

Spatial dynamics of benthic competition on coral reefs

Stuart A. Sandin · Dylan E. McNamara

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Abstract The community structure of sedentary organisms is largely controlled by the outcome of direct competition for space. Understanding factors defining competitive outcomes among neighbors is thus critical for predicting large-scale changes, such as transitions to alternate states within coral reefs. Using a spatially explicit model, we explored the importance of variation in two spatial properties in benthic dynamics on coral reefs: (1) patterns of herbivory are spatially distinct between fishes and sea urchins and (2) there is wide variation in the areal extent into which different coral species can expand. We reveal that the size-specific, competitive asymmetry of corals versus fleshy algae highlights the significance of spatial patterning of herbivory and of coral growth. Spatial dynamics that alter the demographic importance of coral recruitment and maturation have profound effects on the emergent structure of the reef benthic community. Spatially constrained herbivory (as by sea urchins) is more effective than spatially unconstrained herbivory (as by many fish) at opening space for the time needed for corals to settle and to

recruit to the adult population. Further, spatially unconstrained coral growth (as by many branching coral species) reduces the number of recruitment events needed to fill a habitat with coral relative to more spatially constrained growth (as by many massive species). Our model predicts that widespread mortality of branching corals (e.g., *Acropora* spp) and herbivorous sea urchins (particularly *Diadema antillarum*) in the Caribbean has greatly reduced the potential for restoration across the region.

Keywords Competition–colonization · Spatial constraints · Herbivory · Size-specificity · Cellular automata

Introduction

Many examples reveal that dramatically different community states can be observed within the same ecosystem (May 1977). East African landscapes can shift from grasslands to *Acacia* forests when ungulate populations are reduced by disease (Prins and van der Jeugd 1993), lakes can range from clear to turbid based on nutrient conditions, food web structure, and history (Scheffer et al. 1993), and Aleutian nearshore communities have existed as either kelp forests or sea urchin barrens, driven largely by the local density of invertivorous sea otters (Simenstad et al. 1978). In many cases, such alternate states are believed to be self-reinforcing, at least at time scales of typical ecological study or management action. Through removal of particular species or additions of others, ecological feedbacks may be changed fundamentally, resulting in the ecosystem transitioning to an alternate state.

The benthic community of coral reefs provides a well-documented case study of an ecosystem that can exist in

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S. A. Sandin (✉)
Center for Marine Biodiversity and Conservation,
Scripps Institution of Oceanography, 9500 Gilman Drive,
La Jolla, CA 92093-0202, USA
e-mail: ssandin@ucsd.edu

D. E. McNamara
Department of Physics and Physical Oceanography/Center
for Marine Science, University of North Carolina, Wilmington,
601 South College Road, Wilmington, NC 28403, USA
e-mail: mcnamarad@uncw.edu

alternate states—one that is dominated by reef-building corals and coralline algae, and another that is dominated by fleshy algae (including both large, erect seaweeds and smaller turf algal assemblages) (Knowlton 1992). The removal of herbivorous fish and sea urchins can favor the uncontrolled growth of fleshy algae (Bellwood et al. 2004; Hughes et al. 1987), and population booms of coral-consuming echinoderms (due in some cases to release from predation) can lead to declines of reef-builders (Dulvy et al. 2004; McClanahan and Shafir 1990). As such, large-scale changes in the structure of the consumer guilds can be linked to self-reinforcing transitions from a system dominated by stony corals to one dominated by fleshy algae (Mumby et al. 2007).

While we are gaining an increasingly precise understanding of the mechanisms that lead to the degradation of coral reefs (i.e., from coral- to fleshy algal-dominance), we know much less about the conditions that are sufficient for recovery (i.e., return to coral-dominance) (Done 1992). In many cases, the recovery of coral populations is inhibited by the competitive exclusion of corals by more rapidly growing fleshy algae (Hughes et al. 2010). A popular hypothesis suggests that reductions of herbivore densities (e.g., due to fisheries removals and/or epizootics) effectively releases fleshy algae from top-down control, enabling persistent exclusion of corals. Following this hypothesis, we may predict that if herbivore densities are increased, the competitive dynamic would shift in favor of corals, in some cases leading to recovery of coral populations. However, conflicting evidence exists linking the restoration of herbivore densities to regrowth of corals.

Consider first the role of herbivorous fish in affecting the growth and recovery of stony corals. Syntheses of data from across regions show weak linkages between fisheries management and coral cover. Correlational studies have found no clear evidence linking patterns in coral cover to herbivore biomass (Newman et al. 2006) or to level of local management (Graham et al. 2011). In general, management of fishes appears only to slow the decline of coral cover, as evidenced by comparing trends within and outside of marine protected areas (Selig and Bruno 2010). The most optimistic evidence linking regrowth of herbivorous fish biomass with coral recovery notes an approximate 0.5% annual increase in coral cover for 3 years within a marine park (Mumby and Harborne 2010). While the enhancement of fish populations, including herbivorous fish, within marine protected areas may limit losses of coral, there is little evidence linking these fish with rapid rates of coral recovery.

Patterns of benthic change differ, however, when considering the role of herbivorous sea urchins. In the Caribbean, *Diadema antillarum* is the historically most dominant herbivorous sea urchin, and basin-wide declines in its population have been linked with rapid increases in fleshy

algal cover (Hughes et al. 1987). Recent evidence reveals a complementary pattern of rapid fleshy algal reductions in response to increases of herbivorous sea urchin densities. Reductions of algal cover in these spatially restricted ‘urchin zones’ is linked with relatively higher densities of coral recruits (Carpenter and Edmunds 2006; Edmunds and Carpenter 2001), higher coral growth rates (Idjadi et al. 2010), and increased coral cover (Myhre and Acevedo-Gutiérrez 2007). These observations suggest a distinction between the effects of herbivory by fishes versus by sea urchins, with the latter showing a more consistent alteration of benthic competition between fleshy algae and corals.

