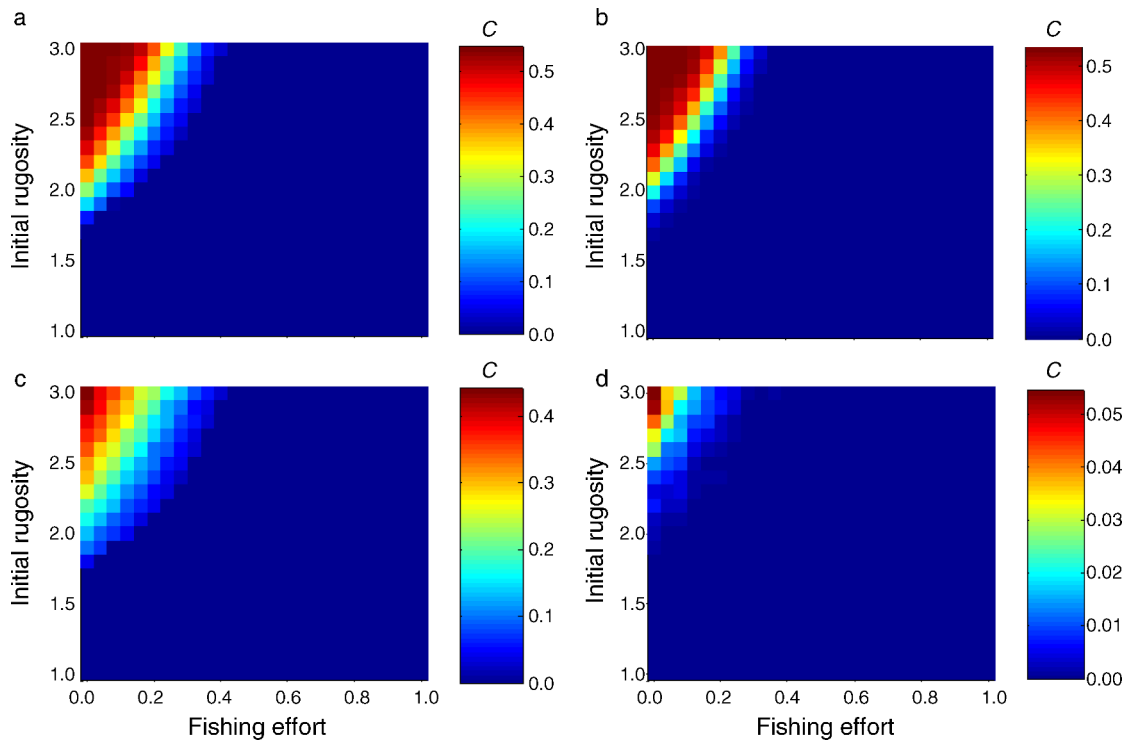


FIG. 7. The simulation structure is the same as the previous figures. Here, each panel displays only the results for mean final coral cover and we demonstrate that as the rate that macroalgae spreads vegetatively over algal turfs (γ) increases (here $\gamma = 1.6$) there is no longer increased resilience to fishing effort for high frequency hurricanes. Even for intermediate levels of hurricane damage, regions with (a) low-frequency hurricanes have greater resilience to fishing effort than do (b) high-frequency hurricane regions. Furthermore, when hurricanes are highly damaging to reef complexity, there is substantially greater resilience to fishing effort when (c) hurricane frequency is low compared to (d) high. This demonstrates that the observed increased resilience to fishing effort for higher frequency hurricanes is only plausible when impact levels and macroalgal spread rates are sufficiently low.

