The analysis of coral reef resilience
– a generic modelling tool –

Andreas Kubicek

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Universität Bremen

Universität Bremen

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“Complexity is the prodigy of the world.
Simplicity is the sensation of the universe.
Behind complexity, there is always simplicity to be revealed.
Inside simplicity, there is always complexity to be discovered”

Gang Yu

Contents

Abstract

Coral reefs, rainforests of the sea, are of greatest ecological and economical importance. Although they cover just a small fraction of sea floor, they provide indispensable functions for the associated flora and fauna, and invaluable services for livelihoods of large human populations in tropical coastal regions. Within the last few decades coral reefs have been increasingly endangered for various reasons, which can be directly or indirectly ascribed to anthropogenic influence. Chronic stresses can undermine the resilience of coral reefs, which then become more susceptible to the effects of pulse stresses, like hurricanes or thermally induced bleaching. Such an event may then diminish relevant ecosystem properties beyond a threshold, and thus trigger a sudden shift to an alternative state, which may not be in favour of corals but an alternative live form that then achieves dominance.

In my thesis I developed a spatially explicit individual-based model to simulate a benthic reef community, typical for a reef in the Western Indian Ocean region. The application was then used to explore key variables and -processes for resilience and to identify potential triggers for phase shifts. Several coral species with contrasting life histories and algae compete for space under different environmental influences. Evoked by direct neighbourhood-interactions and individual responses to environmental conditions, the system performs dynamic self-organisation, and properties of superordinate hierarchical levels (population, community) emerge as a consequence. In multiple scenarios I tested the influences of (i) two different perturbation types (bleaching and mechanical disturbances), -intensities and frequencies, as well as (ii) various levels of grazing and recruitment on the dynamics of coral reef communities.

As the results show, perturbations can generate heterogeneous outcomes. While extreme temperature events render a disadvantage for more susceptible branching coral species, these species can dominate under high frequencies of mechanical disturbance events, because they recolonize empty space faster, due to their faster growth rates. Low disturbance levels always benefit the dominance of massive growth forms and a combination of both perturbations at intermediate levels leads to high evenness in the community composition. The results additionally confirm, that herbivory and recruitment are crucial processes for the resilience and persistence of coral reefs.

This study also highlights the importance of a diversified analysis of coral reef dynamics to understand the full magnitude of consequences, caused by environmental change. The presented application renders an excellent tool (a) to integrate current knowledge, which can be kept up to date with little effort and (b) can be coupled with other modelling systems that operate on different spatial and temporal scales. Complexity and non-linear dynamics of coral reef functioning can thus be simulated and analysed with a high level of detail and informative value.

Zusammenfassung

Korallenriffe, die Regenwälder der Meere, sind von höchster ökologischer und ökonomischer Wichtigkeit. Obwohl sie nur einen kleinen Teil des Meeresbodens bedecken, erfüllen sie unverzichtbare ökologische Funktionen für die assoziierte Flora und Fauna und bieten eine unbezahlbare Existenzgrundlage für eine Vielzahl von Menschen in tropischen Küstenregionen. Im Laufe der letzten Jahrzehnte sind Korallenriffe jedoch aus verschiedenen Gründen, die direkt oder indirekt mit anthropogenen Einflüssen zusammenhängen, zunehmend bedroht. Chronischer Stress untergräbt die Resilienz von Korallenriffen, die dadurch anfälliger für akute Bedrohungen wie Wirbelstürme oder temperaturbedingte Korallenbleiche sind. Solche Ereignisse können Ökosystem-Eigenschaften dann so stark verändern, dass sie einen Schwellenwert unterschreiten und dadurch einen plötzlichen Übergang zu einem alternativen Zustand auslösen, der ungünstig für Korallen ist und zur Dominanz einer anderen Lebensform führen kann.

Während meiner Doktorarbeit habe ich ein räumlich-explizites Individuen-basiertes Modell entwickelt, um eine für den West-Indischen Ozean typische, benthische Korallenriffgemeinschaft zu simulieren. Mit Hilfe des Simulationsmodells wurden Schlüsselgrößen und -prozesse für Resilienz untersucht und potenzielle Auslöser für *phase shifts* identifiziert. Mehrere Korallenarten mit unterschiedlichen ökologischen Merkmalen und Algen konkurrieren unter verschiedenen Umweltbedingungen um Raum. Durch direkte Nachbarschafts-Interaktionen und individuelle Reaktionen auf Umweltbedingungen erfährt das System eine dynamische Selbstorganisation und als Konsequenz daraus entstehen Eigenschaften auf übergeordneten hierarchischen Ebenen (Population, Gemeinschaft). In mehreren Szenarien habe ich dann getestet, welche Einflüsse (i) verschiedene Störungstypen (Korallenbleiche und mechanische Zerstörung), -intensitäten und -frequenzen sowie (ii) unterschiedliche Fraß- und Rekrutierungslevel auf die resultierenden Dynamiken der untersuchten Gemeinschaften haben.

Die Ergebnisse zeigen, dass Störungen unterschiedliche Folgen haben können. Während extreme Temperaturanstiege für sehr Bleiche-anfällige verzweigte Korallenarten einen Nachteil bedeuten, dominieren diese Arten, sobald mechanische Störungen gehäuft auftreten, da sie schneller wachsen und freien Raum neu besiedeln können. Unter einem geringen Einfluss von Störungen sind massiven Korallenarten immer im Vorteil, und in Kombination bewirken die beiden untersuchten Störungstypen bei mittlerer Intensität eine hohe *evenness* in der Gemeinschaftsstruktur. Die Ergebnisse bestätigen außerdem, dass Herbivorie und Rekrutierung von Korallen bedeutende Prozesse für die Resilienz und den Bestand von Korallenriffen sind.

Diese Studie zeigt die Wichtigkeit auf, Korallenriffdynamiken diversifiziert zu analysieren, um das volle Ausmaß der Konsequenzen einer sich verändernden Umwelt zu begreifen. Die hier vorgestellte Anwendung ist ein ausgezeichnetes Werkzeug, um (a) aktuelles Wissen über Korallenriffe zu integrieren und (b) mit anderen Modellanwendungen, die auf unterschiedlichen räumlichen und zeitlichen Skalen operieren, gekoppelt zu werden. Komplexität und nicht-lineare Dynamiken der Funktionsweise von Korallenriffen können so sehr detailliert und mit hoher Aussagekraft simuliert und analysiert werden.

Preface

Goals & motivation

Coral reefs all around the world have been subject to unprecedented change during the last few decades and for most of these unique ecosystems this means decline at tremendously fast rates. They are of great ecological and economical importance, fulfil important ecological functions, such as providing habitat for numerous organisms and feature substantial ecosystem services, which guarantee the livelihood of vast human populations in tropical coastal areas. Their potential economic value is estimated between US$ 29.8 billion year^{-1} (Cesar *et al.* 2003) and US$ 375 billion year^{-1} (Costanza *et al.* 1997, but see Dixon 1998), and the annual fish catch, for example in South-East Asia amounts to 20-33 tons km^{-2} with estimates of 44 tons km^{-2} for isolated island reefs (Austin *et al.* 1996). Although the knowledge on specific properties of coral reefs is extensive, we are still far from understanding the whole extent of their functioning.

Much is known

Coral reefs are among the most intensively studied marine ecosystems in the world and some examples shall highlight, how much is known on specific topics of these unique ecosystems. Life history related properties, such as growth patterns, reproductive traits and dispersal (Veron 2000), the symbiosis with zooxanthellae (Rowan 1998, Baker 2003) and bacteria (Rohwer *et al.* 2002), as well as the process of calcification (Goreau 1963, Gattuso *et al.* 1999) are investigated for many different scleractinian coral species, which are the primary structure builders in reefs. Direct interactions between corals, algae, fish and several invertebrates have been analysed in many different combinations (Hay 1984, McCook *et al.* 2001, Mumby 2009). The ecology of commercially important, reef-associated fish (Nagelkerken *et al.* 2000, 2002) and invertebrate species is well understood, which however does not guarantee reasonable or sustainable use (Uthicke and Benzie 2000, Jackson *et al.* 2001). Also functional traits of fish communities have been explored intensively during the last few decades (Dorenbosch 2006, Walker *et al.* 2009). Darwin's paradox, which terms the high productivity of coral reefs in low-nutrient waters (Crossland 1983), lost much of its paradoxical character, since considerable work has been done on nutrient cycling of sponges (De Goeij *et al.* 2009), corals (Wild *et al.* 2004) and other invertebrates (Szmant-Froelich 1983). Connectivity between reefs and other habitat types (e.g. mangroves, seagrass beds) plays an important role in assessing the size and shape of marine protected areas and this field has also gained a lot of attention within the last two decades (Almany *et al.* 2009). It is known, that menaces for coral reefs are manifold and consequences of changing external conditions, like extreme temperatures or alterations of nutrient concentrations (Szmant 2002) or the pH (Hoegh-Guldberg *et al.* 2007, De'ath *et al.* 2009) have already been identified. As it is common for ecosystems, all of these processes are intertwined, which breeds highly complex responses to environmental change given the vast biodiversity and involved interrelations of coral reefs. At this point we leap into the not-so-well-known.

More is unclear

Although responses to environmental change are known for single species and their one-on-one interaction outcomes can be predicted, the whole picture blurs as soon as we throw all these species and variable environmental parameters together, and add relations and feedback processes spanning over multiple hierarchical levels. This opens up the arena for completely new questions, such as: (i) How is spatial competition altered if not only two individuals, but a community with several coral species and algae interacts? (ii) How do direct competition, specific life history properties and specific susceptibilities to changing external conditions affect the spatial configuration and the community composition in a reef patch? (iii) How do perturbations affect each other and the response of the coral community if they occur alone or simultaneously? – Do they enhance or compensate each other's effects? (iv) How do changes of larval input and a decrease in herbivory affect reef performance?

Model framework

Within this work I designed a model framework, in which different hypotheses, that deal with complexity and non-linearity in coral reefs, can be tested. I employed individual-based modelling (IBM) to create an application, that simulates spatial competition in a coral reef community, allows to integrate an optional number of coral species, and facilitates a detailed parametrization of competing algae and different environmental factors. Design and development were done in close collaboration with the Institute for Marine Sciences (IMS) of the University of Dar es Salaam, Zanzibar, Tanzania. The application was used to simulate spatial competition for a site-specific community composition under various regimes of environmental conditions to identify and analyse key functions of resilience and major causes for coral-algae phase shifts. The future goal is to provide an open-source generic tool which aids the analysis of local coral reef dynamics and may help to implement appropriate management measures for particular situations. In the following implemented organisms, as well as relevant principles of coral reef ecology and ecological modelling are introduced in more detail.