Importantly, the spatial patterning of resource use is distinct between herbivorous fish and sea urchins, with fish more wide-ranging and sea urchins more spatially constrained. As vagile consumers, herbivorous reef fish common to the Caribbean can explore relatively large home ranges (75–300 m²) in search of preferred diet items (Mumby and Wabnitz 2002; Semmens et al. 2005). Fish are selective within these areas, targeting diet items based on algal taxonomy (Burkpile and Hay 2008) and even nutrient content among individuals of a single algal species (Boyer et al. 2004). Home ranges of herbivorous fish, however, tend to increase with decreasing fish density (Mumby and Wabnitz 2002; van Rooij et al. 1996), suggesting intra-guild resource partitioning and relatively evenly spaced herbivory across large spatial scales (10s–100s of m²). In contrast, sea urchins are much more constrained in their movements; individual black-spined sea urchins in the Caribbean (*Diadema antillarum*) typically forage within an area of just 1 m² (Carpenter 1984). Thus, when sea urchins are at low densities, they create a mosaic of intensely grazed and essentially ungrazed areas, driven primarily by the distribution of individuals rather than by the distribution of algal resources. These observations, combined with evidence of taxon-specific responses to herbivore restoration, suggest that a more focused consideration of spatial dynamics may be critical to better understand transitions between alternate states in coral reef systems.

It is well known that spatial dynamics critically affect the population dynamics of sedentary organisms, both on land and underwater. Recruitment and early survivorship of organisms can be affected strongly by the local-scale distribution of heterospecifics (Harrington et al. 2004; Horn 1975) and conspecifics (Connell 1971; Janzen 1970; Vermeij and Sandin 2008). At later stages, adults can compete for space through preemption of resources (Buss and Jackson 1979; Harper 1977) or by directly causing harm to neighboring competitors (e.g., allelopathy) (Gross 2003). The importance of spatial dynamics is particularly acute for clonal organisms. Jackson (1977) identified a number of key distinctions between the competitive abilities of

solitary versus clonal strategies, not the least of which being the pattern of growth and space preemption. When space is liberated, most solitary species depend on the recruitment and growth of sexually produced offspring to fill available space. Clonal organisms also can colonize space through recruitment and growth of propagules, but such recruits can be produced either sexually or asexually (as by fragmentation). Further, clonal organisms neighboring free space can colonize this area through non-sexual growth in colony size (Jackson 1977). Note that in many ecosystems this ability to laterally fill space is not limited to clonal organisms, as many plant and algal species grow vegetatively to occupy neighboring free substrate (Harper 1977; Sousa et al. 1981).

Disturbances, both abiotic (e.g., storms) and biotic (e.g., herbivory), can dramatically alter the spatial patterning of sedentary species. Abiotic disturbances are largely random events that are best described probabilistically across a landscape. Biotic disturbance is more predictable and context-specific. Vagile herbivores, for example, are selective organisms that forage in non-random patterns across space. When herbivores are constrained in their movements, explicit spatial patterning of their prey can emerge (e.g., foraging ‘halos’ made by sea urchins) (Ogden et al. 1973; Randall 1961). Further, when consumers exhibit strong preferences for particular types of food, shifts in competitive hierarchies among prey can occur. Herbivores thus hold potential to alter spatial patterning of sedentary organisms (Adler et al. 2001).

The benthic environment of coral reefs reveals a spatially explicit ecology in which sedentary corals and algae compete for limited space (Connell 1997). In general, reef organisms fit the expectations of the competition–colonization trade-off (Levins and Culver 1971)—stony corals are long-lived and are generally good competitors while fleshy algae (including both turf algae and macroalgae) are ephemeral and rapid colonizers. The competitive distinction between stony corals and fleshy algae is modified by consumers (Carpenter 1986; Lewis 1986). Reef herbivores (including both fishes and sea urchins) limit algal growth, but when herbivores are removed the competitive distinction is reduced and corals can lose their advantage. Removals of herbivores can precipitate rapid growth and expansion of algal assemblages (Hughes et al. 2007) or more subtle effects including the effective failure of coral recruitment leading to a slow transition to algal-dominated landscapes (Birkeland 2004). As such, the competitive advantage for corals is not fixed, but instead is size-dependent; while adults are good competitors for space, juveniles are particularly susceptible to algal competition via overgrowth and other mechanisms.

A spatially explicit simulation model was constructed to explore population dynamics of sedentary individuals

living on a benthic landscape. The model was parameterized to describe dynamics of a Caribbean coral reef environment, though many of the ecological trade-offs explored here can be extrapolated to gain insights into other environments. Unlike existing models of coral reefs, we explicitly consider the spatial dynamics of benthic species, exploring how spatial patterns of herbivory and of coral growth interact to affect competitive dynamics and outcomes. We target our analyses on the process of reef restoration, namely the potential for regrowth of stony corals in an environment from which such corals have been lost.

