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REPORT

Phase shifts and the stability of macroalgal communities on Caribbean coral reefs

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Abstract Caribbean coral reefs are widely thought to exhibit two alternate stable states with one being dominated by coral and the other by macroalgae. However, the observation of linear empirical relationships among grazing, algal cover and coral recruitment has led the existence of alternate stable states to be questioned; are reefs simply exhibiting a continuous phase shift in response to grazing or are the alternate states robust to certain changes in grazing? Here, a model of a Caribbean forereef is used to reconcile the existence of two stable community states with common empirical observations. Coral-depauperate and coral-dominated reef states are predicted to be stable on equilibrial time scales of decades to centuries and their emergence depends on the presence or absence of a bottleneck in coral recruitment, which is determined by threshold levels of grazing intensity and other process variables. Under certain physical and biological conditions, corals can be persistently depleted even while increases in grazing reduce macroalgal cover and enhance coral recruitment; only once levels of recruitment becomes sufficient to overwhelm the population bottleneck will the coral-dominated state begin to emerge. Therefore, modest increases in grazing will not necessarily allow coral populations to recover, whereas large increases, such as those associated with recovery of the urchin *Diadema antillarum*, are likely to exceed threshold levels of grazing intensity and set a trajectory of coral recovery. The postulated existence of alternate stable states is consistent with field observations of linear relationships between grazing, algal cover and coral recruitment when coral cover is low and algal exclusion when coral cover is high. The term 'macroalgal dominated' is potentially misleading because the coral-depauperate state can be associated with various levels of macroalgal cover. The term 'coral depauperate' is preferable to 'macroalgal dominated' when describing alternate states of Caribbean reefs.

Keywords Equilibrium · Hysteresis · Regime shift · Alternate stable state

Introduction

In the last three decades, one of the most widely reported phenomena to occur on Caribbean reefs is the general fall in the cover of living coral and rise in macroalgae (Kramer 2003; Cote et al. 2005). The trend is by no means ubiquitous with exceptional, coral-dominated reefs being found either in isolated patches (Idjadi et al. 2006) or representing depth strata of entire reef systems (e.g. Bruckner and Bruckner 2003). However, the prevailing ecological balance between macroalgae and corals has changed for a variety of reasons, some of which continue to be debated (Aronson and Precht 2006; Burkepile and Hay 2006; Littler et al. 2006; Mumby and Steneck 2008). Major factors driving the bloom in macroalgae include the loss of corals by disease (Bythell and Sheppard 1993), hurricanes (Bythell et al. 1993) and coral bleaching (Kramer et al. 2003); reductions in top-down grazer controls of algae after the die-off of the urchin *Diadema antillarum* (Lessios et al. 1984) and overfishing of herbivorous fishes (Hughes 1994) and local deterioration of water quality (Littler et al. 1993).

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The change in reef community structure in favour of macroalgae is an example of a phase shift (Done 1992). The stability of this phase shift is a matter of great concern, because macroalgal-dominated reefs have been viewed (by some) to represent a stable community state of coral reefs (Hatcher 1984; Knowlton 1992; Bellwood et al. 2004; McManus and Polsenberg 2004). Specifically, if macroalgal dominance is an alternate state of the ecosystem to coral dominance, and if both states are stable, then it could be challenging to reverse the trajectories of many Caribbean reefs and facilitate a rise in living coral. Alternate states of the system become stable because they are reinforced by self-perpetuating positive or negative feedback mechanisms (Holling 1973; Scheffer and Carpenter 2003; Mumby and Steneck 2008). In the case of a shift to a coral-depleted state, for example, macroalgal levels can become high enough to limit coral recruitment, thereby starting a bottleneck in the coral population (Fig. 1). Once adult corals are lost, either because of disturbance or chronic mortality, coral cover is likely to decline because the bottleneck constrains the rate at which adults are replaced. The fall in coral cover liberates new space for macroalgal colonisation and essentially decreases the intensity of grazing (i.e. the rate at which each patch of substratum is regrazed tends to decline as available area increases). The drop in grazing intensity allows macroalgal cover to increase further, thus strengthening the bottleneck in the coral population, and further reinforcing the feedback (Fig. 1).

Whether coral- and macroalgal-dominated reefs represent alternate stable states of the system has not been proven. An alternative scenario is that the phase shift represents a linear continuum of reef state without feedback mechanisms. If that is the case, then a reduction in macroalgal cover may facilitate a rise in coral cover fairly easily. Indeed, in their review of alternate stable states, Petraitis and Dudgeon (2004) raise the possibility that coral–algal phase shifts may not necessarily involve alternative stable states. The authors point out that the increase in coral recruitment observed in Jamaica, following the local recovery of *Diadema* and reduction in macroalgae (Edmunds and Carpenter 2001), might imply a simple phase–shift relationship, namely, that the return to coral dominance could be a simple phase shift brought about by an increase in grazing. Further, there is widespread evidence that macroalgal cover and grazing are strongly negatively related in the Caribbean (Williams and Polunin 2000; Kramer 2003; Newman et al. 2006; Mumby et al. 2007b) and that reduced macroalgal cover is associated with elevated densities of juvenile corals (Edmunds and Carpenter 2001; Mumby et al. 2007a). Therefore, given this evidence, do reefs exhibit alternate stable states or are phase shifts easily reversible phenomena?

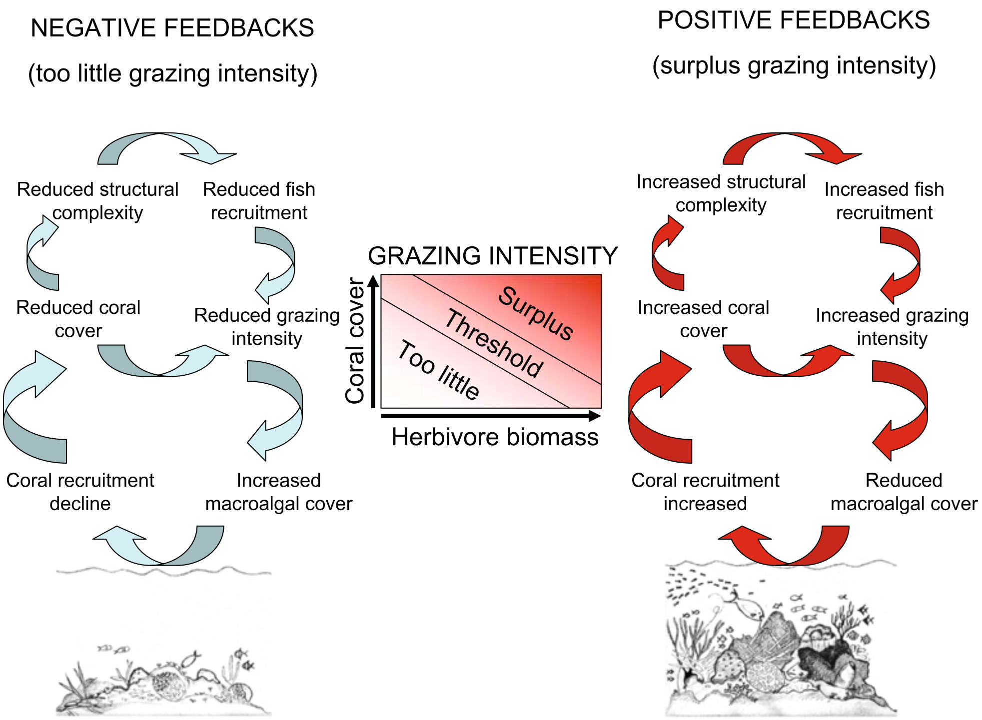

Fig. 1 Schematic representation of positive and negative feedback loops on coral reefs (*source*: Mumby and Steneck 2008, used with permission)

Determining the stability properties of coral reefs from field experiments is almost prohibitively difficult, largely because of ethical considerations in performing large-scale manipulations and the logistical constraint that many coral species have long generation times (Petraitis and Dudgeon 2004). In a recent article, we explored the stability of Caribbean coral populations by using a mechanistic ecological model (Mumby et al. 2007a). The model included many important ecological processes, and each was parameterised from empirical data. The model appeared to behave reasonably as it was found to fit an independent field dataset from Jamaica from the 1970s to the 1990s. We concluded that Caribbean coral populations exhibit two alternative stable states under certain physical and biological conditions. Stability was inferred because each state formed a zone of attraction that resisted certain fluctuations in grazing or the strength of coral–algal competition.