Reefs

Coral reefs feature extraordinary biodiversity (Connell 1978, Hughes *et al.* 2002), high productivity in oligotrophic waters (Hatcher 1990, 1997), and provide shelter, nursing-, and foraging-habitats for considerably large amounts of organisms (Ray 1988). Three types of coral reefs are distinguished: (a) fringing reefs which are close to the shore with a more or less shallow lagoon in-between, (b) barrier reefs which are further offshore and whose lagoon is deeper, and (c) atolls, circular (annular) coral reefs that encircle a lagoon (Darwin 1842).

Coral reefs are distributed all along the Tropical Belt, where a delicate range of sea surface temperatures, light conditions, and aragonite availability allows corals to thrive (Kleypas *et al.* 1999). Some of the hotspots for coral reefs are (i) the Coral Triangle which comprises Indonesia, Malaysia, Papua New Guinea, Philippines, Solomon Islands and Timor-Leste (Veron *et al.* 2009), (ii) the Great Barrier Reef (GBR) in front of the North-Eastern part of Australia, (iii) the Caribbean in the Gulf of Mexico and (iv) the Western Indian Ocean (WIO) region (Veron 2000). Among these reef systems the Australian GBR is probably the only one which is not subject to intensive human use, apart from tourism contributing about AUS$ 1.5 billion to the Australian economy, and carried out in a comparably sustainable way (Harriott 2003). In all other regions, and especially in developing countries, reef systems are heavily impacted by anthropogenic influence (Burke *et al.* 2011). In the WIO region, where large parts of the data for the here presented model are retrieved from, reefs and adjacent ecosystems like mangroves are directly used, not for tourism, but for livelihoods of coastal human populations. Fishing, harvesting of invertebrates (Salm 1983), and often destructive fishing techniques (Muhando 2009), coral mining (Dulvy *et al.* 1995) and deforestation of mangroves, both for firewood and to create space for aquacultures (Alongi 2002, Rönnbäck *et al.* 2002) are just a few examples for the intensive anthropogenic influence.

For a long time coral reefs have been considered as oases in otherwise unproductive marine deserts with the prevailing opinion that reefs were closed, fragile climax systems found in areas with only little environmental fluctuation (Hatcher 1997). But today we know that they are dynamic systems closely associated and interlinked with their environment, like adjacent seagrass and mangrove systems (Nagelkerken *et al.* 2002), with which they are in a constant exchange of abiotic and biotic components. For example, many fish species frequent one, two or all of these habitats throughout their life time (Cocheret de la Morinière *et al.* 2003, Nagelkerken 2007). For some species mangroves serve as nurseries before they continue their adult life on the coral reef. Among these are e.g. parrotfishes (Scaridae), some of which are important grazers on reef systems (Mumby 2006, Mumby and Hastings 2008) and limited to intra-reef movement, when adult (Hobson 1972). Other

Fig. 1 **Ukombe Reef** close to the South-Western coast of Unguja Island, approximately 15 km South from Zanzibar town.

species leave the reef during nights to forage in adjacent habitats and return at daytime to rest in schools and shelter from predators (Hobson 1973). Reefs are also influenced by terrestrial water run-off and river outlets transporting sediments, nutrients and different pollutants (ISRS 2004), which can be buffered by intact mangrove systems at the land-ocean interface (Jupiter *et al.* 2003). The awareness for connectivity as being crucial for sustainability and persistence of coral reefs has increased tremendously in the last 20 years and is nowadays indispensable in management (McCook *et al.* 2009, Almany *et al.* 2009).

Coral reef communities

The true hard corals (Scleractinia), cnidarians of the class Anthozoa and the subclass Hexacorallia, are the primary structure builders in tropical coral reef systems, and set the stage for many different organisms. These hermatypic corals fix carbon, which they assimilate and apply for the production of calcium carbonate skeletons, hard structures, that provide the typical three-dimensional structure in coral reefs (Fig. 1). They live in a close symbiosis with unicellular algae, dinoflagellates of the genus *Symbiodinium*, the so-called zooxanthellae. Via photosynthesis zooxanthellae produce carbohydrates and high-caloric value lipids (Muscatine and Cernichiari 1969, Battey and Patton 1984), which they trade for carbon dioxide and nitrate, and thus contribute a considerable amount to the energy budget of their animal host (Szmant and Gassman 1990, Dubinsky and Jokiel 1994).

The growth morphology of a scleractinian coral strongly depends on its polyp characteristics, like size, growth rate and reproductive mode (Vaughan and Wells 1943). This constitutes many different formations, among which are submassive (e.g. of the family Faviidae, the brain corals), foliacous (e.g. *Turbinaria* sp., the salad coral), laminar or tabular (e.g. *Acropora hyacinthus*), and free-living (e.g. from the genus *Fungia*) (Veron 2000). For the model application I concentrated on two growth morphologies: massive with a hemispherical shape (e.g. *Porites lutea* and *Porites lobata*), and branching with a tree-like shape (e.g. *Acropora muricata* and *Pocillopora damicornis*), two groups with quite contrasting live histories. While massive corals feature relatively low growth rates (see Chapter 2, Tab. 1), they are generally competitively superior in direct contact with branching colonies, and less susceptible to extreme temperature events and breakage by surge or currents (Chapter 2, Tab. 3).

Dispersal in sessile benthic organisms is primarily conducted by reproductive stages, and corals feature several asexual and sexual reproduction modes (Veron 2000). For sexual reproduction a general distinction is made between brooding and broadcasting species. Brooding species like *Pocillopora damicornis* are hermaphroditic – male and female polyps are situated on the same colony; oocytes are fertilized in the polyp and fully developed planula larvae are released into the water column (Harrison and Wallace 1990). They mostly reproduce several times a year and produce relatively low numbers of propagules. Broadcasting species are either hermaproditic (see above) or gonochoric, where male and female polyps are situated on different colonies (Harrison and Wallace 1990). Either way, female polyps produce oocytes and male polyps produce sperm, all released into the water column where they possibly meet and the oocytes get fertilized. Here the fertilization probability is higher for hermaphroditic species because eggs and sperm are often ejected in bundles (Veron 2000). In contrast to brooders, spawning in broadcasting species occurs only once or twice a year with many propagules being released (Harriott 1983, Clark 1998) and larvae are distributed in a wider range compared to brooding species. This normally happens with high intra- and interspecific synchrony at many sites (Babcock *et al.* 1986, van Woesik 2010), depending on multiple triggers (Guest *et al.* 2008), but can also occur asynchronously (Baird *et al.* 2000, Mangubhai and Harrison 2008). The fertilized oocytes then develop into planula larvae, which are distributed passively by ocean currents but also can actively swim (Harrison and Wallace 1990, Stake and Sammarco 2003). After several days they eventually settle on suitable habitat, either randomly or, as found for many species, triggered by chemical cues of crustose coralline algae that promote larval settlement and metamorphosis (Heyward and Negri 1999, Negri *et al.* 2001, Harrington *et al.* 2004). Once settled, the larva transforms into a coral polyp, which starts calcifying and reproducing asexually by budding, thus founding a new colony, matures and contributes to the next generation.

Interactions between corals are generally decided by respective defensive traits or in case of two conspecifics the larger colony will overgrow the smaller one. Many massive species are, for instance, equipped with effective sweeper tentacles and digestive filaments and also dominate in direct competition due to their sheer structure, while branching corals rely on their fast growth rates and thus colonization speed (Burkepile and Hay 2009). Structurally a branching coral is inferior in direct competition with a massive coral of roughly the same size, unless it has extraordinary defensive traits. A smaller massive colony, though, will be overgrown by the branches, and thereby shaded and weakened. If two massive colonies touch, the larger one will always overgrow the smaller one, but other factors, like the momentary fitness may influence the competitive outcome. For example, Rinkevich and Sakai (2001) found that *P. lutea* is competitively inferior to *P. lobata* if fragments of approximately the same size are located next to each other.

Algae become increasingly important in the study of coral reefs, as they may be promoted by global climate change. In this work I distinguish macroalgae and algal turfs. Although I am aware of the fact that some crustose coralline algae can have positive effects on coral recruit settlement and survival (Heyward and Negri 1999, Negri *et al.* 2001, Birrell *et al.* 2008b), here algal turfs contain all filamentous and crustose algae and are treated as hindering for coral larvae settlement, hence negative for coral recruitment (Birrell *et al.* 2005, Kuffner *et al.* 2006). Macroalgae are a standard component in coral reefs and provide good services in moderate numbers (Mejia *et al.* 2012). Nevertheless, during the last few decades they have become more and more abundant in many sites and can be classified as the primary competitors for hard corals in general. In direct comparison macroalgae lead a life on the fast lane; they colonize fast, grow fast, and die fast (Diaz-Pulido and McCook 2004) and besides sexual reproduction they can also disperse by fragmenting. On top, many of these species have strong defensive compounds (Rasher and Hay 2010), are vectors for diseases (Nugues *et al.* 2004) or attract corallivore invertebrates (Wolf *et al.* 2012). Direct competition often results in reduced growth, survival, and fecundity for the coral (Burkepile and Hay 2009). Furthermore, seaweeds can overgrow dead coral skeletons (Diaz-Pulido and McCook 2002), directly harm a coral colony by abrasion or indirectly by shading (McCook *et al.* 2001), or hamper the reproductive output and/or settling of coral larvae (Birrell *et al.* 2008a, Diaz-Pulido *et al.* 2009). Algal abundances are controlled by herbivores, among which invertebrates and fishes constitute a large fraction (Carpenter 1986, McClanahan and Shafir 1990, Mumby *et al.* 2006), but on the other hand sea urchins (McClanahan and Muthiga 1988, Done 1992) and grazing fishes also facilitate considerable bioerosion and fragmenting damage on reef structures (Glynn 1997).