Materials and methods

Model development

The model domain is a grid of square cells with periodic boundary conditions. Each cell is occupied by one of four benthic types: stony corals, turf algae, macroalgae, or crustose coralline algae. These types were defined to capture the dominant spatial dynamics of benthic reef organisms, particularly involving patterns of recruitment, mortality, and competition for space. Corals (C) have low recruitment rates, but adults are long-lived and are dominant competitors for space (Hughes 1984). Turf algae (TA) are the assemblage of finely cropped erect and filamentous algae (e.g., species of *Polysiphonia*, *Ceramium*, *Sphacelaria*, and juvenile macroalgae). TA have high recruitment rates relative to corals but are poor competitors for space (Diaz-Pulido and McCook 2002). Macroalgae (MA) compose the assemblage of erect, fleshy algae that can emerge from the uncontrolled growth and succession of a TA assemblage (e.g., species of *Sargassum*, *Lobophora*, and *Dictyota*) (Carpenter 1990). MA are intermediate competitors for space, inferior only to adult corals in their competitive abilities. Each C, TA, and MA can grow clonally (or vegetatively), laterally expanding to adjacent cells. Finally, crustose coralline algae (CCA) are foundational species on the reef, living beneath other benthic types (e.g., species of *Porolithon* and *Neogoniolithon*). When space is cleared by mortality or herbivory, the cell state becomes CCA. Because this definition of CCA formally includes open space, we are ignoring the possible facilitating or competitive effects of certain CCA species toward coral recruitment and other benthic organisms (Harrington et al. 2004; Vermeij 2006). Although there is much variability of species within each benthic type, these designations were used to capture important dynamical differences in dominant spatial interactions with a minimum set of variables and parameters.

Interactions of benthic types are parameterized based on a grid cell size of 10 × 10 cm on a 5 × 5 m domain, using

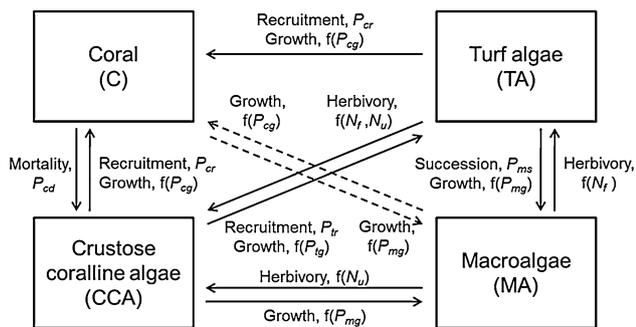


Fig. 1 Flow chart of coral reef benthic interactions. Transitions among the four functional groups are due to recruitment, mortality, herbivory, growth and succession. Important parameters are included in each link and represent transition probabilities or parts of state-dependent functions defining transition probabilities [denoted as $f(x)$]. State-dependent competitive dynamics are indicated by *dashed lines*. Parameters are defined in Table 1

discrete time steps of 0.025 year. A schematic of modeled species interactions is provided in Fig. 1, with basal parameter values in Table 1.

Recruitment and succession

Benthic types can arrive to an area through recruitment of mobile propagules. Because of their small size, settlers of all

functional types typically are competitively inferior to established adults (Vermeij and Sandin 2008). As such, recruitment of corals and algae is enhanced in areas of low competition. In this formulation, we assume that the assemblages of CCA and TA are the inferior competitors for space.

At each time interval, the probability of TA recruiting to a cell occupied by CCA is defined as P_{tr} . Similarly, the probability of C recruiting to a cell occupied by either CCA or TA is defined as P_{cr} . Note that the assumption that coral recruitment probabilities are equal for areas of each CCA and TA is in contrast to field studies documenting lower recruitment to areas of TA than CCA (Harrington et al. 2004; Kuffner et al. 2006). We have repeated analyses taking recruitment hierarchy into account (not shown here) and found no qualitative shift in the results presented. Thus, to limit the number of free parameters, we use this simplified description of coral recruitment dynamics. Note that true recruits of corals or turf algae are much smaller than the size of a cell in this model (100 cm²; results shown are not sensitive to a wide range of cell sizes capturing typical benthic type dynamics, from 10s to 100s of cm²). In sum, the parameters P_{cr} and P_{tr} are the composite probability of a C or TA recruit arriving, surviving, and growing to the size of the cell.

We include no specific term for MA recruitment because what is typically called MA grows from juveniles living in

Table 1 Parameter definitions for simulation model

Parameter	Definition	Value	Units	Source
P_{cr}	Probability of recruitment for C	0.01 ^a	year ⁻¹	Edmunds et al. (2004)
P_{tr}	Probability of recruitment for TA	0.80 ^b	year ⁻¹	Diaz-Pulido and McCook (2002)
G_C	Growth term for C	0.01 ^c	m year ⁻¹	Huston (1985)
G_{TA}	Growth term for TA	1.0 ^d	m year ⁻¹	McClanahan et al. (2002)
G_{MA}	Growth term for MA	0.5 ^e	m year ⁻¹	McClanahan et al. (2003)
P_{ms}	Probability of succession from TA to MA	0.33 ^f	year ⁻¹	Carpenter (1990)
P_{cd}	Probability of mortality of C	0.15 ^g	year ⁻¹	Hughes (1984)
C_{th}	Contiguous threshold for coral	900 ^h	cm ²	Bak and Meesters (1999)
R_u	Urchin grazing radius	45	cm	Carpenter (1984)
$N_{C,max}$	Maximum colony size for massive corals	7,000 ⁱ	cm ²	Soong (1993)

The values presented correspond to the baseline values used for simulations when alternative values are not defined. Probabilities describe dynamics for contiguous 100 cm² area of benthos

^a Calculated as the mean density of recruits, multiplied by the probability of surviving until reaching 100 cm². Similar estimate is derived through monitoring recruitment and growth on settlement racks (Vermeij 2006)

^b Based on rate of turf algal recruitment to recently bleached corals

^c Approximate median value of linear extension of adult corals, across Caribbean taxa