The present study aims to reconcile the potential paradox that a mechanistic model of Caribbean reefs finds coral-depauperate states to be insensitive to certain changes in grazing, whereas a wealth of empirical and experimental evidence suggests that macroalgal cover is strongly negatively correlated with grazing (Lewis 1986; Williams and Polunin 2000; Kramer 2003; Mumby et al. 2006). In other words, how can a modelled 'macroalgal-dominated, coral-depauperate state' resist changes in grazing, whereas empirical studies show that macroalgal cover is directly related to grazing? Furthermore, does the recovery of corals after modest *Diadema* recovery imply that Caribbean reefs exhibit easily-reversible phase shifts rather than alternate stable states as mooted by Petraitis and Dudgeon (2004)? Resolving these issues will help clarify whether the suggestion of alternate stable states is consistent with field observations for Caribbean systems.

Methods

A simulation model was originally designed to represent mid-depth *Montastraea*-dominated forereefs which typically harbour the highest biomass and diversity of reef organisms (Mumby et al. 2008). Since white band disease has depleted populations of large, branching corals (Aronson and Precht 2001), stylised massive growth forms of coral were simulated together with rates of recruitment, growth, reproduction and mortality. The model is a square lattice of 2,500 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). Although the reef has a continuous (toroidal) lattice of 2,500 cells, the lattice structure merely helps define probabilistic rules of coral recruitment and vegetative algal growth. Individual cells comprise multiple coral colonies and algal patches so that interactions occur at colony scales as they do in situ. Corals can recruit to individual patches of cropped algae (which in this model harbour little sediment) but not macroalgae. Macroalgae have a 70% chance of becoming established if dead coral (cropped algae) is not grazed for 6 months (mostly based on *Dictyota*), and this increases to 100% probability after 12 months of no grazing (mostly based on *Lobophora*). Rates of algal dynamics were acquired from detailed centimetre-resolution observations of algal dynamics with and without grazing (Box 2008). Once established, macroalgae also spread vegetatively over cropped algae (de Ruyter van Steveninck and Breeman 1987).

The modelling of grazing is carried out at two scales. First, the simulation model requires an overall *grazing impact*, which defines the proportion of reef effectively maintained in a cropped algal state during a 6-month iteration of the model. In other words, given the overall balance between algal production and grazing, the grazing impact is the proportion of a reef that is grazed sufficiently intensively that algae are kept in a cropped state rather than developing into a macroalgal canopy within a 6-month period. A '6 monthly' value of grazing impact is needed for model implementation because many of the parameters, such as the vegetative growth of corals and macroalgae, are derived at monthly scales that are many orders of magnitude greater than the instantaneous grazing rate of fishes (seconds). Grazing is spatially constrained (Williams et al. 2001; Mumby 2006; Mumby et al. 2006). An unfished community of parrotfishes grazes a maximum of 40% of the seabed per 6-month time interval. The dynamic basis of this grazing threshold is poorly understood seeing as most measures of grazing take place at scales of seconds and most studies of algal dynamics take place on monthly scales. Nonetheless empirical studies (Mumby 2006), and experimental results scaled to the complex forereef (Williams et al. 2001), have identified a grazing limit of 30–40% of the reef during 6 months. This value allows for a numeric positive response by parrotfish after severe coral mortality events during which colonisation space for algae increases dramatically. For example, an increase in parrotfish biomass over 5 years maintained the cover of cropped algae at Glovers Reef at 30–40% after Hurricane Mitch caused extensive coral mortality and liberated new settlement space for macroalgae (Mumby et al. 2005) (i.e. grazing impact remained at around 30% 6 $month^{-1}$ even though coral cover dropped from around 60–20%, suggesting that the approach is robust during phase changes). The reasons for this are not fully understood. All parrotfish species graze algal turfs and in doing so constrain the colonisation and vegetative growth of macroalgae. Direct removal of macroalgae occurs through the grazing of larger sparisomid species (Mumby 2006).

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

Substratum	Constraints	Range (cm^2)
Brooding coral (e.g. *Porites astreoides*) (BC)	Up to three individuals per cell	$1 \leq \mathrm{BC} \leq 2{,}500$
Spawning coral (e.g. *Siderastrea siderea*) (SC)		$1 \leq \mathrm{SC} \leq 2{,}500$
Cropped algae [filamentous, coralline red algae and short turfs (<5 mm height)], 0–6 months (A_6)		$0 \leq A_6 \leq 2{,}500$
Cropped algae, 6–12 months (A_{12})		$0 \leq A_{12} \leq 2{,}500$
Macroalgae (e.g. *Dictyota pulchella*, *Lobophora variegata*), 0–6 months (M_6)		$0 \leq M_6 \leq 2{,}500$
Macroalgae, 6+ months (M_{12})		$0 \leq M_{12} \leq 2{,}500$
Ungrazeable substratum (e.g. sand), U	Fills entire cell if present	$U = 0$ or $U = 2{,}500$

All substrata represented as area (cm^2)

Minimum values of grazing (5% 6 month^{-1}) were estimated using a second, instantaneous model of grazing behaviour parameterised for the size distribution of parrotfishes from a heavily fished site in Jamaica (Mumby et al. 2006). This second model measures grazing behaviour which is the instantaneous grazing behaviour of a parrotfish species or community measured as a percentage of horizontal reef area grazed per hour and is sensitive to species, length and life phase (Mumby et al. 2006). Grazing affects all algal classes such that macroalgae are converted to the class 'cropped algae' and grazed cropped algae are maintained in the same state. This parameterization is appropriate for reefs in which the dominant macroalgal genus is *Dictyota* and where sparisomids dominate the grazer community, such as in Belize. The most common sparisomids (*Sparisoma viride* and *Sparisoma aurofrenatum*) both feed extensively on this macroalga.

Competitive interactions between corals and macroalgae reduce the growth rate of each taxon. Macroalgae have an ability to overgrow corals but are not a major source of coral mortality in the model (Nugues and Bak 2006). Corals are subjected to size-dependent partial-colony mortality (including parrotfish lesions and minor disease) and whole-colony mortality. Coral recruits experience additional mortality from parrotfish predation (Box and Mumby 2007) but reach an escape in size at 5 cm^2 diameter (Meesters et al. 1997). All simulations assume no stock–recruitment relationship and corals recruit at maximum levels irrespective of stock size (i.e. up to 4 per 0.25 m^2). Previous studies with the model have found it to be insensitive to the type of stock–recruitment relationship used, largely because of high post-settlement mortality (Mumby 2006). Individual cells in the lattice are updated in random sequence. All parameters are fitted from empirical studies (Table 2). Sensitivity analyses reveal that model predictions are robust to stochastic variation in parameter values and able to represent long-term fluctuations in the health of reefs in Jamaica for which data were available (Table 3).

Model experiments

In order to illustrate the key dynamics of corals and macroalgae, a simple simulation was implemented in which coral cover was set initially at 35% (with an equal mix of brooders and spawners) and macroalgal cover at 10%. A total of 36 reefs were created, each having a unique but fixed level of grazing impact ranging from 5% 6 month^{-1} to 40% 6 month^{-1}. Sources of acute disturbance were removed although chronic levels of background partial-colony mortality, whole-colony mortality and algal overgrowth of coral were free to occur. In essence, the simulation represents the natural trajectory of reefs between acute disturbance events, i.e. when free of further acute disturbance does the reef degrade, remain at equilibrium or become healthier?