DISCUSSION

Developing a complete understanding of the effect of coral reef stressors is important in determining management methods to promote coral resilience and maintain the ecosystem-based services founded on these corals (Bellwood et al. 2004). Furthermore, there is a need for greater knowledge of the interaction between multiple stressors as well as their long-term impacts (Hughes and Connell 1999). We develop a model-based approach to determine the interaction of hurricane impacts and exploitation of Caribbean reef grazers (specifically parrotfish) and the expected medium-term effects to aid in developing management guidelines for various regions in the Caribbean. Over longer time scales other stressors due to global change would have to be included (Anthony et al. 2011). We do argue that our approach and general lessons would apply if more stressors were included. Similarly, the ideas and concepts developed here will apply more generally to other issues of management in the face of multiple stressors.

We first provided an analysis of the expected dynamics of coral–algae interactions given that habitat quality (measured by rugosity) is a parameter subject to slow changes from processes including production by reef-building corals and bioerosion. We conclude that

patches with high levels of complexity are more resilient to storm impacts and coral recovery is promoted for a wide range of fishing effort levels. Subsequently, we explicitly include changes in rugosity and directly implement hurricane impacts using jump processes allowing us to account for inter-hurricane changes to rugosity.

Our results demonstrate that coral has greater resilience to fishing effort when hurricane frequency is high. However, although high coral cover may be observed for more-aggressive fishing effort levels, it is assumed damaging hurricanes reduce rugosity and pose future threats to maintaining complexity and therefore limiting important ecosystem services that are founded on reef complexity. Thus, if fishing effort is increased or hurricanes become less frequent or more intense, a system in this state is likely to approach coral depletion. Therefore, our results indicate that in regions with frequently occurring hurricanes, management should put greater emphasis on determining whether restorative methods to build vertical relief are cost effective. However, active reef restoration may be invoked at a small scale but scaling up such interventions may be prohibitively expensive. Moreover, we demonstrate that these effects diminish as impact levels increase as well as

when macroalgal growth rates increase. We note that managers should adapt their policy implementations according to shifts in local hurricane frequencies.

Furthermore, reefs experiencing low frequency hurricanes demonstrate less resilience to fishing effort but maintain higher levels of complexity when the system is in a coral-dominated state. Thus, when expected hurricane frequency is low there is a need for greater emphasis on fishing regulations to promote resilience and prevent phase shifts to coral-depleted states. Additionally, for each level of impact and frequency there is an observed band of increased variability near the transition of high coral and coral-depleted states for both the ending values of coral cover and rugosity. To avoid this great uncertainty, it is recommended to maintain fishing effort levels well below this region of transition. However, for all hurricane frequencies increasing intensity poses greater risk to maintenance of structural complexity, a necessity to providing refugia for grazers and serving as a coastal barrier to impacts. Thus, in addition to fisheries management the consequences of global warming need to be considered as there is evidence that hurricane intensity may increase with global warming, resulting in increased relevance of the policy recommendations of high hurricane frequencies through time (e.g., Webster et al. 2005).

ACKNOWLEDGMENTS

This work was supported by the National Science Foundation under Grant #EF-0742674 to A. Hastings and an ARC Laureate Fellowship, Pew Fellowship, and EU FORCE project to P. J. Mumby. We also thank John Bruno and Matthew Spencer for their helpful comments on this manuscript.