^d Linear growth rate required to fill settlement tiles given TA recruitment rate above

^e Estimated from rate of macroalgal space filling in cleared areas of reef

^f Based on rate of macroalgal emergence from turf algal gardens after mass mortality of *Diadema antillarum* on Jamaica

^g Approximate mean mortality across size classes and seasons

^h Approximate threshold for coral survival and growth on disturbed reefs

ⁱ Median (and modal) maximum size for seven species of massive Caribbean corals

the TA assemblage (Carpenter 1990). Because turf algal assemblages include juvenile erect, fleshy algae, algal succession can lead to the shift of TA to MA (Burkepile and Hay 2010). At each time step, there is a probability P_{ms} that a TA cell will transition to an MA cell due to succession. This successional dynamic can occur if a TA cell is not overgrown by a neighboring type during a particular time step. If a TA cell could be overgrown by a neighboring cell (a successful probabilistic draw for a neighboring cell), the eventual winning type will be determined by the rules of competition (as described below).

Growth

Many organisms on coral reefs have flexible growth, with the capacity to laterally spread (Jackson 1977). We assume overgrowth corresponds to relative abilities to compete for light (height of organisms) and to compete for space. Overgrowth of a cell is computed based on the growth rate of the neighboring functional type (G_x , where x denotes the functional type C, MA, or TA) and the number of neighboring cells occupied by the functional type (n_x , an integer which is geometrically bound from 0 to 4). Based on the cell sizes used in this simulation, typical growth rates would not lead to complete overgrowth of a neighboring cell within one time step, even with the possibility of multiple cells jointly contributing to this overgrowth. As such, the probability of a cell being overgrown by functional type x is defined as $1 - (1 - G_x)^{n_x}$. When an individual cell is bordered by multiple functional types, three outcomes are possible: (1) no overgrowth, (2) overgrowth by only one type, and (3) potential overgrowth by more than one type. Scenario (1) occurs in the simulation when no bordering functional type realizes a random numerical draw above the defined overgrowth probability. Scenario (2) occurs when only one bordering type realizes a successful numerical draw. Scenario (3) occurs when more than one type realizes a successful draw. In this case, the rules of direct competition define the winner of the cell. We assume that CCA can be overgrown by TA, MA, and C; that TA can be overgrown by MA and C; and that MA and C have a size-specific competitive dynamic, as described below.

Competition between C and MA is more complex due to the distinct competitive abilities of each type. MA has the advantage of erect growth, affording the ability to overtop and shade benthic competitors (McCook et al. 2001). Further, MA can reduce fitness of nearby corals through the direct transmission of pathogens (Nugues et al. 2004) and/or release of compounds leading to microbial fertilization (Smith et al. 2006) or direct allelopathy (Rasher and Hay 2010) of neighboring coral colonies. Small C colonies,

with high perimeter to area ratios, are particularly susceptible to physical and chemical/microbial mechanisms in the competition for benthic space with MA. Once established as a large colony, however, C are good competitors for space and can prevent overgrowth along colony borders. In essence, a large C colony has a relatively low perimeter to area ratio and thus partial mortality caused by neighboring MA is less likely to result in whole-colony mortality (Meesters et al. 1996).

Given these biological mechanisms, the fates of a C cell and an MA cell that border one another are determined by the size of the C colony. If the C cell in question is part of a small colony (i.e., smaller than a threshold number of contiguous cells, C_{th}) then the cell can be overgrown by MA. Instead, if the C cell is part of a large colony (i.e., composed of at least C_{th} contiguous cells), the C cell will retain its state. On the other side of the border, if an MA cell is adjacent to a large C colony (composed of at least C_{th} contiguous cells), it will be overgrown by C with a probability defined above by the patterns of C growth. These dynamics mimic observations of corals with low perimeter to area ratios growing effectively when found in regular contact with macroalgae (Lirman 2001; Tanner 1995). If the adjacent C colony is smaller, the MA cell will not be overgrown by this neighboring C cell.

Mortality

Natural mortality affects all organisms. However, because algae occupy space with an assemblage of individuals, natural mortality is unlikely to simultaneously affect all individuals living within a particular area. In contrast, because corals are clonal organisms, this functional type is likely to suffer spatially autocorrelated natural mortality. Colonies or sections of colonies occupying 0.01 m^2 can die due to factors such as disease or undetermined senescence (Rinkevich and Loya 1986). In the model, the probability of coral mortality is defined as P_{cd} and results in the transition of a cell from C to the basal state of CCA (or open space). Here, we do not include full-colony mortality, as is possible from coral bleaching and rapidly-spreading diseases.

Herbivory

Fleshy algal cells (TA and MA) are particularly susceptible to removal by herbivores. A suite of herbivorous fishes and invertebrates can remove large sections of algae. On Caribbean reefs, the principal herbivores are fishes (mainly parrotfishes and surgeonfishes) and sea urchins (dominated by *D. antillarum*). Note that we ignore the microherbivores, e.g., amphipods, gastropods, and herbivorous

polychaetes, as their effects are quantitatively minor relative to that of fish and sea urchins (Carpenter 1986).

While the bulk consumption rates of fishes and sea urchins have been compared (Carpenter 1988; Ogden 1976), less attention has been paid to the spatial patterns of such herbivory. We address these differences here. Because of their high mobility, fish can explore wide areas of the benthic landscape in their search for food. As such, the assemblage of herbivorous fishes can be assumed to forage in an ideal-free manner across the benthic landscape. Fish will randomly explore the landscape and consume TA and MA cells at their maximum rate, if sufficient cells are available in this state, or at a rate defined by the total of TA and MA cells, if less than the maximum is available.