In order to explore whether the model, which exhibits alternate stable states, can reproduce the observed continuous negative correlation between macroalgal cover and grazer impact (Williams and Polunin 2000), a simple experiment was conducted. Taking the range of coral cover reported by Williams and Polunin (2000) (6–36%), the dynamics of a similar set of reefs, with starting cover ranging from 5% to 35% in 5% increments, were simulated for a full range of fish grazing levels (i.e. 7 levels of initial coral cover × 36 levels of grazing = 252 reefs). After a 10-year period, a reef was selected at random for each level of fish grazing and the corresponding cover of macroalgae determined (e.g. for grazing level 9% 6 month^{-1}, macroalgal cover might have been extracted for the reef initialised with 5% coral cover). This approach avoided introducing a systematic bias between coral cover and grazing impact on macroalgal cover. The approach is also conceptually similar to a field study that randomly (or pseudo-randomly) samples a number of reefs, each on their own trajectories, but within

Table 2 Basic parameterisation of simulation model for mid-shelf reefs without significant sediment input and sparisomid-dominated grazing

Parameter	Details
Coral recruitment	Corals recruit to cropped algae, A_6 and A_{12}, because algal turfs are not heavily sediment-laden. Recruit at size 1 cm^2. Recruitment rate of brooders and spawners (respectively): 2 and 0.2 per 0.25 m^2 of cropped algae per time interval. Recruitment rate was adjusted for rugosity (~2) and the cover of cropped algae at Glovers Reef (Mumby 1999)
Coral growth	Coral size is quantified as the cross-sectional, basal area of a hemispherical colony (cm^2). Brooding corals (BC) have a lateral extension rate of 0.8 cm year^{-1} and spawning corals (SC) grow slightly faster at 0.9 cm year^{-1} (based on median rates for *Porites astreoides*, *Porites porites*, *Siderastrea siderea*, *Montastraea annularis*, *Colpophyllia natans* and *Agaricia agaricites*) (Maguire and Porter 1977; Highsmith et al. 1983; Huston 1985; Chornesky and Peters 1987; Van Moorsel 1988)
Coral reproduction	Excluded, assume constant rate of coral recruitment from outside reef (i.e. no stock-recruitment dynamics)
Colonisation of cropped algae	Cropped algae arises (i) when macroalgae is grazed and (ii) after all coral mortality events (Jompa and McCook 2002a) except those due to macroalgal overgrowth (see coral–algal competition below).
Colonisation of macroalgae	Macroalgae have a 70% chance of becoming established if cropped algae are not grazed for 6 months (mostly *Dictyota*) and this increases to 100% probability after 12 month of no grazing (mostly *Lobophora*). Rates acquired from detailed centimetre-resolution observations of algal dynamics with and without grazing (Box 2008)
Macroalgal growth over dead coral (cropped algae)	In addition to arising from cropped algae that are not grazed (above), established macroalgae also spread vegetatively over cropped algae (mostly *Lobophora* as *Dictyota* spread shows little pattern with grazing (Mumby et al. 2005)). The probability that macroalgae will encroach onto the algal turf within a cell, $P_{A\to M}$, is given by (1) where $M_{4\text{cells}}$ is the percent cover of macroalgae within the von Neumann (4-cell) neighbourhood (de Ruyter van Steveninck and Breeman 1987). This is a key method of algal expansion and represents the opportunistic overgrowth of coral that was extirpated by disturbance. $P_{A\to M} = M_{4\text{cells}}$ (1)
Competition between corals	If corals fill the cell (2,500 cm^2), the larger coral overtops smaller corals (chosen at random if more than one smaller coral share the cell). If corals have equal size, the winner is chosen at random (Lang and Chornesky 1990)
Competition between corals and cropped algae	Corals always overgrow cropped algae (Jompa and McCook 2002a)
Competition between corals and macroalgae 1: effect of macroalgae on corals	(a) Growth rate of juvenile corals (area <60 cm^2) set to zero if $M_{4\text{cells}} > 80\%$ and reduced by 70% if $60\% < M_{4\text{cells}} \leq 80\%$. Parameters based on both *Dictyota* and *Lobophora* (Box and Mumby 2007) (b) Growth rate of juvenile and adult corals (area $\geq$ 60 cm^2) reduced by 50% if $M_{4\text{cells}} < 60\%$ (Tanner 1995; Jompa and McCook 2002a) (c) Limited direct overgrowth of coral by macroalgae can occur (Lirman 2001; Hughes et al. 2007). Nugues and Bak (2006) found that the upper 95% CL of the mean area of overgrowth ranged from 0 to 18 cm^2 pa across a ~7 cm length of coral edge, with an overall mean of 8 cm^2 pa. This translates to 4 cm^2 in each 6-month time step of the model. Overgrowth (cm^2), $O_{C\to M}$, was scaled to entire colonies using (2) where $M_{4\text{cells}}$ is the proportion of macroalgae in the von Neumann 4-cell neighbourhood and P_i is the perimeter of the coral. $O_{C\to M} = M_{4\text{cells}} \times P_i/7 \times 4$ (2) Note that Nugues and Bak (2006) did not find significant effects of *Lobophora* on all coral species studied. Whilst this was the correct interpretation of their data, the published results strongly suggest that an effect does exist and that a larger sample size may well have resulted in significant differences. Other studies have found negative effects of macroalgae on both massive (Lirman 2001) and branching corals (Jompa and McCook 2002b).
Competition between corals and macroalgae 2: effect of corals on macroalgae	The vegetative growth rate of macroalgae, $P_{A\to M}$, is reduced by 25% when at least 50% of the local von Neumann neighbourhood includes coral (de Ruyter van Steveninck et al. 1988; Jompa and McCook 2002a) $\textit{proportion of coral}, C = \frac{(\text{BC}+\text{SC})}{2500}$ (3a) $P_{A\to M} = 0.75 \times M_{4\text{cells}}$ if $C \geq 0.5$ (3b) $P_{A\to M} = M_{4\text{cells}}$ if $C < 0.5$ (3c)

Table 2 continued

Parameter	Details
Grazing by fishes and impact of fishing	An unfished community of parrotfishes grazes a maximum of 40% of the seabed per 6-month time interval. During a given time interval, cells are visited in a random order and all algae consumed until the total grazing impact is reached. All turf and macroalgae are consumed (and converted to A_6) until the constraint is reached. Fishing can reduce the instantaneous grazing intensity of parrotfish communities by at least sixfold (Mumby et al. 2006) to 5% 6 month^{-1}
Partial-colony mortality of corals	Size-dependent, following empirical observations from Curaçao before major bleaching or hurricane disturbances (Meesters et al. 1997). State variables reported in literature converted to dynamic variables using least squares optimisation until equilibrial state in model matched observed data. Implementation uses equations (4a) and (4b) where P_{pm} is the probability of a partial mortality event, A_{pm} is the area of tissue lost in a single event and χ is the size of the coral in cm^2: $P_{\text{pm}} = 1 - [60 + (-12\ \ln(\chi))] \quad (4\text{a})$ $\text{Ln}\left[\left(A_{\text{pm}} \times 100\right) + 1\right] = -0.5 + (1.1\ \ln(\chi)) \quad (4\text{b})$
Whole-colony mortality of juvenile and adult corals	Incidence of mortality in juvenile corals (60–250 cm^2), 2% per time interval (~4% per annum). Halved to 1% (2% pa) for mature colonies (>250 cm^2) (Bythell et al. 1993). These levels of mortality occur in addition to macroalgal overgrowth. Algal overgrowth and predation affects juvenile corals (see above and below).
Predation on coral recruits	Instantaneous whole-colony mortality occurs from parrotfish predation at a rate of 15% each 6-month iteration of the model (Box and Mumby 2007) Predation is confined to small corals of area $\leq 5\ \text{cm}^2$, based on Meesters et al. (1997) where between 60% and 95% of bite-type lesions were of this size
Hurricane impact on juvenile and mature corals (>60 cm^2): whole-colony mortality	Whole-colony mortality of larger corals is represented using a quadratic function (5) where x is the cross-sectional basal area of colony (Bythell et al. 1993; Massel and Done 1993). Small colonies avoid dislodgement due to their low drag, intermediate-sized corals have greater drag and are light enough to be dislodged, whereas large colonies are heavy enough to prevent dislodgement $P_{\text{hur}} = -0.0000003x^2 + 0.0007x + 0.0551 \quad (5)$
Hurricane impact on mature corals (>250 cm^2): partial-colony mortality	The extent of partial mortality, M_{hur}, is modelled using a Gaussian distribution with mean of 0.30 and standard deviation of 0.20. Each value of M_{hur} represents the percentage of original colony tissue that is lost due to the hurricane. If $M_{\text{hur}} \leq 0$, there is no mortality. If $M_{\text{hur}} \geq 1$, the entire colony is lost (though this is a rare event). Data from monitoring of impact of Hurricane Mitch in Belize.
Hurricane impact on juvenile corals (1–60 cm^2)	Scouring by sand during a hurricane may cause 80% whole-colony mortality in juvenile corals (Mumby 1999)
Hurricane impact on macroalgae	Hurricanes reduce the cover of macroalgae to 10% of its pre-hurricane level (Mumby et al. 2005)
Hurricane frequency	Hurricanes were simulated using a binomial model which when implemented in discrete time approximates a poisson random distribution. Maximum long-term incidence of severe hurricanes ~10 years in Florida and 20 years in Mesoamerica (Treml et al. 1997; Gardner et al. 2005)