Reefs at risk

Coral reefs are on a global retreat, and threats, which can explain their decline are numerous. Natural disturbances, like hurricanes, temperature-induced bleaching or coral diseases have hit coral reefs for centuries, but the systems seemed to have a high resilience and enough time to recover (Pearson 1981). Additionally, such disturbances were mostly local events and larval input for the recovery of populations was still maintained from outside reefs. Nowadays, threats like thermal bleaching often act on regional or global scales, occur in combinations and therefore often superimpose local disturbances and each other's impacts. They also prevent recovery, because they occur in too short time intervals (see also Chapter 2, Hughes and Connell 1999). Direct anthropogenic influences, like mechanical disturbances by anchorage, boat crashes, coral mining or blast fishing destroying the reef structure (Davis 1977, Dulvy *et al.* 1995, Rogers and Garrison 2001, Dinsdale and Harriott 2004), or poison fishing, compromising the physiology of organisms (Barber and Pratt 1998), take their toll. A reduction of grazing intensities due to overfishing (Daskalov *et al.* 2007) as a result of an increasing demand for food (Burke *et al.* 2011) or due to the loss of a key herbivore, like the 1983 die off of *Diadema antillarium* in the Caribbean (Lessios *et al.* 1984) may increase algal densities and, in the long run impede coral survival. Additionally, there are indirect imposed effects, like agricultural run-off and sewage, containing nutrients and pollutants (ISRS 2004) which exert similar effects as poison on corals and may even advantage algal proliferation (Schaffelke and Klumpp 1998, Fabricius 2005). Deforestation of coastal forests and mangrove systems increases sediment loads, which suffocate the reef (Muzuka *et al.* 2010). Last but not least, global climate change has a huge impact: the concentration of atmospheric greenhouse gases and with it global temperatures have increased tremendously in the last three decades and a resulting West-East temperature gradient causes an elevated likelihood for a higher frequency of extreme events, such as El Niño or hurricanes (Timmermann *et al.* 1999, Harley *et al.* 2006, Hansen *et al.* 2006). Very high or very low sea surface temperatures induce bleaching of many different coral species and we know that some species will go extinct earlier than others (Hughes *et al.* 2003), especially if intervals between bleaching events are too short to allow recovery. CO_2 concentrations in the atmosphere have increased and will not decrease in the near future (Nakicenovic *et al.* 2000), the gas dissolves into the seascape and decreases the pH in the water column. Thereby calcium carbonate structures are either eroded or cannot be produced sufficiently, any more (Hoegh-Guldberg and Bruno 2010), impeding coral survival.

Resilience, stability and phase shifts

To define stability as a concept for ecological systems has caused confusion because mathematically stability often has been assumed to relate to equilibrium conditions (Holling 1973). Holling (1973), therefore adopted the definition of resilience from physics for ecology, which "determines the persistence of relationships within a system and is a measure of the ability of these systems to absorb changes of state variables, driving variables, and parameters, and still persist." In his view resilience and stability are two important properties of an ecosystem where resilience allows change but stability tends to return the system into the equilibrium state, from which it has been deflected by a perturbation. The above definition allows to integrate non-linear processes which are common in nature, and hence to see ecosystems as complex adaptive systems (Lansing 2003) facing constantly changing influences from the outside with internal adaptations. In such a definition a system is always bound in a transitional state of some sort and never reaches an equilibrium point, but fluctuates around it.

Within a coral reef, resilience is provided by the species diversity (Loreau *et al.* 2003), functional redundancy (Nyström *et al.* 2008), various life histories of reef participants (Vermeij *et al.* 2007) and the fact that species act on different spatial and temporal scales (Hobson 1973, Burkepile and Hay 2010). In other words, for a reef resilience can be seen as an insurance for the system to not fall into an alternative state with unfavourable conditions.

If in an ecosystem a bifurcation point or a critical threshold for a given changing property is reached the system can undergo a sudden phase shift to an alternative state which may become stable (Scheffer *et al.* 2001, Scheffer and Carpenter 2003). Under chronic environmental stress, for example in an overfished reef site, when decreased resilience levels prevail, such a threshold can be reached at even lower rates of change. In a coral reef these are often coral-algal phase shifts but may also result in the dominance of an alternative life form, such as corallimorpharians, sponges, soft corals or sea urchins (Norström *et al.* 2009). In some cases newly established feedback processes lock the system in these permanent states (Nyström *et al.* 2012). Nevertheless, even though a reversal is possible, hysteresis prevents the system from achieving it by simply re-establishing pre-shift conditions (Scheffer *et al.* 2001). For a backward-shift, circumstances would have to be made even more favourable for corals than before the shift. In a reef which has undergone a coral-algal phase shift due to overfishing, a no-take area which would constitute high herbivore densities over a few decades, might serve the purpose (see also Chapter 3).

Individual-based modelling

Individual-based modelling (IBM) emerged in the 1970s and found its early applications in the terrestrial (Kaiser 1976) as well as in the aquatic context (DeAngelis *et al.* 1979). Soon it proved to be an exceptional tool for the representation and simulation of complex ecological dynamics, because it allows a spatial representation of heterogeneous entities with individualistic behaviour in a heterogeneous environment (Breckling 2002).

In IBM the environment is mostly represented as a two-dimensional grid which allows to place different properties in the individual cells. Values of environmental variables can then be treated universally for the whole grid (e.g. water temperature in a reef patch) or vary from cell to cell (e.g. nutrient availability for plants), customized for the demand of detail of the analysis. Individual organisms are described in classes, blueprints, which contain all the relevant information on life history traits and also the behavioural and physiological rules for an organism. If the focal organisms would be, for example corals, then the properties may be the species, the initial size of an individual coral colony, a specific growth rate, its reproductive mode etc. The behavioural rules could then describe their direct interaction with their neighbours as well as their environment, like it is done in the presented application. At program start an optional number of coral individuals (copies) is implemented, each featuring its particular combination of initial variable values. In every time step, each individual's neighbourhood is checked and an appropriate (re)action chosen for the interaction with each neighbour, as well as for environmental conditions. Thereby the system exhibits dynamic self-organisation and higher level properties, like population structure or community composition, emerge in consequence of small scale interactions.

Because in an IBM arbitrary entities can be chosen, allowing a realistic representation of focal organisms, field data can be used directly, without the need of pre-processing. This also allows a straightforward communication with people who have no strong background in computer science, making IBMs excellent tools for management measures that include local communities in developing countries. Although the development of an application with IBM requires a lot of time and knowledge of the studied system, it is nevertheless a promising technique for the analysis of ecological complexity because it allows to represent large amounts of components and processes in adequate detail with a low degree of abstraction – and that amount increases with computing power.

Outline of the chapters

The following part outlines the four first author publications, which are part of this thesis. All necessary equipment as well as field trips and attendances to relevant scientific meetings, which supported the preparation and advancements of the here presented work were provided by the Leibniz Center for Tropical Marine Ecology (ZMT) in Bremen.

Chapter 1

Andreas Kubicek, Esther Borell

Modelling Resilience and Phase Shifts in Coral Reefs – Application of Different Modelling Approaches

This chapter gives an overview of different model applications in coral reefs, each of which features distinct techniques, foci, assumptions, and goals. Functioning, advantages and limitations of the different applications are described in detail, and compared in a final discussion.

Chapter 2

Andreas Kubicek, Christopher A. Muhando, Hauke Reuter

Simulations of long-term community dynamics in coral reefs – How perturbations shape trajectories

In this chapter the model application is introduced. It contains a detailed model description, validation and sensitivity analysis and shows the effects of different modes of perturbations, namely temperature induced bleaching of corals or mechanical disturbances in different intensities and frequencies. It gives insights on community responses to different perturbations and highlights the advantages of a divergent analysis of coral reef dynamics.

Chapter 3

Andreas Kubicek, Hauke Reuter

Multiple feedbacks in coral reefs

Due to their high complexity coral reefs feature many different feedback loops. The model application is used to analyse several interconnected feedback systems, and how they react on changes of environmental variables. In this article potentials for coral-algae phase shifts are examined and also, how a recovering reef would perform, if released from unfavourable conditions.

Chapter 4

Andreas Kubicek, Fred Jopp, Broder Breckling, Christoph Lange, Hauke Reuter

Hierarchically structured validation of individual-based models: How to consider qualitative, compositional and quantitative implications

Individual-based model applications mostly operate over several hierarchical levels which complicates the validation with traditional methods, where model output can be simply compared to empirical data, taken at the same level. This article introduces an alternative methodology for the validation of individual-based models, where processes are mostly implemented on very low hierarchical levels, e.g. for the organisms, and higher level properties emerge from small-scale interactions. The presented approach demonstrates several options, of how to validate the model on each of the emerging higher levels, such as the population or the community, in order to increase the informative value of such applications.

Chapter 1

Modelling Resilience and Phase Shifts in Coral Reefs – Application of Different Modelling Approaches

Andreas Kubicek and Esther Borell

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Chapter 17
Modelling Resilience and Phase Shifts in Coral Reefs: Application of Different Modelling Approaches

Andreas Kubicek and Esther Borell

Abstract Tropical coral reefs are among the most diverse habitats with great ecological and economic importance. These highly dynamic ecosystems are frequently subject to natural disturbance events (e.g. hurricanes) which can lead to dramatic changes in reef properties if the systems' resilience is already reduced by anthropogenic impacts such as increased levels of nutrients or over-fishing. Due to their high complexity many relations in coral reef dynamics are still poorly understood and ecological modelling becomes increasingly prominent as a tool to close these knowledge gaps. This article gives an overview on different modelling techniques that address the investigation of coral reef dynamics and discusses advantages and disadvantages of respective applications.

17.1 Introduction

Tropical coral reefs are complex ecological habitats, that are the most diverse of all marine ecosystems, with estimates of benthic and pelagic organisms ranging from 600,000 to more than 9 million species worldwide (Reaka-Kudla 1997). Scleractinian corals (stony corals, Cnidaria, Anthozoa) are the main reef builders. They fix calcium carbonate, which produces the majority of the habitat structure for other reef organisms. Coral reefs are dynamic systems within a wider network of closely interlinked habitats such as mangroves and seagrass beds, (Nagelkerken et al. 2002; Mumby and Hastings 2008), which are frequently subjected to natural disturbances (Connell 1997; Buddemeier and Smith 1999). However, the nature and temporal pattern of disturbances have changed severely over the past few decades coinciding with global climate change (Veron et al. 2009) and increasing anthropogenic activities in coastal areas (Mora 2008), often exceeding the regenerative capacity of reef systems (Bellwood et al. 2004).