Sea urchins, in contrast, are limited in their movements, creating characteristic ‘urchin halos’ around preferred shelter areas (Ogden et al. 1973). Assuming that sea urchins can explore a radius in the landscape of R_u , the food available to a particular individual is simply the number of cells in state TA or MA in its halo. Urchins are assumed to visit all cells in their halo every 0.1 year. Note that we assume that herbivores show no preferences among algal types, a pattern expected given sufficient diversity of herbivorous species (Burkpile and Hay 2008).

In order to focus analyses on the spatial effects of herbivory, we assume that all herbivory alters benthic types similarly. In particular, we assume that herbivory by fishes and by sea urchins converts both MA and TA to CCA. We thus model herbivory by means of scraping and ignore the possible mechanisms of cropping and browsing (thereby converting MA to TA) as is common to herbivorous damselfish and other smaller fish species.

Analyses

Comparing modes of herbivory

Model simulations were conducted by exploring reef development starting from a range of initial conditions with respect to coral and algal coverage using parameter values from Table 1. To compare the effects of spatial constraints in herbivory, we modeled two extreme cases—herbivory by (1) fish only (spatially unconstrained) and (2) sea urchins only (spatially constrained). To avoid systematic bias, we maintained a comparable potential for herbivory for each herbivore type (measured as maximum number of fleshy algal cells consumed per unit time by the herbivores). In particular, we assume that 0.4 sea urchins m^{-2} have the potential to graze 25% of the benthos per 0.1 year [derived from the per capita area of foraging (defined by R_u) of *Diadema*; Table 1], which is comparable to the foraging capacity of a mixed assemblage of herbivorous fishes at a biomass of 7 $g\ m^{-2}$ (Hoeoy and Bellwood 2008).

Comparing coral growth patterns

The clonal growth of corals leads some species to grow monotonically and essentially without limits (e.g., branching acroporids). In contrast, the skeletal plans of many massive corals have structural limits to the spatial extent to which an individual colony can grow (e.g., *Montastraea*, *Diploria*). Such limited growth will set up an explicit contrast between the spatial dynamics of such ‘branching’ versus ‘massive’ growth morphologies.

Massive corals were modeled by making the growth term for corals (G_C , as described above) a function dependent on the size of an individual colony, G'_C . In order to capture the dynamics of massive corals, it was imperative to record the colony identity of each coral cell in the landscape (i.e., a historical record linking adjacent cells formed by clonal growth). Growth of corals in this case has two space-dependent elements: (1) the number of contiguous neighboring coral cells (as before, positively related to coral growth), and (2) size of the specific coral colony (negatively related to coral growth). Growth of massive corals is modeled following a logistic equation, $G'_C = G_C (1 - \#C/N_{C,max})$, where $\#C$ is the number of coral cells connected in one colony and $N_{C,max}$ is the maximum size for a massive colony. Branching corals were modeled with size-dependent competition with MA (1), but without defined size-dependent growth (2). Simulations run below only include either massive or branching corals, not both.

Sensitivity analyses

We conducted sensitivity analyses to test whether results were generalizable beyond one set of starting conditions and beyond the parameter values listed in Table 1. To identify the model attractors, each model was started at 100 starting states that spanned the range of benthic states. Note that we use the word “attractor” in this rule-based model to refer to the region (or regions) of state space to which the model evolves over time (Wolfram 1984). To clarify the figures, results from a subset of starting states that reveal all attractors are presented. Further, to test the dependence of model outcomes to parameter values, a sensitivity analysis was performed. We found little sensitivity of model results to changes in parameter values (Electronic Supplementary Material), suggesting that the models are robust within this region of parameter space.

Results

Model simulations of benthic organisms growing clonally (corals) and vegetatively (algae) revealed an endogenous tendency to form transient spatial patterns. Landscapes

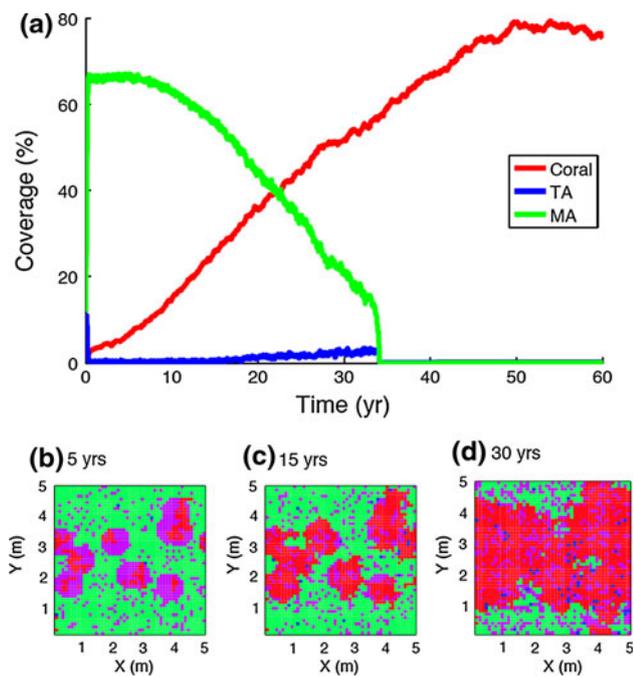


Fig. 2 **a** Time series of benthic community development over 60 years showing percent coverage for coral, turf algae (TA) and macroalgae (MA) starting from a random initial configuration of 10% of each type (remaining 70% coverage was by crustose coralline algae, CCA) and including both herbivorous fish and sea urchins. Snapshots of benthic landscape at **b** 5, **c** 15 and **d** 30 years showing coverage by coral (red), turf algae (blue), macroalgae (green) and CCA (purple). Note that ephemeral single cells of CCA are largely caused by spatially uncorrelated herbivory by fish while larger circles of CCA are caused by spatially correlated herbivory by sea urchins, consistent with so-called ‘urchin halos’

begun with C, MA, and TA each randomly covering 10% of the landscape (with the remaining 70% set as CCA) and run in the presence of a mixed herbivore assemblage showed the emergence of spatial clustering of coral during an initial 10-year phase (Fig. 2, and evidenced by a variance-to-mean ratio of coral density across the landscape ephemerally exceeding 1.0, not shown). Once the C achieved sufficient coverage to outcompete algal species, coral spread to become pervasive across the domain.