some initial range of possible starting conditions. The strength and direction of relationship between grazing impact and macroalgal cover were then evaluated using the Pearson Product-Moment correlation coefficient. The entire process was simulated 100 times, and the mean correlations and inter-quartile ranges are comparable to published data from Williams and Polunin (2000). Note that absolute values of macroalgal cover were not compared between model and field data because additional field data would be required to fully parameterize the model for site-specific conditions such as sediment level and the cover of other taxa such as sponges, and such data were not available.

Results and discussion

Alternate stable states and the equilibrial dynamics of corals and macroalgae

Equilibrial dynamics of corals

The first model experiment tracked the trajectories over time of 36 reefs, each initialised with the same coral cover (35%) but at various levels of fish grazing. A striking pattern in reef trajectories developed over time as a function of grazing impact (Fig. 2a, b). Those reefs with

Table 3 Sensitivity of model, defined as difference in threshold grazing at 10% live coral cover between standard parametrisation and that with adjusted parameter

Parameter	Value			Threshold grazing		Abs disparity	
	Min	SD	Max	Min	Max	Min	Max
Basal size at which corals become fully mature (cm^2)	225	250	275	34.5 (0.2)	35.0 (0.3)	0.3	1.2
Growth rate of brooders (cm^2 year^{-1})	0.6	0.8	1.0	42.3 (0.3)	29.1 (0.1)	22.2	15.9
Growth rate of spawners (cm^2 year^{-1})	0.7	0.9	1.1	36.1 (0.1)	33.3 (0.3)	4.3	4.6
Probability of macroalgal colonisation if cropped algae not grazed in 6 month (%)	60	70	80	33.6 (0.2)	35.6 (0.2)	2.9	2.9
Growth rate of coral recruits zero if $M_{4\text{cells}} >$ X(%), where X is…	72	80	88	34.8 (0.2)	34.5 (0.1)	0.6	0.3
Growth rate of coral recruits reduced by X(%) if 60% $< M_{4\text{cells}} \geq$80%, where X is…	63	70	77	34.8 (0.2)	34.6 (0.1)	0.6	0.0
Growth rate of pubescent and adult corals reduced by X%…	45	50	55	34.7 (0.2)	33.9 (0.2)	0.3	2.0
Growth rate of pubescent and adult corals reduced by 50% if $M_{4\text{cells}} <$X%…	35	40	44	34.4 (0.1)	33.3 (0.2)	0.6	3.8
Effect of corals on macroalgal growth rate reduced by X%…	22.5	25	27.5	34.3 (0.2)	34.6 (0.3)	0.9	0.0
Effect of corals on macroalgae reduced by 25% when neighbourhood of coral >X(%)	45	50	55	37.4 (0.1)	37.3 (0.2)	8.0	7.8
Whole-colony mortality of pubescent corals (%year^{-1})	2	4	6	37.2 (0.2)	38.1 (0.2)	7.5	10.1
Whole-colony mortality of mature corals (%year^{-1})	1	2	3	32.3 (0.2)	36.6 (0.2)	6.6	5.7
Predation rate on coral recruits in each 6-month iteration of model (%)	13	15	17	36.4 (0.2)	36.6 (0.2)	5.1	5.8
Rate macroalgae overgrows live coral (cm year^{-1})	6	8	10	30.2 (0.2)	41.3 (0.1)	12.7	19.3
Spatially extensive grazing	0.3			42.7 (0.2)		23.4	

Standard model has a grazing threshold of 34.6% (SE 0.2), implying that 34.6% of the reef must be grazed each 6 month to prevent the reef from falling below the unstable equilibrium. All sensitivity analyses report mean grazing threshold from 10 simulations. Absolute (Abs.) disparity expresses absolute difference in threshold as a percentage of the standard grazing threshold. Results given for both the minimum and maximum values of each parameter simulated except spatially extensive grazing in which the model implementation was varied rather than parameter values

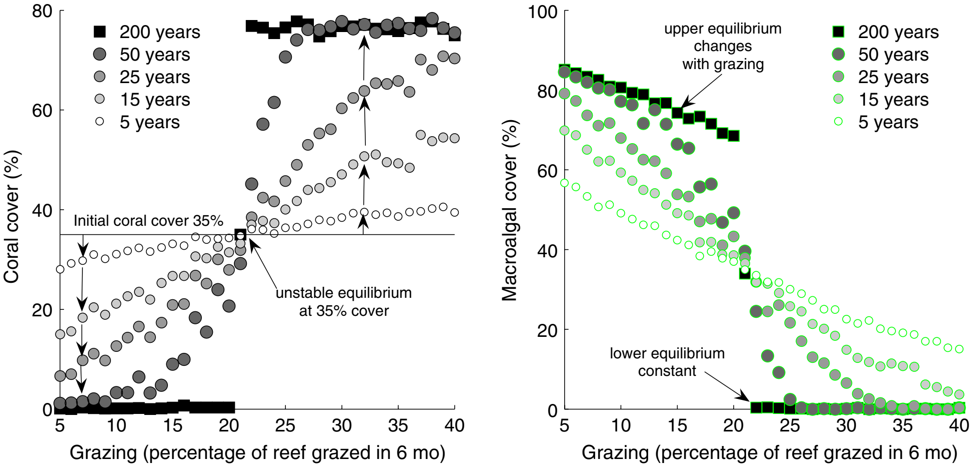

Fig. 2 Temporal trajectories of reefs under chronic disturbance and varying fish grazing starting from an initial coral cover of 35%. Transient cover is represented using circular markers and stable equilibria by squares. Plots shown simultaneously for **a** coral cover and **b** macroalgal cover

grazing of <20% 6 month^{-1} exhibited a gradual decline in coral cover and the rate of decline increased at lower levels of grazing impact (Fig. 2a). A contrasting pattern of coral cover occurred once grazing levels exceeded 20% 6 month^{-1}. Here, coral cover increased and did so at an increasingly faster rate as grazing levels rose (Fig. 2a). Thus, reefs with higher grazing exhibited recovery (coral colonisation and growth outweighing mortality), whereas reefs at lower grazing exhibited degradation (mortality outweighing processes of colonisation and growth). The reef at the fulcrum or threshold level of grazing (around 20% 6 month^{-1}) remained at the initial coral cover of 35% and was therefore at equilibrium. Viewing these dynamics allows some terminology to be assigned. Transient dynamics are those that occur as the reef moves towards a stable equilibrium (transients are shown in circles and equilibrial dynamics as squares in Fig. 2). The equilibrium at 35% coral cover and grazing of 20% 6 month^{-1} is considered to be *unstable* because reefs slightly to either side of this point are attracted towards either high or low coral cover. Indeed, most reefs eventually reach one of two possible *stable* equilibria in the absence of acute

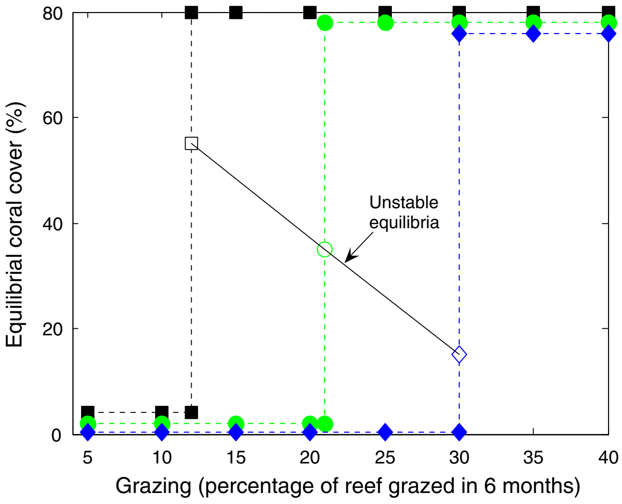

Fig. 3 Identification of system equilibria for three levels of starting coral cover; 55% (*black squares*), 35% (*green circles*) and 15% (*blue diamonds*). Stable equilibria are denoted using solid markers and unstable equlibria using open markers. Unstable equilibria lie between two alternate stable states. In order to aid inspection of the graph, the stable equilibria for each initial coral cover have been offset artificially above one another, whereas in reality all stable equilibria fall at the level indicated for 15% cover

disturbance; a high coral cover state or a coral-depauperate state.