A. Kubicek (✉)
Department of Ecological Modelling, Leibniz Center for Tropical Marine Ecology GmbH (ZMT), Fahrenheitstrasse 6, 28359 Bremen, Germany
e-mail: andreas.kubicek@zmt-bremen.de

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Chronic alterations of a reef environment including increased levels of nutrients, overfishing and the release of toxic compounds can severely undermine reef resilience and thus the ability of reef communities to cope with new disturbances superimposed onto those already existing (Nystroem et al. 2000). Reduced resilience inhibits or delays reef regeneration after a disturbance event, which can lead to long-lasting or even irreversible changes in community structure; so-called phase shifts to alternative stable states (Hughes and Connell 1999; Hughes et al. 2007). The resultant alternative state is manifest in either a new dominant coral species (Aronson et al. 2004) or an alternative life-form, like corallimorpharians (Kuguru et al. 2004), ascidians, soft corals, sponges and urchin 'barrens' (Norstroem et al. 2009) and very often algae (McManus and Polsenberg 2004). Regardless of the nature of these shifts, they generally all culminate in a conspicuous loss of benthic invertebrate and fish diversity as well as a decrease in inorganic carbonate deposition, which in turn reduces reef complexity, overall species richness and increases shoreline erosion.

Important factors that mediate resilience include (1) the degree of diversity within functional groups, functional redundancy and the response diversity within each group, (2) demographic structure of populations, (3) recruitment success, and (4) ecosystem connectivity, i.e. exchange processes among reefs or between reefs and adjacent habitats within a given seascape.

When diversity of coral reef species is high and species interact in a highly structured environment, feedback loops occur over a wide range of scales. Thus, descriptive approaches using mean average measures or starting from reduced statistical assumptions might not be appropriate for analysing the complex structure and underlying processes. Here modelling may help to integrate the multitude of components, relevant variables and parameters to describe and visualize complex ecological processes and the driving forces which shape the resilience of a system. Models may also be used to simulate the behaviour of specific system components in response to a changing environment (Fig. 17.1).

In the following subsections we describe different approaches to modelling reef resilience including examples of a trophic model which is based exclusively on differential equations (Sect. 17.2) and a Cellular Automaton (CA) model which allows spatial explicit analysis (Sect. 17.3). Section 17.4 introduces how Individual Based Modelling (IBM) can facilitate the implementation of direct individual interactions of organisms and Sect. 17.5 gives an example of a grid based community model which combines differential equations and a CA approach. We have chosen these examples to illustrate and discuss the possible advantages and drawbacks of presently applied ecological modelling techniques.

17.2 Equation-Based Modelling of a Coral Reef Food Web

McClanahan (1995) developed a differential equation model to evaluate the impact of fishing on Kenyan coral reefs. The model simulates the food web of a virtual reef ecosystem of undefined spatial extent in which corals and algae comprise the primary

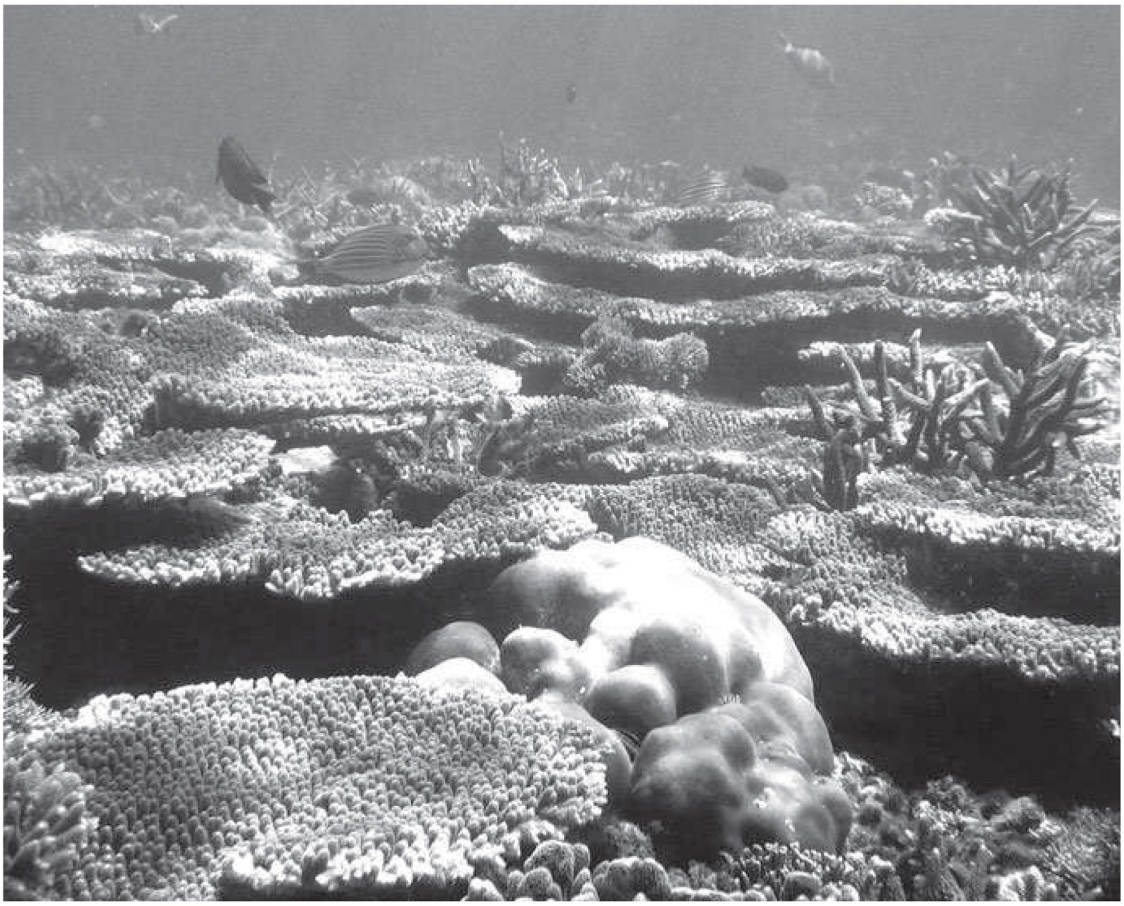

Fig. 17.1 Intact coral reef, Sulawesi/Indonesia (Photo by E. Borell)

producers, herbivores consist of sea urchins and herbivorous fish and predators are composed of invertivorous and certain piscivorous fish as well as humans, i.e. fishermen.

Model relationships and parametrisation were all based on empirical studies and local fisheries data. To keep the model at an operational size, McClanahan considered only a limited number of the system's key components and their interactions and left out other food web pathways such as phytoplankton, detritus or corallivores and top predators, such as sharks. Gross and net reef production is calculated by combining production and respiration for both algae and corals. Although the model considers that both groups fix calcium carbonate from the seawater, corals in the model calcified at rates ten times greater than algae and thus represented the major calcium carbonate depositors. Sea urchins and herbivorous fish competed for algae and in the process of foraging eroded reef structure with the erosion by urchins being tenfold higher than that of fish.

Invertivores controlled the abundance of urchins and in the model switched to an unspecified alternative food source upon depletion of sea urchins. This had the effect that invertivores did not experience bottom-up control, which decreased fluctuations in model dynamics. Herbivorous fish were controlled by piscivores. At the very top end of this web were humans who ultimately constitute a somewhat arbitrary control of all fish present in the system. All processes in this model were described by utilizing a matrix of interlinked differential equations (Chap. 6).

Through variation of the state variables 'fishing experiments' were performed in order to assess the effects of fishing intensity and catch selection on fisheries yield, community structure and ecological processes. McClanahan performed a total of five simulation runs to specifically determine (1) the model's prediction of successional dynamics, (2) the effect of removing all bony fish, (3) the effect of removing only piscivores, (4) the effect of removing all fish except invertivores, and (5) model predictions of a scenario where sea urchins (or fishing) do not have a detrimental effect on live coral. Model simulations of different scenarios revealed that the modification of a single variable in this web of highly interrelated components has important ramifications for reef development. One of the major findings of the model (and later verified by field studies) was that coral reefs are prone to have more than one equilibrium state for realistic parameter ranges (see Chap. 6), influenced by the extent of fishing or the abundance of piscivores (Fig. 17.2). The simulation results showed that if all fish groups were harvested, two equilibrium states could occur, one governed by herbivorous fish and the other by sea urchins. A third ecological state was manifest by high algal and low coral cover associated with the low abundance of either herbivorous fish or sea urchins. The fisheries management strategy that is predicted to produce the highest yields whilst maintaining high primary productivity and calcium carbonate deposition was to harvest piscivores and herbivorous fish and to leave invertivores unharvested. For this case, the model predicted the amount of piscivores to quickly decline, taking predation pressure off the herbivorous fish and channelling the majority of algal production into herbivorous fish, while invertivores kept the sea urchin abundance low. When fishing levels were highest, algal biomass was predicted to increase and

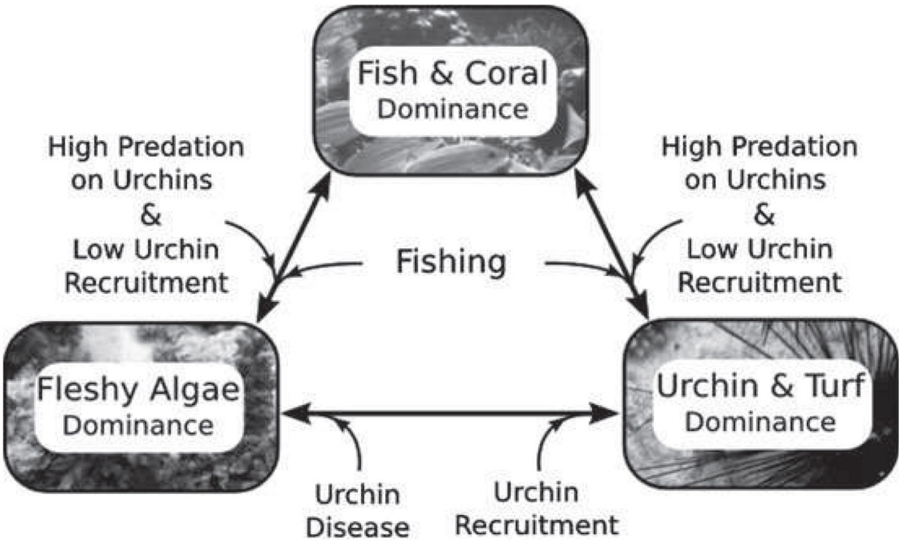

Fig. 17.2 Transition processes between different equilibrium states of the coral reef ecosystem indicated by model simulations and field studies. Adapted from McClanahan (1995)

competitively exclude corals. Calcium carbonate deposition would remain high because of the proportion of calcifying algae and because bioerosion would decrease due to low sea urchin and fish abundance.