To isolate the influence of the two types of herbivory in the model, simulations were run including fish and sea urchins in isolation. By definition, herbivores increased the mean mortality of turf and macroalgae. While fish foraged in a random manner, sea urchins created distinct ‘halos’, i.e., areas that were foraged regularly and had strongly reduced fleshy algal cover (e.g., Fig. 2).

The benthic configuration of simulations run from a range of initial conditions for ‘branching’ coral and MA coverage (where, in all cases, each benthic type was scattered randomly across the domain in a manner similar to what might be found after a destructive storm event) with typical densities of herbivorous fishes revealed two

attractors, one dominated by corals and one by fleshy algae (Fig. 3a). Simulations started with at least 20% coral cover ultimately arrived at the ‘coral’ attractor (~75% coral cover and <5% macroalgae) while simulations started with lower coral cover arrived at the ‘macroalgae’ attractor (~85% macroalgal and <5% coral) indicating a basin of attraction for each attractor. When simulations were run with herbivorous sea urchins instead of fish, one attractor emerged. Regardless of starting configuration of the benthos, all simulations arrived at a coral-dominated state (~80% coral and ~10% macroalgae; Fig. 3b).

The pattern by which a coral grows affects its ability to compete for space with fleshy algae. In contrast to simulations using ‘branching’ corals (Fig. 3a, b), simulations with the same level of herbivory due to fish or sea urchins but including ‘massive’ corals had only algal-dominated attractors. The attractor for models with only herbivorous fish and massive corals was dominated by macroalgae (>80%) with little coral (Fig. 3c). The attractor with sea urchins and massive corals was at approximately 75% macroalgae and 15% coral (Fig. 3d).

The density of herbivores significantly changed the results of the simulations. Starting with a randomized landscape composed of 10% each ‘branching’ coral, MA and TA, there was a clear change in results as fish density increased (Fig. 4a). At low densities, the attractor was a macroalgal-dominated state, with coral covering <5% of the benthos. However, when herbivorous fish biomass was 21 g m⁻² or greater, the attractor was essentially reversed, with coral cover exceeding 80% and macroalgae rare. Across a similar range of herbivory potential, no distinct threshold effects were observed for sea urchins, with all attractors being dominated by corals (>70%; Fig. 4b). Simulations using ‘massive’ corals showed the same behavior in attractor state as fish density was increased (Fig. 4c); however, unlike for branching coral, variations in sea urchin density altered the attractor (Fig. 4d). For all sea urchin densities, the final coral state was directly related to the available algal-free space in the domain resulting from sea urchin grazing. As the density increased above 1.2 sea urchins m⁻², the overlap of urchin halos (which were randomly assigned in the domain) buffered the effect of increasing sea urchin density, causing the final coral coverage to asymptote.

Discussion

Model results showed clear transitions in outcomes of benthic competition as a function of spatial constraints when the model was run using a realistic range of parameter values. Similar patterns of context-specificity of benthic dynamics have been noted by Mumby et al. (2007) and