The example given here identified an unstable equilibrium (threshold) occurring at a coral cover of 35% and a grazing level of 20% 6 month^{-1}. In order to locate other thresholds, the simulation model was run for 200 years for every combination of coral cover and grazing. For many levels of grazing, three equilibria emerged; a stable coral-depauperate state, an unstable equilibrium at intermediate coral cover and a stable coral-rich state (shown in detail in Fig. 3 which identifies two additional unstable equilibria to that identified in Fig. 2). Unstable equilibria were identified where coral cover remained within two percentage units of the initial value during the 200-year simulation (Fig. 3), thereby discriminating unstable equilibria from non-equilibrium points nearby. For the range of grazing associated with herbivorous fish on exposed forereefs (i.e. 5–40% 6 month^{-1}), unstable equilibria fell along a diagonal line from an upper left bifurcation (>70% coral cover and grazing 5% 6 month^{-1}) to a bottom right bifurcation, located at low coral cover (<5%) and a relatively high grazing level of 30% 6 month^{-1} (all equilibria shown in Fig. 4a). The two bifurcations delimit a zone of system instability, termed the 'bifurcation fold', such that corals can either exhibit recovery trajectories, remain constant, or exhibit decline; the outcome depends on whether the reef sits above, on, or below the threshold, respectively. Thus, a single level of grazing (e.g. 15% 6 month^{-1}) can be associated with either reef recovery, stasis, or decline, the direction being determined by coral cover (Fig. 4a). Such bistability, or the existence of two possible community states from a single level of a process (grazing) is the very essence of alternate states (Petraitis and Dudgeon 2004). Such systems exhibit hysteresis; the level of grazing needed to maintain the coral-dominated system differs dramatically from that needed to return to coral dominance once the system has flipped. In order to view this graphically (Fig. 4a), consider a reef at 70% coral cover and grazing impact of 10% 6 month^{-1}. The reef lies above the threshold unstable equilibrium and is stable. Now imagine that a mass coral bleaching event causes a sudden reduction in coral cover to a level below the threshold, such as 20%. The reef will now begin to shift towards a coral-depauperate state unless grazing levels can be elevated from 10% 6 month^{-1} to approximately 30% 6 month^{-1} to cross the threshold. Thus, a very different level of grazing is needed to reverse the loss of coral.

In short, the model implies that two stable alternate states of the system exist if grazing levels lie between 5% 6 month^{-1} and 30% 6 month^{-1} (Mumby et al. 2007a).

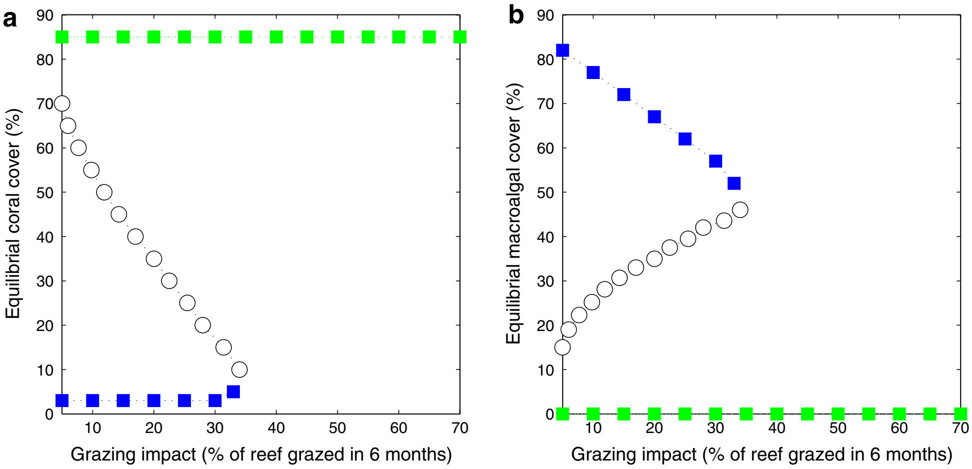

Fig. 4 Positions of stable (*solid squares*) and unstable (*open circles*) equilibria for *Montastraea* reefs at 7–15 m depth with high productivity and little sediment input. Equilibria determined after 200-year simulations and shown simultaneously for corals (**a**) and macroalgae (**b**). Colour coding of stable equilibria denotes the corresponding states of coral and macroalgae

Once grazing exceeds the upper bifurcation (30% 6 month^{-1}), the system has only one stable equilibrium at high coral cover. It should, of course, be borne in mind that acute disturbances will prevent many reefs ever reaching that equilibrium, but the trend would tend to be one of recovery between successive disturbances.

A key point evident from Fig. 4a is that the locations of unstable equilibria covary with coral cover and grazer impact. This is because macroalgal cover is driven by grazing intensity, and grazing intensity depends on both the community composition of herbivorous fish (what is termed grazing impact in the model) and the area of available substrate. Thus, as the cover of corals or other ungrazable substrata increase, grazing intensity will tend to intensify and constrain macroalgal cover even if the number of herbivores remains unchanged (Williams et al. 2001). It is for this reason that unstable equilibria covary with coral cover and grazing impact (Fig. 4); coral cover and grazer biomass interact to determine grazing intensity, macroalgal cover and coral recruitment.

Unstable equilibria form threshold states of the system around which the trajectory can be one of recovery or decline. It is important to bear in mind that grazing is plotted on the *x*-axis for convenience and that the impact of many other ecosystem processes, such as nutrification, is to alter the shape of the bifurcation fold and the positions of thresholds. For example, if algal growth rates were elevated by nutrient flux, threshold values would tend to move towards the upper right end of the plot (see sensitivity analysis, Table 3).

Equilibrial dynamics of macroalgae

The trajectories of macroalgae during the first simulation experiment largely mirrored those of corals, albeit moving in the opposite direction (Fig. 2b). Once again, an unstable equilibrium occurred associated with a coral cover of 35% and grazing impact of 20% 6 month^{-1}. However, the equilibria of macroalgae differed to corals in one important respect. For the ‘macroalgal-dominated’ or ‘coral-depauperate’ equilibrium, macroalgal cover varied linearly with grazing, whereas coral cover did not (Fig. 4b). For example, whenever a reef started out below the unstable equilibrium, the final equilibrial coral cover was vanishingly low irrespective of grazing level. However, unlike corals, the equilibrial macroalgal cover began to change linearly as grazing increased and eventually crossed a threshold beyond which it became excluded by corals (Fig. 2b). Thus, the key difference between the stable equilibria of corals and macroalgae is that the coral-depauperate state is insensitive to changes in grazing (at least until a threshold is crossed), whereas the macroalgal-dominated state changes linearly with grazing until a threshold is crossed. The reason for the difference is that there is insufficient coral in the coral-depauperate state to limit macroalgae. In this case, the cover of macroalgae is set by the balance of grazing and algal production (i.e. what is termed grazing impact in the model).