LITERATURE CITED

- Alvarez-Filip, L., N. K. Dulvy, J. A. Gill, I. M. Côté, and A. R. Watkinson. 2009. Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. *Proceedings of the Royal Society B* 276:3019–3025.
- Andréfouët, S., P. Mumby, M. McField, C. Hu, and F. Muller-Karger. 2002. Revisiting coral reef connectivity. *Coral Reefs* 21:43–48.
- Anthony, K. R. N., J. A. Maynard, G. Diaz-Pulido, P. J. Mumby, P. A. Marshall, L. Cao, and O. Hoegh-Guldberg. 2011. Ocean acidification and warming will lower coral reef resilience. *Global Change Biology* 17:1798–1808.
- Arnold, S. N., R. S. Steneck, and P. J. Mumby. 2010. Running the gauntlet: inhibitory effects of algal turfs on the processes of coral recruitment. *Marine Ecology Progress Series* 414:91–105.
- Bellwood, D. R., T. P. Hughes, C. Folke, and M. Nyström. 2004. Confronting the coral reef crisis. *Nature* 429:827–833.
- Blackwood, J. C., A. Hastings, and P. J. Mumby. 2010. The effect of fishing on hysteresis in Caribbean coral reefs. *Theoretical Ecology*. [doi: 10.1007/s12080-010-0102-0]
- Box, S. J., and P. J. Mumby. 2007. The effect of macroalgal competition on the growth and survival of juvenile Caribbean corals. *Marine Ecology Progress Series* 342:139–149.
- Brown, B. E., and Suharsono. 1990. Damage and recovery of coral reefs affected by El Niño related seawater warming in the Thousand Islands, Indonesia. *Coral Reefs* 8:163–170.
- Bythell, J. C., E. H. Gladfelter, and M. Bythell. 1993. Chronic and catastrophic natural mortality of three common Caribbean reef corals. *Coral Reefs* 12:143–152.
- Bythell, J. C., Z. M. Hillis-Starr, and C. S. Rogers. 2000. Local variability but landscape stability in coral reef communities following repeated hurricane impacts. *Marine Ecology Progress Series* 204:93–100.
- Bythell, J., and C. Sheppard. 1993. Mass mortality of Caribbean shallow corals. *Marine Pollution Bulletin* 26:296–297.
- Champagnat, N., and A. Lambert. 2007. Evolution of discrete populations and the canonical diffusion of adaptive dynamics. *Annals of Applied Probability* 17:102–155.
- Edmunds, P. J. 1991. Extent and effect of black band disease on a Caribbean reef. *Coral Reefs* 10:161–165.
- Edwards, H. J., et al. 2010. How much time can herbivore protection buy for coral reefs under realistic regimes of hurricanes and coral bleaching? *Global Change Biology*. [doi: 10.1111/j.1365-2486.2010.02366.x]
- Emslie, M. J., A. J. Cheal, H. Sweatman, and S. Delean. 2008. Recovery from disturbance of coral and reef fish communities on the Great Barrier Reef, Australia. *Marine Ecology Progress Series* 371:177–190.
- Froese, R., and D. Pauly, editors. 2011. FishBase. (www.fishbase.org)
- Hoegh-Guldberg, O., et al. 2007. Coral reefs under rapid climate change and ocean acidification. *Science* 318:1737–1742.
- Hughes, T. P., and J. H. Connell. 1999. Multiple stressors on coral reefs: a long-term perspective. *Limnology and Oceanography* 44:932–940.
- Huston, M. 1985. Variation in coral growth rates with depth at Discovery Bay, Jamaica. *Coral Reefs* 4:19–25.
- Jompa, J., and L. J. McCook. 2002. Effects of competition and herbivory on interactions between a hard coral and a brown alga. *Journal of Experimental Marine Biology and Ecology* 271:25–39.
- Kleypas, J. A., and C. Langdon. 2007. Coral reefs and changing seawater chemistry. Pages 73–110 in J. T. Phinney, O. Hoegh-Guldberg, J. A. Kleypas, and W. Skirving, editors. *Coral reefs and climate change: science and management*. AGU monograph series. Coastal and estuarine studies. Volume 61. American Geophysical Union, Washington, D.C., USA.
- Knowlton, N. 1992. Thresholds and multiple stable states in coral reef community dynamics. *American Zoologist* 32:674–682.
- Lapointe, B. E., B. J. Bedford, and R. Baumberger. 2006. Hurricanes Frances and Jeanne remove blooms of the invasive green alga *Caulerpa brachypus* forma *parvifolia* (Harvey) cribb from coral reefs off Northern Palm Beach County, Florida. *Estuaries and Coasts* 29:1559–2731.
- Lee, S. C. 2006. Habitat complexity and consumer-mediated positive feedbacks on a Caribbean coral reef. *Oikos* 112:442–447.
- Merton, R. C. 1971. Optimum consumption and portfolio rules in a continuous-time model. *Journal of Economic Theory* 3:373–413.
- Mumby, P. J. 2006. The impact of exploiting grazers (Scaridae) on the dynamics of Caribbean coral reefs. *Ecological Applications* 16:747–769.
- Mumby, P. J. 2009. Phase shifts and the stability of macroalgal communities on Caribbean coral reefs. *Coral Reefs* 28:761–773.
- Mumby, P. J., N. L. Foster, and E. A. Glynn Fahy. 2005. Patch dynamics of coral reef macroalgae under chronic and acute disturbance. *Coral Reefs* 24:681–692.
- Mumby, P. J., and A. R. Harborne. 2010. Marine reserves enhance the recovery of corals on Caribbean reefs. *PLoS ONE* 5:e8657.
- Mumby, P. J., A. R. Harborne, J. Williams, C. V. Kappel, D. R. Brumbaugh, F. Micheli, K. E. Holmes, C. P. Dahlgren, C. B. Paris, and P. G. Blackwell. 2007a. Trophic cascade facilitates coral recruitment in a marine reserve. *Proceedings of the National Academy of Sciences USA* 104:8362–8367.