McClanahan's model has the general applicability to assess coral reef food web interactions through a somewhat holistic approach rather than focusing on a limited number of organisms and interactions. However, a major shortcoming of this type of modelling is presented by the fact that it is highly aggregated. Treating several components under the umbrella of one variable, i.e. the grouping of various components according to functional types or trophic groups severely reduces natural variability and may therefore easily mask processes which are crucial attributes to the system's dynamics. Considering that different species or functional groups of algae and corals, do exhibit very different types of tolerance to a given environmental condition, the lack of distinction can lead to the oversimplification of a given scenario.

17.3 Spatial Competition Between Coral Species: Application of a Cellular Automaton Modelling Approach

Langmead and Sheppard (2004) designed a classical cellular automaton model (Chap. 8) to assess the effect of natural background disturbance (e.g. sedimentation, predation) on a coral community on a Caribbean fore-reef slope. Each disturbance event can be set to occur over different spatial scales and at varying levels of intensity. The model comprises ten different coral species that compete for space. Each of the species has a specific pattern of recruitment, growth, mortality rate and aggression (i.e. competitive potential).

The simulation area of the model reef comprises a torus with a total size of 9 m^2 that is subdivided into 1 cm^2 cells corresponding to a median sized coral polyp. Each of these cells can contain either bare substratum or one of ten coral species at a time.

The model was exclusively parameterized with data obtained from the literature. Coral growth was based on annual skeletal extension rates of each species and was expressed as radial expansion. Growth was determined by the rules for competitive interactions between corals: Colonies could only grow into adjacent cells if they were either unoccupied (bare substratum) or occupied by a competitively subordinate species (species were ranked according to their aggressiveness). Depending on the differential susceptibilities to disturbance and varying mortality rates, each species was assigned a probability of mortality if impacted by disturbance. Based on data for larval settlement in the study area, each coral species was set to be present at a specific density and the number of potential recruits was then determined annually using a Poisson probability distribution. Recruitment success was determined by larvae abundance and the amount of free space in the plot as recruits are only allowed to settle on bare substratum.

To gain a better understanding of the spatial extent of disturbance (i.e. the fraction of the plot that is disturbed) and the size of disturbed patches, two different scenarios were created: First, the spatial extent of disturbance was varied at five intervals ranging from 0 to 0.6 while the size of disturbed patches was kept constant. In the second scenario, the total disturbed fraction of each plot per year was kept constant and the size of disturbed patches was varied. The sizes of disturbed patches followed a power law model in which frequency of disturbance events is related to their spatial extent; i.e. smaller disturbances were set to occur more often than larger ones.

Recruitment and background disturbances were updated yearly while growth and competitive interactions were iterated once every 3 months.

Simulations were run for 500 years (complete cycle of the model) and percentage cover of each species was taken on an annual basis. The data derived from the model simulations were fed into a Bray–Curtis matrix in order to determine the sensitivity of the variables on species diversity, species composition and mortality in response to each of the model parameters.

The results showed that in the absence of disturbance, the reef was occupied by competitively dominant species and that those species featuring low aggression and low growth rates were lost after short periods of time. Intermediate levels of background disturbance favoured high coral diversity, which supports the classic hypothesis of intermediate disturbance (Grime 1973). Accordingly, the amount of bare substratum increased with higher levels of disturbance and was accompanied by a decrease in biodiversity.

The relative importance of total colony mortality to partial colony mortality changed with colony size class. Total mortality was more important for small colonies while large colonies were most sensitive to partial mortality. For sensitive species, competitiveness, i.e. aggressive potential had the greatest influence on community composition. Growth was also an important factor whereas mortality and recruitment had the least impact on the model.

Model evaluation showed that only five out of the ten simulated species were comparable to actual field observations. Despite this relatively weak congruence (mainly resulting from insufficient data), for coral population size structures, the model was able to accurately represent growth and distribution for seven out of the ten species. The results indicate that size structure of populations is a much more precise indicator for testing the predictive abilities of the model than the simple comparison of coral cover.

Another important aspect of the results was the apparent relationship between the threshold of partial and total colony mortality and modal colony size on a log-scale, which demonstrates that colony size and age may be decoupled earlier than was previously thought (e.g. see also Bak and Meesters 1998). Also, the results indicate that size of disturbed patches was as important in structuring coral communities as the overall amount of disturbance (Fig. 17.3). This poses an important consideration when looking at recovery mechanisms of reefs since the spatial extent of cleared substratum is rarely directly quantified in the field, but is usually determined indirectly through differences in coral cover. Even though

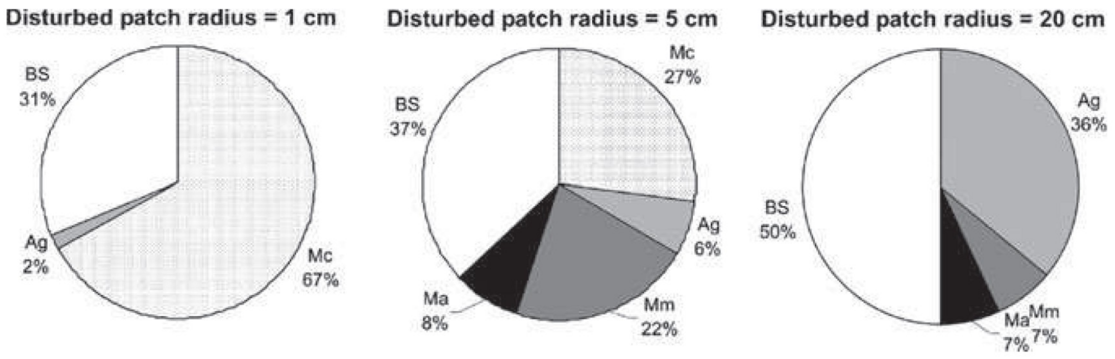

Fig. 17.3 Effect of disturbed patch size on community composition while the total fraction of disturbed reef area was kept constant. Mean percent cover at 500 years for the most abundant species (Mc *Montastraea cavernosa*, Ma *Montastraea annularis*, Mm *Meandrina meandrites*, Ag *Agaricia* spp.) and bare substratum (BS). [From Langmead and Sheppard (2004)]

some interesting information can be deduced from this approach, the overall applicability of the model in a broader context of coral reef dynamics and effects of disturbance events is limited due to its small size and the lack of other key components such as grazers and algae, which can play a crucial role in structuring coral reef communities.

17.4 Macroalgal Growth Patterns Simulated with an Individual-Based Model

Many macroalgae exhibit non-deterministic phenotypic growth, which enables them to thrive under different environmental conditions. Yniguez et al. (2008) designed an individual-based (or agent-based, see Chap. 12) model (SPREAD, Spatially-Explicit Reef Algae Dynamics) to investigate the effects of key growth factors (nutrients, light, temperature) as well as disturbance and mortality on the growth rates and growth morphology of the calcifying algae *Dictyota* and *Halimeda* spp. at four different sites (two inshore and two offshore reefs) within the Florida Keys Reef Tract. Model performance was empirically evaluated with local growth rate and structure for *H. tuna* at these sites.

To determine the effects of different environmental conditions on the growth patterns of the algae, Yniguez et al. (2008) used single modules (see Fig. 17.4) as the interacting components in their model rather than representing whole algal individuals. The emergent properties of superordinate hierarchies such as the whole individual organism, the population or the algal community were thus derived from interactions of single modules. The model environment was composed of a three-dimensional cubical grid (edge length ~30 cm) and subdivided into 1 cm^3 cells. Each cell contained information about light and space availability, nutrients and temperature. Temperature and nutrients were kept uniform for all cells at each time step but changed with season. Light availability was determined for each cell

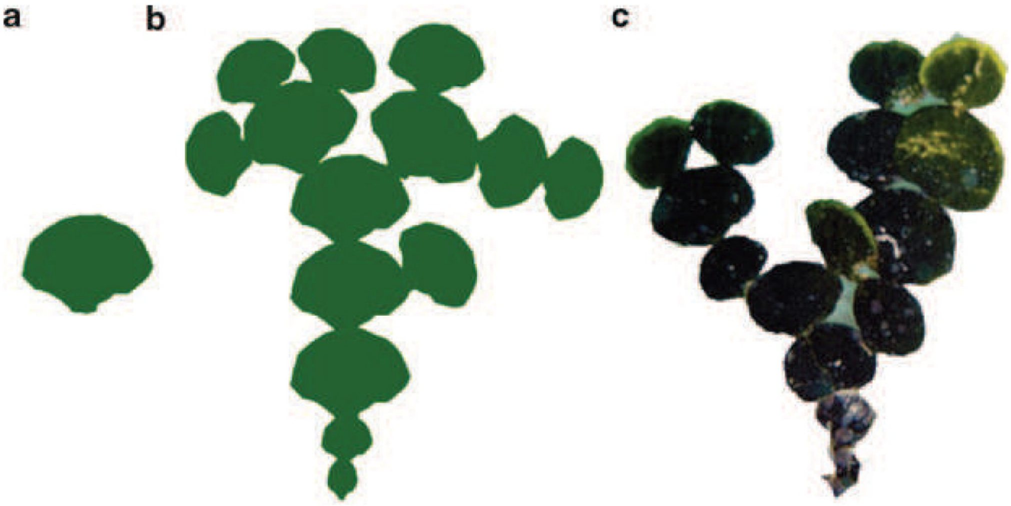

Fig. 17.4 *Halimeda tuna* – a single module as interacting components in the model (**a**) the modelled growth pattern (**b**) and a photograph of the actual alga (**c**). Taken from Yniguez et al. (2008)

individually depending on depth and shading effects of existing modules. At the start of the simulation, the initial values for state variables and the number of model organisms were set corresponding to field observations. The model used discrete daily time steps. Each module had direct information of its position within the grid and was able to retrieve/'sense' environmental parameters for both its own cell and its neighbourhood. Based on this information, probabilities for growth (defined as the production of a new module by an existing one) and growth pattern were calculated and newly produced modules positioned. If existing modules were situated at the edge of an alga they could be randomly selected for fragmentation, which implied an additional mortality probability for the fragment. At the end of an iteration the three-dimensional grid was transformed into a two-dimensional square to calculate the percentage of cover for each species.