Transient dynamics of corals and macroalgae

In order to complete the description of equilibrial dynamics of corals and macroalgae, it is important to distinguish the rates of transient and equilibrial dynamics between taxa. Coral generation times typically involve decadal to century time scales (Hudson 1981) and therefore increases in coral cover occur slowly (Fig. 1a). Unlike corals, macroalgal dynamics occur on two inherent time scales. Macroalgae themselves exhibit fast transient dynamics with generation times on a scale of weeks to months (de Ruyter van Steveninck and Breeman 1987). Such fast dynamics allow macroalgae to equilibrate rapidly (on the order of months) to the present coral cover and grazing regime (Williams et al. 2001). However, a second, slow dynamic tracks the availability of settlement substratum and follows changes in coral cover. The equilibria plotted for corals and macroalgae in Fig. 4 reflect the long-term equilibria of the system, determined at the slow time scale over which corals reach equilibria.

Reconciling alternative stable states with a linear empirical relationship between grazing and macroalgal cover

Low coral cover is the key to reconciling model predictions of alternative stable states with linear empirical relationships between grazing and macroalgal cover. Given the recent history of intense disturbance in the Caribbean, the coral cover on many reefs today is low and typically <20% (Kramer 2003). If herbivorous fish can only graze approximately 40% of the reef (Williams and Polunin 2000; Mumby 2006) then settlement substratum is rarely going to be a limiting resource for macroalgae and the fast dynamics of algae enable them to equilibrate rapidly to the available settlement substratum and grazing regime, allowing negative correlations to emerge between grazing and macroalgal cover.

A model experiment simulated the transient dynamics of coral and macroalgal cover for low initial coral covers (5–35%) and a variety of fish grazing levels (Fig. 5). Random resampling of reefs for each level of grazing (see, for example, Fig. 6) led to a mean negative correlation between macroalgal cover and grazing of -0.74 ($P < 0.001$) which compares favourably to the value of -0.82 found by Williams and Polunin (2000). Moreover, the mean inter-quartile range of macroalgal cover from

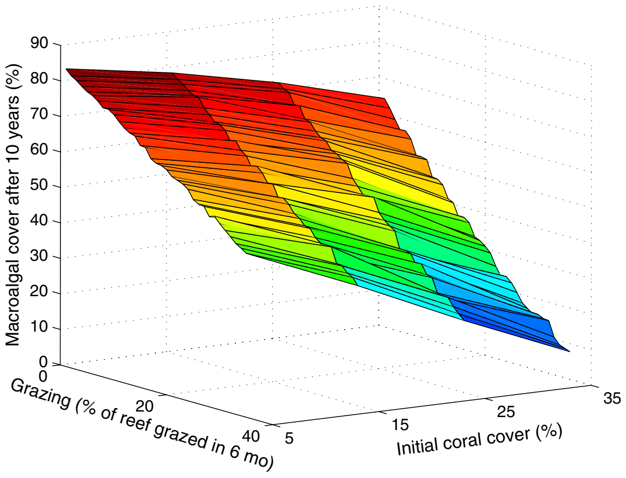

Fig. 5 Model-derived transient macroalgal cover after 10 years of simulations as a function of grazing and initial coral cover

samples of 36 reefs (result = 25% cover) matched the variation reported by Williams and Polunin (2000). In short, a model coral ecosystem that displays alternate stable states was able to reproduce the continuous negative relationships between macroalgal cover and grazing found in the field. Such empirical relationships are therefore consistent with the existence of multiple stable states on Caribbean reefs.

The model predicts that macroalgal cover can vary considerably within a coral-depauperate state. This is an important outcome because ‘coral-depauperate’ reefs do not necessarily have to be totally dominated by macroalgae, nor are they totally devoid of coral. The key feature of a stable coral-depauperate reef state is that coral recruitment rates are not high enough to maintain the population (Fig. 1). However, juvenile corals do exist in this coral-depauperate state and their density increases with grazing (Fig. 7), which also explains the positive relationship between the rate of increase of transient coral cover and grazing observed in Fig. 2a. Indeed, the model prediction of a positive correlation between grazing impact and recruitment density (Fig. 7) is borne out empirically by a study of coral recruitment along a gradient of parrotfish grazing (Mumby et al. 2007b).

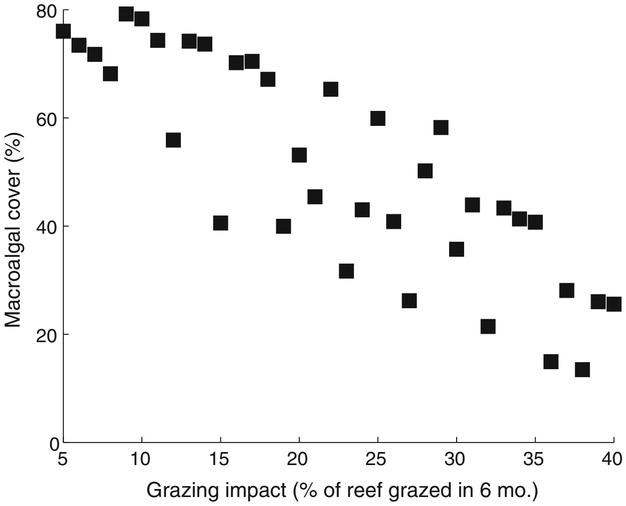

Fig. 6 Example of relationship between grazing and macroalgal cover for reefs under nonequilibrial conditions (i.e. after just 10 years of simulations with initial coral cover = C, where $5\% \leq C \geq 35\%$). For each level of grazing impact a reef was chosen at random to plot macroalgal cover

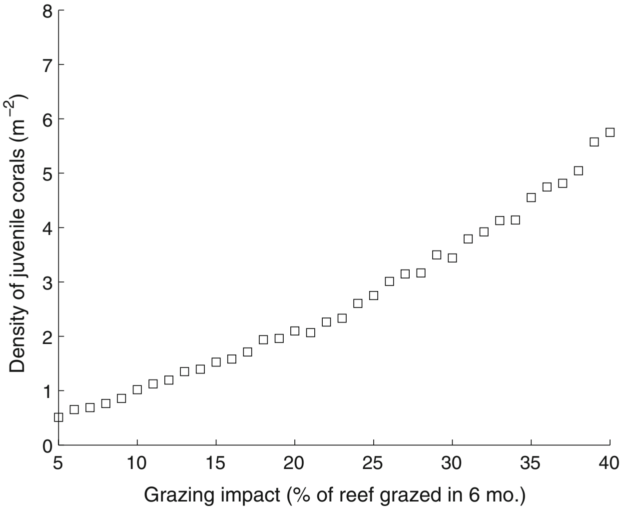

Fig. 7 Relationship between fish grazing impact and the density of juvenile corals (colony area <60 cm^2) under nonequilibrial time scales of 10 years and at 5% initial coral cover

Empirical surveys of macroalgal cover may discover even lower levels of cover than those found by the model for a variety of reasons. These include very recent physical disturbance, seasonal reductions in macroalgal cover (Hoyt 1927), high cover of substrates that are not grazed (e.g. sponges), which serve to intensify grazing in the same manner as live coral, and the occurrence of mobile sediment that can prevent the colonisation of both corals and algae. The latter process may be particularly important in hardbottom habitats where both coral and macroalgal cover are low; arguably, such areas are not reefs at all.

Given the variability in macroalgal cover that can occur during a coral-depauperate stable state, it would perhaps avoid confusion in future if the scientific community adopted the term ‘coral-depauperate state’ rather than ‘macroalgal-dominated state’.

Reconciling phase shift reversal after *Diadema* recovery with alternate stable states

The coral bifurcation plot (Fig. 4a) must be revisited to answer the question raised by Petraitis and Dudgeon (2004) that recovery of *Diadema* could, in principle, indicate a simple phase–shift relationship with grazing rather than one that involves alternate stable states. The plot implies that increases in grazing within the bifurcation fold will not necessarily reverse the coral–algal phase shift. For example, increases in grazing from 5% 6 month^{-1} to 20% 6 month^{-1} on a reef with only 10% coral cover will lead to a modest reduction in algal cover but not enable a recovery of the coral population because the reef would remain below the unstable equilibrium. However, if grazing increased beyond the bifurcation fold (i.e. to at least 35% 6 month^{-1}) algal cover would be sufficiently reduced that coral recruitment would attain levels necessary to allow a gradual increase in coral cover and eventually reverse the phase shift. The issue, therefore, is how the change in grazing relates to the position of critical thresholds. In a recent article, a modest recovery of *Diadema* in a system lacking many herbivorous fish was posited to shift grazing levels to at least 45% 6 month^{-1} and therefore enables corals to recover (Mumby et al. 2007a). Thus, a recovery of coral after a return of *Diadema* is fully consistent with the existence of alternate stable states: urchin recovery increases grazing so dramatically that the system moves beyond the zone of bistability.

