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Mechanics of multiple feedbacks in benthic coral reef communities

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ABSTRACT

Coral reefs are subject to extraordinary alterations under changing environmental conditions and increasing human resource use. Here we use a generic, spatially explicit, individual-based model to analyze fundamental interrelations and feedback loops relevant for coral reef dynamics, including recruitment, herbivory, benthic interactions, and fisheries. We assess the influence of three different fishing regimes (i.e. no-take, non-destructive and destructive fishing) and larval connectivity on the resilience of a coral reef community and explore respective thresholds. Simulation results show that changes in one of these parameters and a resulting imbalance in one feedback loop can disorder the whole interplay of regulating processes. Under many analyzed conditions alterations of herbivory or recruitment may induce a self-enhancing degradation of a coral dominated ecosystem state. Model results show that reefs can persist under non-destructive fishing with adequate larval connectivity but isolated reef sites are threatened at current modes of perturbations, because low larval recruitment does not allow for sufficient post-disturbance recovery. At high connectivity levels, fast growing species dominate and may displace other species. Often, these species increase three-dimensional structure, and thus, refuges for herbivores. However, this also reduces functional redundancy and if the dominant species (here *Acropora muricata*) is highly susceptible to thermally induced bleaching an extreme temperature event may cause overall coral extirpation and a regime shift to algal dominance. The model constitutes a virtual laboratory for reef studies, gives insights on how particular effectors may trigger cascades in the coral community, and hence highlights the necessity to analyze mechanisms not only separately, but within the whole system's context to fully grasp complex responses in ecosystems.

1. Introduction

Coral reefs feature extraordinary biodiversity and a complex structure of interconnections between organisms and their environment, which creates numerous feedback loops within as well as among hierarchical levels (Mumby and Steneck, 2008; Nyström et al., 2012). Corals compete for space with macroalgae (McCook et al., 2001) and other benthic organisms (Norström et al., 2009). Coral community composition largely determines the rugosity (three-dimensional structure) of a reef patch (Alvarez-Filip et al., 2011; Luckhurst and Luckhurst, 1978), and in consequence influences herbivore densities, and hence, algal coverage (Graham et al., 2006; Hay, 1981). The performance of individual species can have strong effects on overall system dynamics and an emerging ecosystem state feeds back on each individual. For example, the population size of a coral species influences its recruitment success in a particular reef setting (Hughes et al., 2000), while size, growth rate, morphology, and current health status affect individual coral colony survival in spatial competition, its reaction to environmental stressors and its trophic relations. When analyzing a coral reef system, it is, hence, highly important to consider how individuals are affected by environmental factors and how self-organization determines spatial distribution, community composition, recruitment success and reaction to changing levels of herbivory under particular external influences (Mumby and Steneck, 2008; Nyström et al., 2012).

Single feedback processes in coral reefs have often been studied in isolation. Mumby et al. (2007) found that mangrove areas providing breeding habitats for important herbivorous parrot fish, had a strong influence on grazing performance, macroalgae densities, and hence, reef trajectories. Nyström et al. (2012) explore various controls for algal proliferation and disturbances to highlight how phase shifts can become persistent. For example high algal cover prevents

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corals from settling and in the long run reduces the brooding stock of corals. Mumby and Steneck (2008) illustrate the importance of understanding complex, interconnected feedback relations of coral cover, structural complexity, herbivore density, macroalgal cover and coral recruitment.

However, with experimental approaches, alone, it is extremely complex and costly to link specific causes to effects on the overall coral reef status and to combine analyzes of feedback loops on system trajectories. Here, modeling can help to integrate current knowledge and new findings (Breckling et al., 2006; Reuter et al., 2008). While some models on broader scales approximate the potential geographic range of coral reefs (Kleypas, 1999; Melbourne-Thomas et al., 2011), others seek to estimate sustainable fishing and management regimes (Gao and Hailu, 2012; McClanahan, 1995; Ruiz Sebastián and McClanahan, 2013), or use approaches on finer scales to study spatial competition among corals (Langmead and Sheppard, 2004), or between corals and other benthic competitors (Buenau et al., 2012; Mumby, 2006). The effects of ocean acidification and warming on reef resilience are studied by Anthony et al. (2011) while Fung et al. (2011) estimate probabilities for phase shifts in various configurations. However, only a few of these models combine a spatial representation with different hierarchical scales, and dynamics of multi-species communities.