- Mumby, P. J., A. Hastings, and H. Edwards. 2007b. Thresholds and the resilience of Caribbean coral reefs. *Nature* 450:98–101.
- Mumby, P. J., and R. S. Steneck. 2008. Coral reef management and conservation in light of rapidly evolving ecological paradigms. *Trends in Ecology and Evolution* 23:555–563.
- Petersen, J. E., and A. Hastings. 2001. Dimensional approaches to scaling experimental ecosystems: designing mouse traps to catch elephants. *American Naturalist* 157:324–333.
- Peterson, C. H., and J. Lubchenco. 1997. On the value of marine ecosystems to society. Pages 177–194 in G. C. Daily, editor. *Nature's services. Societal dependence on natural ecosystems*. Island Press, New York, New York, USA.
- Petraitis, P. S., and S. R. Dudgeon. 2004. Detection of alternative stable states in marine communities. *Journal of Experimental Marine Biology and Ecology* 300:343–371.
- Renken, H., P. J. Mumby, I. Matsikis, and H. J. Edwards. 2010. Effects of physical environmental conditions on the patch dynamics of *Dictyota pulchella* and *Lobophora variegata* on Caribbean coral reefs. *Marine Ecology Progress Series* 403:63–74.
- Rogers, C. S., T. H. Suchanek, and F. A. Pecora. 1982. Effects of hurricanes David and Frederic (1979) on shallow *Acropora palmata* reef communities: St. Croix, U.S. Virgin Islands. *Bulletin of Marine Science* 32:532–548.
- Sheppard, C., D. J. Dixon, M. Gourlay, A. Sheppard, and R. Payet. 2005. Coral mortality increases wave energy reaching shores protected by reef flats: Examples from the Seychelles. *Estuarine, Coastal and Shelf Science* 42:223–234.
- Webster, P. J., G. J. Holland, J. A. Curry, and H. R. Chang. 2005. Changes in Tropical Cyclone Number, Duration, and Intensity in a Warming Environment. *Science* 309:1844–1846.
- Williams, I. D., N. V. C. Polunin, and V. J. Hendrick. 2001. Limits to grazing by herbivorous fishes and the impact of low coral cover on macroalgal abundance on a coral reef in Belize. *Marine Ecology Progress Series* 222:187–196.
- Woodley, J. D., et al. 1981. Hurricane Allen's impact on Jamaican coral reefs. *Science* 214:749–755.

APPENDIX A

Parameterization of $K(M + T, R)$ (*Ecological Archives* A021-121-A1).

APPENDIX B

Bifurcation diagram for fishing effort vs. rugosity (*Ecological Archives* A021-121-A2).

APPENDIX C

Determining hurricane impact to coral cover (*Ecological Archives* A021-121-A3).

APPENDIX D

All simulation results (*Ecological Archives* A021-121-A4).