Implications for reef studies

A mechanistic model of Caribbean reef dynamics that exhibits bistability has been found to be consistent with field observations of coral cover, macroalgal cover, grazing and patterns of coral recruitment: the low cover of coral on many Caribbean reefs allows simple linear relationships to emerge between these variables over short, transient time scales. Predictions of the ecological model are also consistent with observed reef state in those relatively rare situations in which coral cover and fish grazing are presently high, such as in Bonaire: the model predicts that macroalgae will be virtually excluded under these conditions (Fig. 4a), which is borne out by field observations from shallow (<20 m) parts of these reefs (Bruggemann et al. 1994; Bruckner and Bruckner 2003).

While use of a mechanistic model does not prove that Caribbean reefs can exhibit bistability under certain levels of fish grazing, there is as yet no field study that has rigorously tested the existence of multiple stable states on a coral reef. Perhaps the best hopes for testing the existence of bistability include improving mechanistic models, finding direct evidence of positive and negative feedbacks and interference competition (Grimm and Wissel 1997) and the use of field monitoring to identify the location of critical thresholds.

Finding field evidence for the existence of critical thresholds will be difficult for a number of reasons. Chief amongst these is that the underlying chronic dynamics of reefs—and therefore the location of the bifurcation fold and thresholds—will vary from one physical environment to another. For example, changes in algal productivity and sediment scour will strongly influence the location of thresholds yet such information is rarely quantified during monitoring or census projects. Moreover, many monitoring and census projects focus on measuring state variables (e.g. coral cover) yet data are also needed on rates of processes (e.g. grazing, productivity). Having said that, large repositories of monitoring data may prove to be invaluable in identifying thresholds, once the process variables have been quantified and categorised among sites. This is because reef *trajectories* differ either side of a threshold and it is these trajectories that must be observed. This can only be done through careful monitoring with high statistical power. Sites exhibiting positive trajectories of coral cover have physical and biological properties that place them above a threshold, whereas reefs exhibiting continued decline in the absence of acute disturbance (including disease outbreaks) lie below a threshold.

The importance of statistical power can be appreciated by considering the rates at which reefs might recover. In an average project lifetime of 5 years, changes in coral cover from a coral-depleted reef would be small, even if grazing levels were manipulated massively through use of a reserve or after urchin recovery (Fig. 8). In the example presented for a reef starting at 15% coral cover (Fig. 8), the maximum change in coral cover expected under chronic disturbance would be <6%, some seven times less than the change that could occur in macroalgae (though the rate of change in coral cover in situ will also be affected by local recruitment rates and the size distributions of corals).

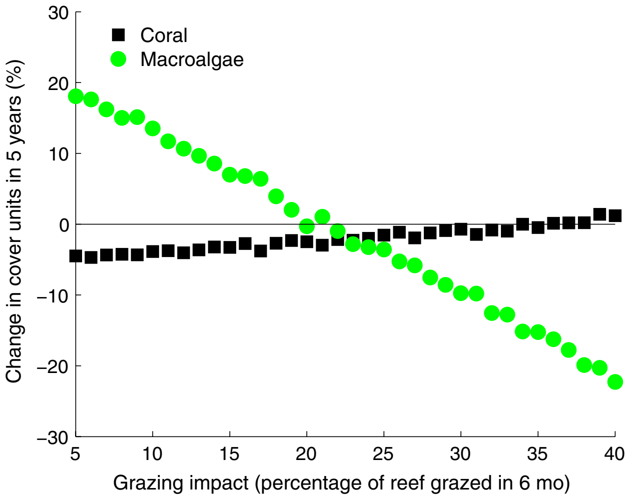

Fig. 8 Effect of grazing on the relative rate of change in the cover of corals versus macroalgae during a management time frame of 5 years. Coral cover started at 15% in all scenarios and either exhibited chronic decline, stasis or limited recovery

Given the slow pace of recovery of many Caribbean reefs (Connell 1997), the variable nature of macroalgal cover at a coral-depauperate state, and the variety of disturbance trajectories on which reefs lie which reinforce non-equilibrial dynamics, it should also be borne in mind that meta-analyses of coral cover are unlikely to provide definitive evidence for or against alternate stable states because reefs do not necessarily cluster into coral-rich and coral-depauperate states on transient time scales (cf. Bruno et al. 2009).

Understanding the mechanisms of hysteresis and locations of bifurcation folds will provide improved guidance for reef management (Nystrom et al. 2008). The existence of stable states means that reefs become more difficult to restore as their health deteriorates (Mumby et al. 2007a) and modest changes to the system, such as minor increases in grazing or reductions to nutrient flux, might not necessarily precipitate the expected benefits to coral populations. A better understanding of thresholds will enable us to assess the cost-effectiveness of potential management interventions and identify those interventions that offer the greatest shift to or from a threshold for a given cost.

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References

Aronson RB, Precht WF (2001) White-band disease and the changing face of Caribbean coral reefs. Hydrobiologia 460:25–38

Aronson RB, Precht WF (2006) Conservation, precaution and Caribbean reefs. Coral Reefs 25:441–450

Bellwood DR, Hughes TP, Folke C, Nystrom M (2004) Confronting the coral reef crisis. Nature 429:827–833

Box SJ (2008) The dynamics of macroalgae on a Caribbean coral reef: modelling the availability of settlement space and dominant algae and evaluation the effect of macroalgal competition on the growth and survival of juvenile corals. PhD Thesis, University of Exeter, p 146

Box SJ, Mumby PJ (2007) The effect of macroalgal competition on the growth and survival of juvenile Caribbean corals. Mar Ecol Prog Ser 342:139–149

Bruckner AW, Bruckner RJ (2003) Condition of coral reefs off less developed coastlines of Curaçao (Part 1: Stony corals and algae). Atoll Res Bull 496:370–394

Bruggemann JH, van Oppen MJH, Breeman AM (1994) Foraging by the stoplight parrotfish *Sparisoma viride*. I. Food selection in different socially determined habitats. Mar Ecol Prog Ser 106:41–55

Bruno JF, Sweatman H, Precht WF, Selig ER, Schutte VGW (2009) Assessing evidence of phase shifts from coral to macroalgal dominance on coral reefs. Ecology (in press)

Burkepile DE, Hay ME (2006) Herbivore vs. nutrient control of marine primary producers: context-dependent effects. Ecology 87:3128–3139

Bythell J, Sheppard C (1993) Mass mortality of Caribbean shallow corals. Mar Pollut Bull 26:296–297

Bythell JC, Gladfelter EH, Bythell M (1993) Chronic and catastrophic natural mortality of three common Caribbean reef corals. Coral Reefs 12:143–152

Chornesky EA, Peters EC (1987) Sexual reproduction and colony growth in the scleractinian coral *Porites astreoides*. Biol Bull 172:161–177

Connell JH (1997) Disturbance and recovery of coral assemblages. Coral Reefs 16:S101–S113

Cote IM, Gill JA, Gardner TA, Watkinson AR (2005) Measuring coral reef decline through meta-analyses. Phil Trans Royal Soc B Biol Sci 360:385–395

de Ruyter van Steveninck ED, Breeman AM (1987) Deep water populations of *Lobophora variegata* (Phaeophyceae) on the coral reef of Curaçao: influence of grazing and dispersal on distribution patterns. Mar Ecol Prog Ser 38:241–250

de Ruyter van Steveninck ED, Van Mulekom LL, Breeman AM (1988) Growth inhibition of *Lobophora variegata* (Lamouroux Womersley) by scleractinian corals. J Exp Mar Biol Ecol 115:169–178

Done TJ (1992) Phase-shifts in coral reef communities and their ecological significance. Hydrobiologia 247:121–132