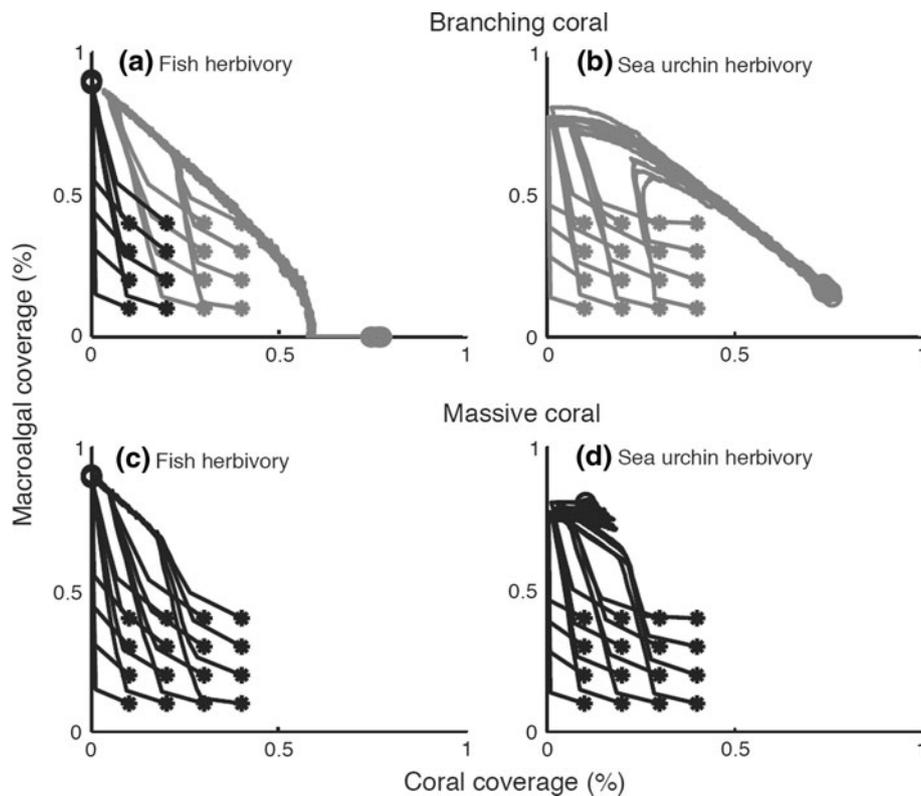
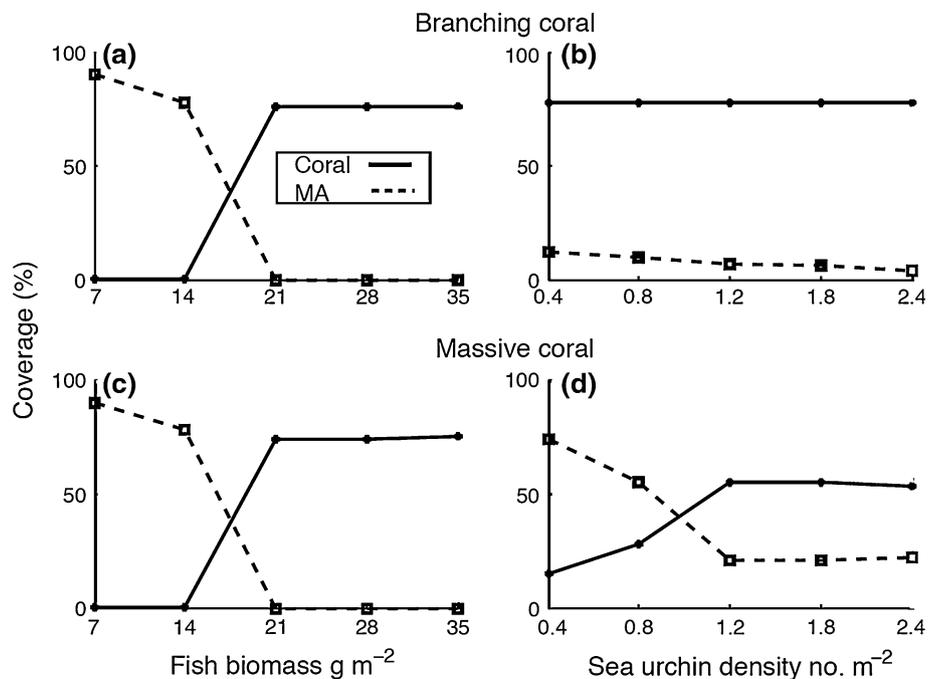


Fig. 3 Partial phase space diagrams showing pathways of simulated benthic community change in two dimensions (cover of corals and macroalgae), factorially comparing results for types of herbivore and types of coral growth morphology. Two types of herbivores are **a, c** fishes with spatially unconstrained herbivory and **b, d** sea urchins with spatially constrained herbivory. Two types of coral growth morphologies are ‘branching’ corals with unlimited clonal growth (*top row*) and ‘massive’ corals with spatially constrained

growth (*bottom row*). Benthic starting conditions (*asterisks*) are varied comparably; endpoints (*open circles*) show simulations after 80 years. Tracks are coded *gray* for arriving at ‘coral-dominated’ attractors (>50% coral cover) and *black* for ‘algal-dominated’ attractors (>50% macroalgal cover). For all simulations, the potential herbivory is held constant in units of maximum cells consumed per unit time (~25% of the landscape, simulated as 7 g m⁻² of herbivorous fish biomass or 0.4 sea urchins m⁻²)

Fig. 4 Sensitivity of attractors to level of herbivory. At each level of herbivory, the two points represent two dimensions of the benthic attractor—coral cover (*stars and full line*) and macroalgal cover (*squares and dashed line*)—for both **a, b** branching and **c, d** massive coral across **a, c** fish density and **b, d** sea urchin density. Note that herbivore densities are standardized to comparable units of maximum number of cells affected by herbivores per model time step. All simulations were started with a randomized landscape containing 10% representation by each TA, MA and coral



Mumby (2009). In contrast to this earlier work, however, we explored the ecological feedbacks associated with the explicit spatial positioning and behaviors of organisms. We found that by linking dynamics spatially, through spatially constrained herbivory and growth, profound shifts occur in the emergent distributions of benthic organisms.

Spatial constraints of herbivory

Grazing can alter the spatial distribution of autotrophs based on the degree of spatial heterogeneity of herbivory (Adler et al. 2001). In the competition for space between corals and fleshy algae, there is a clear effect of the spatial pattern of herbivory on benthic dynamics (Figs. 2 and 3). In simulations including only herbivory by fish, we found strong context-specificity in the emergent benthic patterning. Depending upon the starting conditions (Fig. 3a) and the density of fish (Fig. 4a), herbivory by fish can lead to anything from domination by corals to domination by fleshy algae. In the presence of herbivorous sea urchins, the emergent benthic patterns are less variable, in general conferring more competitive advantages to corals relative to fleshy algae (Figs. 3 and 4). These results suggest that sea urchins are more efficacious than fish at controlling macroalgae and favoring coral growth. Fish travel broadly, exploring relatively large home ranges and foraging in spatially disjointed areas of fleshy algae. Sea urchins instead forage in a limited area, leading to spatially and temporally constrained herbivory within their home range (Fig. 2). Importantly, corals are strong competitors for space with fleshy algae only after coral colonies have reached a sufficiently large size (Bak and Meesters 1999). As such, the success of corals depends largely upon consistent control of fleshy algal growth in areas neighboring juvenile coral colonies. Herbivory by sea urchins provides such a consistent, fleshy algal-free area for corals to settle and reach maturity. In contrast, the probability is low that a particular area will be cropped of fleshy algae consistently by fish herbivory alone for the >2 years needed for coral maturation, unless the density of herbivorous fish is large (Fig. 4a, c).