A total of 30 replicate simulations (each over a period of 1,000 days) per site revealed striking similarities for morphometric characteristics of model *H. tuna* and field data such as the number of segments per individual alga between different sites and the relationship between growth (segment production) rates and depth. *H. tuna* from the deepest site featured the highest growth rates and the highest number of produced modules per individual, while individuals of the shallowest site had low growth rates and low numbers of segments. Despite small divergences between model prediction and field data, the natural inter-site differences in growth morphometrics were well reflected by the model. Due to its fine-tuned nature this technique is not yet applicable to larger scale simulations mainly due to limitations in computing capacity. Similar methodologies were already applied in the study of plant architecture and morphology by utilizing so called L-Systems (see also Chap. 11). This approach is novel in the marine context and can contribute valuable information regarding small scale processes, which can be fed into larger scale models when depicting natural variability.

17.5 Ecosystem Model for Phase Shifts in Caribbean Coral Reefs

The current collapse of many coral reefs in the Caribbean is thought to be a combined effect (Bellwood et al. 2004) of overfishing of herbivorous fish (Hughes 1994), coral diseases (Bythell and Sheppard 1993), hurricanes (Bythell et al. 1993), coral bleaching (Kramer et al. 2003) and local deterioration of water quality (Littler et al. 1993). Macroalgal blooms on the overfished reefs in the Caribbean were, until the early eighties mainly prevented by a single species of sea urchin *Diadema antillarum*. The mass mortality of *D. antillarum* in 1983 (Lessios 1988), left parrotfish (Scaridae) as the main herbivores on many Caribbean reefs.

To gain a better understanding of the relative importance of fishing of parrotfish and parrotfish grazing for coral-algal dynamics, Mumby (2006) merged different modelling approaches within one application that facilitates the integration of interactions within and between different trophic levels of a typical Caribbean coral reef community. The main model in this study constitutes a grid based spatial explicit simulation model for a hypothetical reef that combines empirical data derived from field studies, experiments and other models. The second model is an equation based approach, which was designed to model the processes of parrotfish grazing in order to parameterize their grazing behaviour in the main simulation model.

The Basic Coral Reef Model

The model addressed the dominant massive reef building coral species (as most branching species were eliminated by the white band disease) on a common Caribbean reef in the *Montastraea annularis* zone at mid-depth (5–15 m) where coral diversity and abundance were found to be highest. The model was parameterized with data from Glovers Reef of Long Cay (LC) in Belize. The virtual reef area comprised a 625 m^2 (25 m × 25 m) lattice made up of 2,500 rectangular cells (0.5 m × 0.5 m). The functional organisation inside the cells resembled that of a classical cellular automaton. Unlike a classic cellular automaton however, the cells were able to accommodate more than one distinct entity, i.e. different organisms and/or dead substratum at the same time. The benefit of such an organisation is that the observer is able to split up populations into smaller groups thereby facilitating a semi-individual model behaviour. Contrary to an IBM, organisms in this model did not interact directly with each other but the trajectory of an organism's behaviour and development was determined by the characteristics of its own cell (i.e. composition of components) and those of its neighbourhood.

The model was iterated every 6 months; an interval that is sufficiently long to allow for meaningful assessments of coral growth and coral distribution. Yet, direct algal cover is the outcome of a dynamic balance between algal production (area for colonization, recruitment rate, and growth) and algal removal (grazing), processes that occur over much shorter time spans. For this reason Mumby (2006) developed a second model to parameterize parrotfish grazing intensity, in which he determined the proportion of area grazed within a 6-month period. The calculations incorporate parameters for fish species, abundances, sizes, sex, and feeding activity (bite rates). According to the results, in an unharvested parrotfish community 30% of the total area was grazed, while in heavily depleted populations the grazed proportion comprised only 10% and for areas of intermediate fishing pressure, this fraction amounts to 20%.

The main model included corals, algae, urchins and parrotfish (Fig. 17.5). However, urchins were excluded from most model scenarios since a large scale recovery of *D. antillarum* populations was considered unlikely and outbreaks of diseases could readily reoccur. Corals and algae (see Table 17.1 for summary of attributes for corals and algae) were placed randomly on the grid until distinct

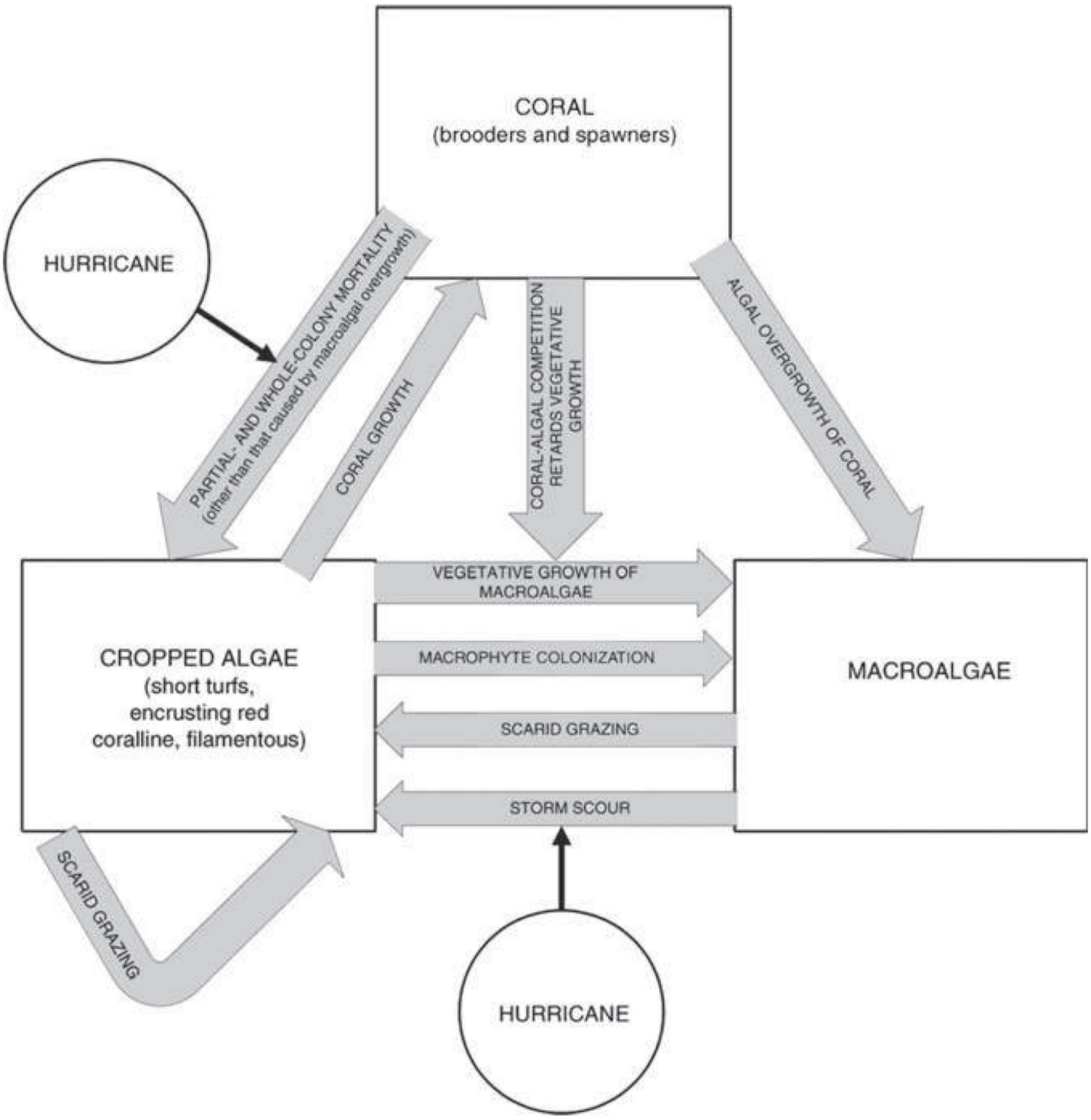

Fig. 17.5 Processes included in the simulation model (*arrows*) that link the major functional categories of reef organisms (*boxes*). Taken from Mumby (2006)

Table 17.1 Major attributes of corals and algae and the main rules utilized in the model

Corals	Algae
General information	
Massive corals Two groups according to reproductive mode: 1) Brooders, e.g. *Porites astreoides* 2) Spawners, e.g. *Siderastrea siderea*	Macroalgae and cropped algae Age classes: Cropped algae 0–6 months Cropped algae 6–12 months Macroalgae 0–6 months Macroalgae 6–12 months
Reproduction/recruitment/dispersal	
Larval production depending on maturity state/size class for high coral cover: juvenile (<60 cm^2) → no larvae pubescent (60–250 cm^2) → ~50 larvae × cm^{-2} adult (>250 cm^2) → ~210 larvae × cm^{-2} Number of recruits that can settle per cell depending on settling ground: Bare substrate → 4 recruits Cropped algae → 2 recruits Macroalgae → 0 recruits → the density of spawning coral recruits is ten times lower than that of brooding ones	Probabilistic overgrowth of cropped algae (A) by macroalgae (M) within a von-Neumann-Neighbourhood, depending on proportions of macroalgae (M_{4c}) and corals (C) if $C \geq 0.5$ PA → M → $0.75 \times M_{4c}$ if $C < 0.5$ PA → M → M_{4c}
Growth	
Constant diametric growth rates: 8 mm × year^{-1} (brooders) 10 mm × year^{-1} (spawners)	If cropped algae are not grazed for 1 year they turn into macroalgae
Mortality	
Periodic – annually Smaller coral colonies are more susceptible to partial and whole-colony mortality than larger ones Stochastic – hurricanes Proportion of corals is subject to partial or whole-colony mortality; based on mean fraction of reef destruction across the Caribbean	Periodic – annually Proportion of algae which are eaten by grazers → depending on grazer density Stochastic – hurricanes Proportion of macroalgae become cropped algae if located on disturbed patch; based on mean fraction of destruction across the Caribbean
Interactions and processes	
If corals reach maximum cell size (2,500 cm^2): →Larger colonies grow over smaller colonies →Corals grow over cropped algae →Corals can displace macroalgae	Macroalgae can grow over cropped algae Macroalgae can grow over corals (depending on coral colony size) and lead to partial or whole-colony mortality

proportions of spatial cover had been reached with the rest being occupied by sand and rubble.