Edmunds PJ, Carpenter RC (2001) Recovery of *Diadema antillarum* reduces macroalgal cover and increases abundance of juvenile corals on a Caribbean reef. Proc Natl Acad Sci USA 98:5067–5071

Gardner TA, Côté IM, Gill JA, Grant A, Watkinson AR (2005) Hurricanes and Caribbean coral reefs: Impacts, recovery patterns, and role in long-term decline. Ecology 86:174–184

Grimm V, Wissel C (1997) Babel, or the ecological stability discussions: an inventory and analysis of terminology and a guide for avoiding confusion. Oecologia 109:323–334

Hatcher BG (1984) A maritime accident provides evidence for alternate stable states in benthic communities on coral reefs. Coral Reefs 3:199–204

Highsmith RC, Lueptow RL, Schonberg SC (1983) Growth and bioerosion of three massive corals on the Belize barrier reef. Mar Ecol Prog Ser 13:261–271

Holling CS (1973) Resilience and stability of ecological systems. Annu Rev Ecol Syst 4:1–23

Hoyt WD (1927) The periodic fruiting of *Dictyota* and its relation to the environment. Am J Bot 14:592–619

Hudson JH (1981) Growth rates in *Montastraea annularis*: a record of environmental change in Key Largo Coral Reef Marine Sanctuary, Florida. Bull Mar Sci 31:444–459

Hughes TP (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. Science 265:1547–1551

Hughes TP, Rodrigues MJ, Bellwood DR, Ceccarelli D, Hoegh-Guldberg O, McCook L, Moltschaniwskyj N, Pratchett MS, Steneck RS, Willis BL (2007) Phase shifts, herbivory, and the resilience of coral reefs to climate change. Curr Biol 17:1–6

Huston M (1985) Variation in coral growth rates with depth at Discovery Bay, Jamaica. Coral Reefs 4:19–25

Idjadi JA, Lee SC, Bruno JF, Precht WF, Allen-Requa L, Edmunds PJ (2006) Rapid phase-shift reversal on a Jamaican coral reef. Coral Reefs 25:209–211

Jompa J, McCook LJ (2002a) Effects of competition and herbivory on interactions between a hard coral and a brown alga. J Exp Mar Biol Ecol 271:25–39

Jompa J, McCook LJ (2002b) The effects of nutrients and herbivory on competition between a hard coral (*Porites cylindrica*) and a brown alga (*Lobophora variegata*). Limnol Oceanogr 47:527–534

Knowlton N (1992) Thresholds and multiple stable states in coral reef community dynamics. Am Zool 32:674–682

Kramer PA (2003) Synthesis of coral reef health indicators for the western Atlantic: results of the AGRRA program (1997–2000). Atoll Res Bull 496:1–58

Kramer PA, Kramer PR, Ginsburg RN (2003) Assessment of the andros island reef system, bahamas (Part 1: Stony corals and algae). Atoll Res Bull 496:77–100

Lang JC, Chornesky EA (1990) Competition between scleractinian reef corals: a review of mechanisms and effects. In: Dubinsky Z (ed) Ecosystems of the world 25: coral reefs. Elsevier, Amsterdam, pp 209–252

Lessios HA, Robertson DR, Cubit JD (1984) Spread of *Diadema* mass mortality through the Caribbean. Science 226:335–337

Lewis SM (1986) The role of herbivorous fishes in the organization of a Caribbean reef community. Ecol Monogr 56:183–200

Lirman D (2001) Competition between macroalgae and corals: effects of herbivore exclusion and increased algal biomass on coral survivorship and growth. Coral Reefs 19:392–399

Littler MM, Littler DS, Lapointe BE (1993) Modification of tropical reef community structure due to cultural eutrophication: the southwest coast of Martinique. Proc 7th Int Coral Reef Symp 1: 335–343

Littler MM, Littler DS, Brooks BL (2006) Harmful algae on tropical coral reefs: bottom-up eutrophication and top-down herbivory. Harmful Algae 5:565–585

Maguire LA, Porter JW (1977) A spatial model of growth and competition strategies in coral communities. Ecol Model 3:249–271

Massel SR, Done TJ (1993) Effects of cyclone waves on massive coral assemblages on the Great Barrier Reef: meteorology, hydrodynamics and demography. Coral Reefs 12:153–166

McManus JW, Polsenberg JF (2004) Coral–algal phase shifts on coral reefs: ecological and environmental aspects. Prog Oceanogr 60:263–279

Meesters EH, Wesseling I, Bak RPM (1997) Coral colony tissue damage in six species of reef-building corals: partial mortality in relation with depth and surface area. J Sea Res 37:131–144

Mumby PJ (1999) Bleaching and hurricane disturbances to populations of coral recruits in Belize. Mar Ecol Prog Ser 190:27–35

Mumby PJ (2006) The impact of exploiting grazers (Scaridae) on the dynamics of Caribbean coral reefs. Ecol Appl 16:747–769

Mumby PJ, Steneck RS (2008) Coral reef management and conservation in light of rapidly-evolving ecological paradigms. Trends Ecol Evol 23:555–563

Mumby PJ, Foster NL, Glynn Fahy EA (2005) Patch dynamics of coral reef macroalgae under chronic and acute disturbance. Coral Reefs 24:681–692

Mumby PJ, Dahlgren CP, Harborne AR, Kappel CV, Micheli F, Brumbaugh DR, Holmes KE, Mendes JM, Box S, Broad K, Sanchirico JN, Buch K, Stoffle RW, Gill AB (2006) Fishing, trophic cascades, and the process of grazing on coral reefs. Science 311:98–101

Mumby PJ, Hastings A, Edwards HJ (2007a) Thresholds and the resilience of Caribbean coral reefs. Nature 450:98–101

Mumby PJ, Harborne AR, Williams J, Kappel CV, Brumbaugh DR, Micheli F, Holmes KE, Dahlgren CP, Paris CB, Blackwell PG (2007b) Trophic cascade facilitates coral recruitment in a marine reserve. Proc Natl Acad Sci USA 104:8362–8367

Mumby PJ, Broad K, Brumbaugh DR, Dahlgren CP, Harborne AR, Hastings A, Holmes KE, Kappel CV, Micheli F, Sanchirico JN (2008) Coral reef habitats as surrogates of species, ecological functions, and ecosystem services. Conserv Biol 22:941–951

Newman MJH, Paredes GA, Sala E, Jackson JBC (2006) Structure of Caribbean coral reef communities across a large gradient of fish biomass. Ecol Lett 9:1216–1227

Nugues MM, Bak RPM (2006) Differential competitive abilities between Caribbean coral species and a brown alga: a year of experiments and a long-term perspective. Mar Ecol Prog Ser 315:75–86

Nystrom M, Graham NAJ, Lokrantz J, Norstrom A (2008) Capturing the cornerstones of coral reef resilience: linking theory to practice. Coral Reefs 27:795–809

Petraitis PS, Dudgeon SR (2004) Detection of alternative stable states in marine communities. J Exp Mar Biol Ecol 300:343–371

Scheffer M, Carpenter SR (2003) Catastrophic regime shifts in ecosystems: linking theory to observation. Trends Ecol Evol 18:648–656

Tanner JE (1995) Competition between scleractinian corals and macroalgae: an experimental investigation of coral growth, survival and reproduction. J Exp Mar Biol Ecol 190:151–168

Treml E, Colgan M, Keevican M (1997) Hurricane disturbance and coral reef development: a geographic information system (GIS) analysis of 501 years of hurricane data from the Lesser Antilles. Proc 8th Int Coral Reef Symp 1: 51–546

Van Moorsel GWNM (1988) Early maximum growth of stony corals (Scleractinia) after settlement on artificial substrata on a Caribbean reef. Mar Ecol Prog Ser 50:127–135

Williams ID, Polunin NVC (2000) Large-scale associations between macroalgal cover and grazer biomass on mid-depth reefs in the Caribbean. Coral Reefs 19:358–366

Williams ID, Polunin NVC, Hendrick VJ (2001) Limits to grazing by herbivorous fishes and the impact of low coral cover on macroalgal abundance on a coral reef in Belize. Mar Ecol Prog Ser 222:187–196