Figure 4 provides evidence of potential thresholds of herbivore densities leading to divergent outcomes of benthic competition. As parameterized, our model predicts a dynamical transition occurring around 21 g m^{-2} of herbivorous fish biomass (Fig. 4), a value higher than the mean biomass of $\sim 15 \text{ g m}^{-2}$ of fish estimated from unprotected sites across the northern Caribbean (Newman et al. 2006). Although quantitative thresholds are needed to help direct management efforts, we recommend care be taken before applying these results to specific cases. This study was formulated to explore dynamical behaviors of reef systems using a simplified model structure and best-

available parameter estimates. This study highlights the qualitative dynamical distinctions emerging across herbivore and coral types but, without more site-specific tailoring of model particulars, quantitative predictions should be viewed cautiously.

These conclusions regarding the distinction between herbivory by fishes and by sea urchins are likely to be conservative. Recall that the baseline simulations were run with identical levels of herbivory, measured as the number of cells that were visited by herbivores per unit time (Table 1; Fig. 3). In our formulation, herbivorous fish roamed the landscape in search of algal resources, finding and foraging specifically in areas with turf or macroalgae. Because sea urchins were spatially constrained, they only had the capacity to visit the cells within their limited home range. Thus, if the cells in the home range were to switch to a coral state, the sea urchin ‘lost’ one area of its foraging range and the landscape as a whole was subject to less herbivory. In the field, we may expect sea urchins to move to avoid the loss of algal foraging area due to previous visitation (Carpenter 1984) or preemption of space by corals, thus leading to new areas being subjected to herbivory and potentially leading to further coral recruitment.

Ontogenetic shifts in competitive dynamics have been discussed as important mechanisms for maintaining species diversity (Grubb 1977). While adults may interact based on adult–adult competitive hierarchies, dynamics become more complex when considering the altered competitive landscapes across combinations of species and life stages. While adult corals may be competitively superior on the reef benthos, recruiting and juvenile corals are in many cases competitively inferior to fleshy algae (Kuffner et al. 2006). Differential patterns of herbivory by fishes and sea urchins appear to alter Grubb’s (1977) so-called ‘regeneration niche’ of corals in reef environments—sea urchins consistently provide suitable habitat for coral recruitment while relatively more fishes are needed to consistently provide similar conditions.

Massive versus branching corals

Clonal organisms display a variety of growth morphologies that vary distinctly in relative performance across biological and physical conditions (Jackson 1979). Two of the prominent morphologies among corals are branching and massive corals. Branching corals are capable of prodigious asexual growth across a landscape. For example, thickets of *Acropora palmata* in Florida have been shown to be genetically identical over more than 100 m of reef, suggesting that these colonies can dominate a landscape in the essential absence of settlement of sexual recruits (Baums et al. 2006). In contrast, individual colonies of massive corals cover much less area than branching corals. As such,

for an assemblage of massive corals to dominate a benthic landscape, sufficiently high settlement and post-settlement survivorship is essential.

The benthic dynamics of landscapes with massive corals were distinct from those with branching corals. Given one level of herbivory by fish, there was a reduced range of benthic starting states that led to coral domination for massive versus branching corals (Fig. 3a, c). Similarly, starting at one consistent benthic configuration, there was a reduced range of sea urchin densities that led to coral domination for massive versus branching corals (Fig. 4b, d). These results further highlight the importance of ontogenetic changes in competitive dynamics. Branching corals are capable of dominating a benthic landscape because a relatively low number of successful recruitment events can result in prodigious spread of corals. In order to realize comparable spread of massive corals, many more successful recruitment events are necessary. While sea urchins can effectively create settlement opportunities for massive corals, these opportunities are spatially limited to only a few colonies residing within and nearby to foraging halos.

Shifts in the composition of coral assemblages in recent decades have been found across the Caribbean (Aronson et al. 2002; Bak and Nieuwland 1995), driven largely in the shallows by the loss of the branching *Acropora* species. Disease and other factors have led to the widespread decline of *Acropora palmata* and *A. cervicornis*, which were the competitively superior shallow-water species in the Caribbean (Aronson et al. 2002). These dominant branching species have been replaced by smaller species of corals, ones with growth more similar to our idealized 'massive' corals. The widespread decline of coral cover and lack of coral recovery across the Caribbean may in part be due to the loss of branching *Acropora* (species capable of rapid and spatially unconstrained clonal growth) in lieu of recruitment-dependent massive corals.

Summary

Spatial patterns of herbivory and growth can have dramatic influences on competitive outcomes of sedentary organisms. Such shifts in competitive dynamics are not limited solely to adult stages but can change through ontogeny. Through spatially explicit simulation models, we have revealed that variation in spatial patterning of herbivory and of coral growth can severely alter the distribution of benthic organisms. We have shown that spatially constrained herbivores are more effective at facilitating competitive coexistence by maintaining areas suitable for coral settlement and recruitment to the adult community. Further, we find that corals more dependent on sexual recruits for population spread are worse competitors with fleshy algae relative to corals with essentially unlimited asexual

growth across space. Thus, changing environments and changing spatial contexts can effect large changes in competitive dynamics among sedentary species. Without an appreciation of this sensitivity to spatial constraints and dynamics, our understanding of emergent properties of coral reefs and other ecosystems will be severely limited.

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