Corals were divided into two functional groups according to their mode of reproduction, comprising either brooders or spawners. Brooding corals produce planula larvae which settle in the vicinity of their parent colony. Spawners (commonly referred to as broadcast spawners) release gametes and the planulae are dispersed in the water column and may migrate many kilometres before settlement.

The model was parameterized with data for *Porites astreoides* and *Siderastrea siderea* for brooders and spawners respectively. Both maturity and reproductive output were expressed as a function of colony-size and the efflux of larvae from reefs was quantified from the size-frequency distribution of coral colonies. Coral recruitment was parametrized with data from an offshore reef in Belize which had high adult coral cover and high biomass of grazing fish. Coral recruitment in the model was set to occur at an initial colony size of 1 cm in diameter with the settlement success being determined by the components of their cell (i.e. rugosity and algal characteristics). A linear stock-recruitment relationship was created based on the assumption of high adult coral cover and optimal larval supply. The massive growth forms of coral colonies were expressed as hemispheres and growth rates were modelled by linear extension rates of the hemispheres (Table 17.1).

Mortality rates of corals were also colony-size dependent where whole colony mortality was generally lower for mature (large) colonies than for smaller ones. Large colonies were able to overgrow smaller colonies in basic interactions once colonies had reached the maximum implied size of a cell. Macroalgae were able to overgrow coral recruits and to cause extensive partial mortality of larger colonies.

Data on hurricane mediated mortality was derived from the impact of Hurricane Mitch on mature colonies of *M. annularis* in Belize where at least 90% of the colonies experienced partial-colony mortality. The frequency of hurricanes could be varied according to geographical area. Since the simulation area of 625 m^2 is relatively small, the chances that a reef would be either completely destroyed or missed entirely by a hurricane were high. For this reason the model used the mean percentage of destroyed reef area for the whole simulation area rather than subdividing it into patches of heavy and light destruction.

Algae were distinguished as either cropped algae (cropped substrata) or macroalgae. Cropped algae included encrusting coralline red algae, fine filamentous algae and algal turfs, which were contained within one category because coral recruitment, i.e. coral settlement and post-settlement mortality is associated with all of these types. If cropped algae were not grazed, spores of macroalgae (here in the model *Dictyota* spp. and *Lobophora variegata*) developed into a fleshy canopy that prevented coral settlement. Macroalgal growth progressed by either of the following pathways: Cropped algae which were not grazed over the period of 1 year turned into macroalgae. Once established, macroalgae were able to overgrow cropped algae in neighbouring cells depending on their relative cover and that of corals within a von-Neumann-Neighbourhood (see also Table 17.1). If coral cover was low, macroalgae could overgrow an area of cropped algae similar in size to the area they occupied, whereby high coral cover reduced this area by 25%.

Simulations and Results

An a priori sensitivity analyses revealed that initial coral cover, grazing and hurricane frequency were all important factors influencing coral cover over a period of 20 years. It is important to bear in mind that the model was only simulated on the reef dynamics of initially 'healthy' reefs. The most important findings of the simulations may be summarized as follows:

First, in the absence of any acute disturbance event and the urchin *D. antillarum*, coral cover always increased when grazing was carried out by an unexploited community of parrotfish. This in turn had a positive influence on recruit survival where highest densities correlated positively with highest coral cover. Second, in the absence of *D. antillarum*, the dynamics of coral cover were highly sensitive to changes in hurricane frequencies. Reefs that experienced hurricanes on a decadal basis showed a net decline in coral cover whereas a hurricane frequency of 20 years allowed for full recovery akin to the initial 30% coral cover. Reefs that were subjected to hurricanes at even lesser frequencies (e.g. 40–60 years) exhibited rapid reef growth. On the other hand, the inclusion of *D. antillarum* enabled reefs to withstand hurricanes on a decadal basis and the results showed that overall diversion in reef recovery (i.e. reef trajectory) between different hurricane frequencies decreased. Third, a reduction in parrotfish biomass lead to substantial changes in reef community. High parrotfish biomass (i.e. high grazing) resulted in a 25% increase in coral cover. Conversely, coral cover decreased from 30 to 7% when parrotfish were heavily depleted. Furthermore, the results demonstrate that grazers (or the depletion of them) is a fundamental and overarching factor in shaping the trajectory of reef development in Caribbean forereefs. All other parameters, such as whole-colony mortality rates, connectivity, larval retention and dispersal had a negligible effect on coral cover. Last, reefs that maintained a healthy parrotfish population showed clear phases of reef growth in between hurricane disturbances which recurred at 40-year intervals. In contrast, reefs with a partially depleted parrotfish population being subjected to the same hurricane frequency exhibited a steady decline in coral cover.

Interestingly, examination of temporal shifts in the relative size-frequency distribution of corals under different disturbance scenarios also indicates that hurricanes and the exploitation of grazers had very contrasting effects on coral populations: Under intense exploitation of grazers, the coral size distribution become bimodal and the population experienced a bottleneck among the juvenile size classes. On reefs with high levels of grazers but frequent hurricane disturbances, populations were characterized by high numbers of juvenile and pubescent colonies while the adult part of the population experienced a bottleneck.

Improvement and Adjustment to Different Questions

This study illustrates that the overall outcome of the model could not have been predicted by simply examining the parametrisation due to the intricate nature of biotic and abiotic interactions across spatial and temporal scales. The results of this model received strong support by proceeding studies using modified versions of the same simulation model. The importance of sea urchins for the ecological balance between corals and macroalgae on Caribbean reefs was confirmed by Mumby et al. (2007) who investigated the susceptibility to and persistence of macroalgal dominance on Caribbean reefs. Mumby and Hastings (2008) extended the model by including vicinity to mangroves as an additional factor and two different depths as additional parameters in order to assess the relative importance of mangroves (they function as nursery grounds for Scarid fish) on the abundance of parrotfish on adjacent reefs. In another recent study Mumby (2009) uses the same model to assess the stability of alternative stable states of Caribbean reefs. Here, the parameters pertaining to external disturbances were omitted and instead the model concentrates on the inherent parameters of coral community dynamics. In contrast to the model discussed here, growth rates, sizes at maturity, overgrowth and mortality were now not set as fixed values but determined probabilistically, which allows for a higher degree of natural behaviour of the model due to a broader range of natural variability. The reef community dynamics were investigated with regard to different levels of grazing intensity ranging from 5 to 40%. Simulations were run in 6 month intervals for a total of 36 single reefs. With this approach, Mumby was able to identify clear threshold levels of grazing intensity (i.e. the level of grazing necessary to prevent the shift to an alternative state) for different sets of initial coral cover and different levels of grazing.

Spatially explicit modelling approaches to understand the impact of grazers on coral reefs have only emerged over the past 5 years. The models by Mumby offer a novel approach to overcome the problem of reef complexity, which to date has complicated experimental studies of the interactions of multiple disturbances. However, a word of warning should be issued regarding the organisation in a lattice. The complexity of the model may lead to complications in the definition of clear rules for interactions between individual organisms which are not located in the same cell. For example, if a coral outgrows its cell, the part that protrudes into the adjacent cell becomes an integral component of that cell and thus ‘fragmented’ from its original colony. It starts to function as a new and smaller entity with rules and trajectories of a juvenile coral colony, since age is determined via size. The fact that most processes are determined via a von-Neumann-Neighbourhood might compensate for the loss in detail to some extent, however, depending on the questions asked, there may still be a risk to ignore certain important processes.

17.6 Summary and Conclusions

The techniques currently available in ecological modelling all bear certain limitations and the choice of a given approach depends on the question of interest.

The exclusive utilization of differential equations (Sect. 17.2) can provide interesting results for different fishing scenarios in a relatively complex simulation environment, that may help to improve fisheries practices. Often these techniques lack resolution, however, as all components are aggregated into functional (larger) groups, which substantially obscure the inherent natural variability among relevant components. This can be compensated through the employment of a cellular automaton as illustrated by Langmead and Sheppard (2004). It allows for spatially explicit analyses through disaggregating populations into single interacting coral polyps. On the downside, because the rules of this CA model do not address cell aggregations (i.e. the whole coral colony) they cannot change in relation to individual colony attributes.

The grid based approach by Mumby (2006) allows to integrate a suite of important components of a coral reef system, which makes it possible to describe the complex characteristic processes for coral reef communities. This application constitutes a novel approach to the analyses of resilience and phase shifts of coral reefs. It builds on the concept of a cellular automaton by implementing distinct procedures within one cell and allows for dynamic changes of certain rules, e.g. larger colonies are less likely to be overgrown by algae than smaller ones. The combination of different modelling techniques does not only improve model performance but also helps to identify some of the deficits in our current research and may reveal how future experiments could be adjusted in order to fill the gaps. Yet, the structure with distinct spatial entities – the cell – limits this approach in its flexibility. The formulation of rules for several cells or across cells becomes very complicated and could be easier accomplished by utilizing a continuous area.

In contrast, individual based modelling (IBM) is free from such limitations because the model area does not have to comprise spatial aggregation of the acting units. Yniguez et al. (2008) give a good example for an applied IBM. In their model the environment is organized as a grid which holds different states for environmental variables. Interactions either between algal modules and/or algal modules with their environment are possible in all directions with dynamic changes of rules in relation to the component's attributes. The utilisation of IBM offers several useful tools to study resilience as object-oriented programming (Chap. 4) provides the possibility for a detailed description of organisms (as objects) in separate subprograms (see also Chap. 12). This constitutes a very fine-tuned approach to model detailed interactions on small scales. In addition, an IBM allows to integrate all earlier developed modelling techniques, like equation based sub-models or CAs, wherever intended or needed to create an application with highly dynamic performance and realistic behaviour.

Understanding the factors supporting resilience and the characteristics of phase shifts is imperative if we want to understand current and future coral reef dynamics. Both resilience and phase shifts comprise highly complex processes that are not yet fully understood. Over the past few years modelling has become a prominent tool to tackle ecological questions in coral reef science. Modelling has not only contributed a great deal to advance our understanding of potential driving forces pertaining to reef resilience, but also helped to identify the current scientific gaps and research deficits in this discipline. Future modelling approaches that merge past and present information derived from previous models, with data of specific sites will substantially enhance our abilities to identify local driving forces of reef dynamics. This may be employed in management programs that can help to improve the sustainable utilisation of resources.