Here we use a spatially explicit, individual-based model, in which corals with different life history traits compete with each other under recurring bleaching events and different fishing regimes to analyze how reef communities and accordingly ecosystem properties change with herbivory, three-dimensional habitat structure, recruitment, and fishing practices. We focus our study on three mechanisms (Fig. 1) which affect several important feedback processes on coral reef systems:

(a) In an unfished reef patch high grazer abundance guarantees (i) sufficient *herbivory* to keep free spaces unoccupied by algae, and thus, (ii) settling ground for coral recruits (Fig. 1a).
(b) *Coral recruitment* is determined by (i) a positive stock-recruitment relationship for coral populations (Hughes et al., 2000), (ii) larval input from neighboring reef sites (Almany et al., 2009; Botsford et al., 2009) and (iii) algal density, which is a decisive factor for coral recruitment success (Birrell et al., 2008; Fig. 1b).
(c) In an *intensively fished* patch grazer densities become dependent on hiding spaces, and hence, 3-dimensional structure (Berkström et al., 2012; Hixon and Beets, 1993). In this study *destructive fishing* represents the situation in which fishermen try to maintain a minimum catch in over-fished habitats (Jennings and Polunin, 1996; Mangi et al., 2007). They frequent the site more often and thereby increase anchor damage and intensify their fishing effort often in combination with destructive fishing techniques (Hlavacs, 2008; Jiddawi and Öhman, 2002; Fig. 1c).

In a resilient ecosystem properties and relationships are maintained even when the system is disturbed (Holling, 1973). In general, feedback loops are crucial to maintain resilience, and hence the persistence and regeneration potential of a coral reef. For example, successful coral recruitment and recruit survival can only be assured by keeping algal densities under control while connectivity and rugosity influence the abundance of herbivores. Within a coral reef, resilience is provided by species diversity (Loreau et al., 2003), functional redundancy (Nyström, 2006), different life histories of reef species (Vermeij et al., 2007) and the fact that species act on different spatial and temporal scales (Burkepile and Hay, 2010; Hobson, 1973). The loss of one specific function may be buffered by others but multiple deficiencies can undermine resilience.

Causes for coral decline, such as global climate change (Hoegh-Guldberg et al., 2007; Hughes et al., 2007) and over-exploitation (Muhando, 2005; Mumby, 2006) often affect regulatory properties within a reef decisively. Superimposing perturbations can shift an already stressed coral reef into an alternative state (McManus and Polsenberg, 2004; Norström et al., 2009; Graham et al., 2015, but

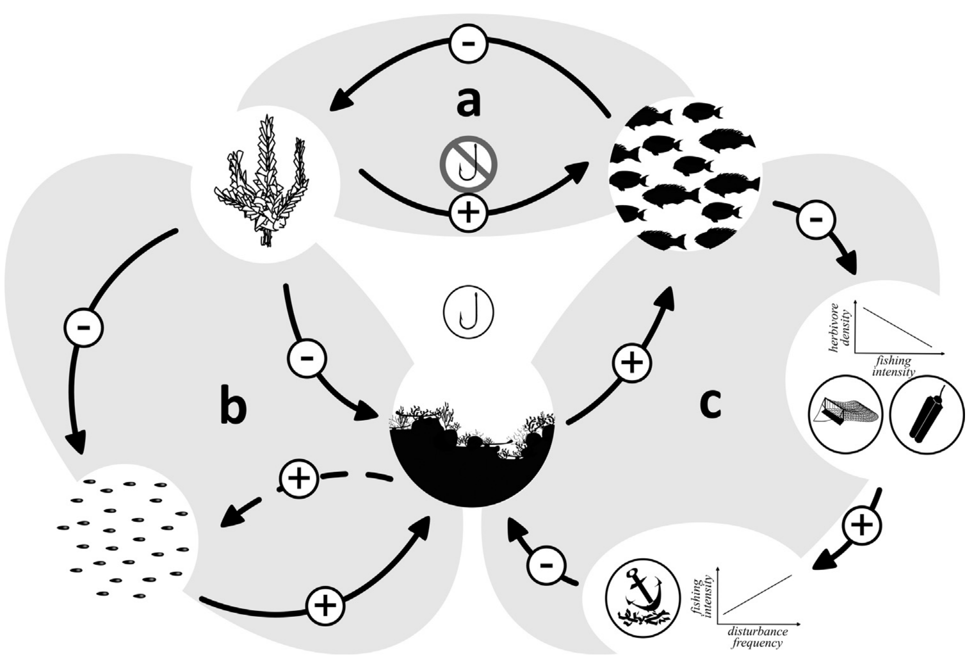

Fig. 1. *The three processes herbivory, recruitment and fishing and their relationships in the model.* (a) In an unfished reef patch fish abundance is high and algae are maintained at low densities. (b) Recruitment success depends on population size of corals, algal densities which impair recruit settling, and connectivity to other reefs (not shown in this graph). (c) Under intensive fishing the grazer density becomes dependent on the rugosity and declining herbivory increases the probability of algae to occupy free space. Under destructive fishing regimes the fishing intensity increases if the fish density falls below a threshold, which increases the frequency of mechanical disturbance events and in turn decreases coral rugosity. As above, this leads to reduced herbivory.