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Chapter 2

Simulations of long-term community dynamics in coral reefs – How perturbations shape trajectories

Andreas Kubicek, Christopher Muhando, Hauke Reuter

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Simulations of long-term community dynamics in coral reefs – How perturbations shape trajectories

Andreas Kubicek[1], Christopher Muhando[2], Hauke Reuter[1]

1) Leibniz Center for Tropical Marine Ecology, Bremen, Germany
2) Institute for Marine Sciences of the University of Dar es Salaam, Zanzibar, Tanzania

Abstract

Tropical coral reefs feature extraordinary biodiversity and high productivity rates in oligotrophic waters. Due to increasing frequencies of perturbations – anthropogenic and natural – many reefs are under threat. Such perturbations often have devastating effects on these unique ecosystems and especially if they occur simultaneously and amplify each other's impact, they might trigger a phase shift and create irreversible conditions.

We developed a generic, spatially explicit, individual-based model in which competition drives the dynamics of a virtual benthic reef community – comprised of scleractinian corals and algae – under different environmental settings. Higher system properties, like population dynamics or community composition arise through self-organization as emergent properties. The model was parametrized for a typical coral reef site at Zanzibar, Tanzania and features coral bleaching and physical disturbance regimes as major sources of perturbations. Our results show that various types and modes (intensities and frequencies) of perturbations create diverse outcomes and that the switch from high diversity to single species dominance can be evoked by small changes in a key parameter.

Here we extend the understanding of coral reef resilience and the identification of key processes, drivers and respective thresholds, responsible for changes in local situations. One future goal is to provide a tool which may aid decision making processes in management of coral reefs.

Keywords: coral reef resilience, disturbance, bleaching, benthic community dynamics, individual-based modelling, Zanzibar

Summary

The degradation of coral reefs is a major threat for tropical coastal environments, worldwide. For this reason we developed a spatially explicit model which simulates competition in a benthic reef community under the influence of various environmental factors.

Here we highlight the impact of two major perturbation types on the long-term dynamics of a standard coral reef off Zanzibar Island, Tanzania. While mechanical disturbances are more inspecific and affect all organisms of the reef similarly, temperature-induced bleaching causes selective impact among coral species within the benthic community. Our results show clearly that complex systems which are organized of a multitude of diverse entities and hence feature complex emergent properties, need to be analyzed on different integration levels rather than seen as a black box.

Our tool may help to disentangle the combined effects of different perturbations and to analyze their respective impact on the benthic community of a coral reef. Hence, it will help to direct future research foci and to coordinate management measures for distinct site specific contexts.

2.1 Introduction

Tropical coral reefs are highly productive but also fragile ecosystems that provide habitats for the coastal fauna and multiple services to local human communities [1]. Due to their high biodiversity, they exhibit a complex pattern of interactions between organisms and their environment with feedback loops within and between trophic as well as different hierarchical levels [2], and thereby facilitate a framework of non-linear dynamics which complicates a holistic analysis. Although extensive knowledge of corals, their responses to environmental change [3] and interaction with other organisms [4], and reef resilience [5] has been gained in the last few decades, the understanding of coral reef functioning is still far from being complete [6].

Reefs are increasingly under threat and many coral species are in danger of becoming extinct [7], due primarily to anthropogenic influence. Globally, coral reef systems are subject to rising sea surface temperatures which increase their susceptibility to bleaching, and to ocean acidification which erodes $CaCO_2$ structures. Both stressors are chronically increasing and can be attributed to climate change [3,5]. Additionally it is predicted that extreme weather events (e.g. el Niño or hurricanes) will strike with increasing frequency [8,9]. Directly imposed human pressure upon coral reefs can have physical – e.g. by the use of destructive fishing techniques [10,11], sedimentation [12], or anchorage [13–15] – or chemical – e.g. nutrients, sewage, pollution [11,16] – consequences.

The overall tendency of coral reef systems to react to changes in environmental conditions and anthropogenic influences can be described by the term resilience. It "… determines the persistence of relationships within a system […] and is a measure of the ability of these systems to absorb change […] and still persist." [17]. In a coral reef it may be determined by species diversity, functional redundancy, life history of reef organisms, species functioning at different spatial and temporal scales, and connectivity to other reefs or habitat types [18,19]. Reduced resilience can impose catastrophic regime shifts [20,21] and in a reef often leads to a phase shift from coral dominated systems to alternative states; i.e. dominance of macroalgae [16,22,23] or of other benthic organisms [24], but see [25].

During the last two decades a series of ecological models have been applied to coral reef ecosystems. Among these we can find applications on various spatial and temporal scales. While Kleypas *et al.* [26] seek to approximate the possible geographic range for coral reefs to exist globally, other applications focus on conservation [27] or sustainable fishing regimes [28,29]. There are yet other models at the regional, local and/or small scale [30–34] with the purpose to explore the influence of environmental conditions on spatial processes and interactions of coral reef community dynamics, and some of these models, like [35] are designed to aid management decisions.

Individual-based modelling (IBM) has proven to be an exceptional tool to tackle ecological questions with adequate detail [36–38] because properties of investigated ecological systems can be described very close to reality. By including, for example, heterogeneously varying individual interactions and spatial heterogeneity, IBMs considerably extend the range of ecological modelling [39]. In this study we focus on individual benthic organisms and their interaction with the environment because these processes and the spatial configuration of a community are the base for environmental responses to perturbations in reality as well. There is a lot of knowledge on properties of individual coral colonies of various species; e.g. which symbionts they possess, how they grow, and how they react to thermal stress [40,41], upon changing environmental settings in general, or if faced with other benthic organisms within their local neighborhood [42–45]. All of these factors are relevant for the understanding of coral reef functioning and should be included in an analysis of local reef dynamics.

To date, the application of individual-based models in the context of coral reefs is very scarce, but interesting models have been developed for some investigations. Yniguez *et al.* [46] described the three-dimensional growth pattern of *Halimeda tuna*, a common macroalga in Florida Key reefs. Sleeman *et al.* [47] utilize an individual-based model to analyze different spatial arrangements of coral transplants in order to improve reef restoration measures. Koehl *et al.* [48] simulated larval transport in turbulent waters, and Brandt and

McManus [49] investigated the spread of the white plague disease in various coral populations. Tam and Ang [50] present a strictly theoretical 3-dimensional model in which they describe disturbance-induced changes in a coral community with three different hypothetical coral growth patterns.

Here, we present a generic multi-species individual-based coral reef model in which scleractinian coral species and algae compete for space. This tool enables the analysis of key functions for coral reef resilience and the identification of major causes of phase shifts for local situations. In our example we apply a basic system with a standard parametrization for a typical Western Indian Ocean reef system.

In order to improve the understanding of how climate change and different modes of human interference affect trajectories of specific reef sites and their resilience we examine community responses under various environmental settings. Hence, we apply (1) different frequencies of major bleaching events, (2) mechanical disturbance regimes, and (3) both perturbations acting together to test the influences on the benthic community.

2.2 Material & Methods

Model description

A) General

In this spatially explicit, individual-based model competition of benthic organisms (i.e. corals, macroalgae and turf) can be represented under various environmental settings (Fig. 1). It consists of a two-dimensional continuous area on which all free space is considered as potential settling ground for all organism groups (see also Appendix, Fig. 1). Individual life histories (e.g. recruitment, growth, death) of corals and algae and their interactions are described and each organism reacts specifically to environmental influences like

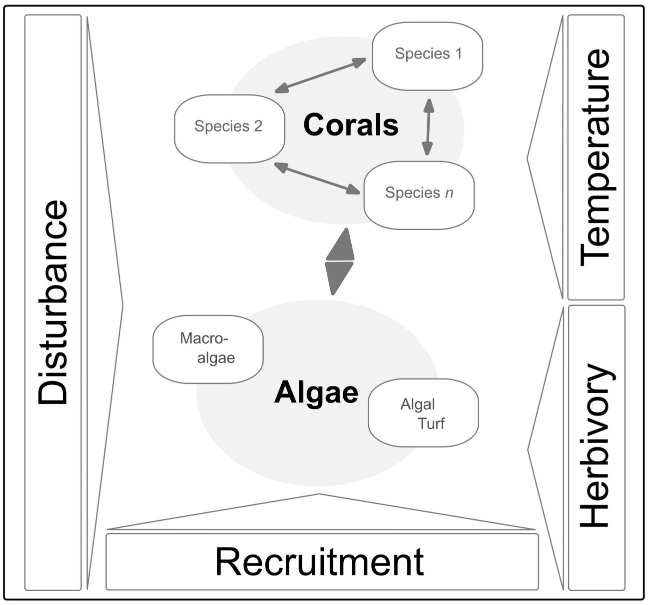

Fig. 1 **Overview of model components.** Different coral species interact with each other and with two different types of algae. Mechanical disturbance affects the whole benthic community whereas high temperature triggers bleaching only in corals and herbivory affects only algae.

temperature and mechanical disturbances (both investigated in detail). In the model, temperature influences the bleaching susceptibility of a coral colony and mechanical disturbance processes kill and remove all organisms inside the disturbed area. Macroalgal density is controlled by grazing through herbivores, which we implemented as a density dependent process. The model has been developed using the MASON multiagent simulation toolkit (see http://cs.gmu.edu/~eclab/projects/mason/) and is available at sourceforge (see http://sourceforge.net/projects/siccom). Details of the model implementation and parametrization will be described in the following sections.

B) Organisms

Corals

Coral species are described with a detailed life history (Fig. 2) which may differ in growth pattern, growth rates, reproductive pattern, and susceptibility to temperature-induced bleaching. The life-cycle of a coral is simulated by considering all major processes; i.e. reproduction, release of gametes, and the settlement of recruits, as well as their growth or mortality due to external factors or interaction with neighbors (Fig. 3). The generic structure of species parameters (see Tab. 1-3) allow the specification of a wide set of different functional coral groups.

CORALS – GROWTH (PATTERN / RATE)

We distinguish between massive and branching growth morphologies. Virtual corals basically grow with a constant rate extending their radius from a center, however, their growth performance is restricted by interaction with neighboring organisms or by their individual fitness (Appendix, Fig. 2). Branching coral colonies are implemented as a 24-point star, of which the axis length represents the colony's extent in a respective direction. Massive corals consist of the same 'skeleton' but here the endpoints of the star are connected to form a polygonal shape. The average radius of a colony is used to calculate the colony's cover and hemispherical surface area. To minimize edge effects, a coral's axis that expands over the borders of the simulation area cannot grow larger than the average radius of its colony.

CORALS – REPRODUCTION

In the model, coral reproduction determines recruitment numbers and depends on the specific reproductive traits. We differentiate between gonochoric broadcasters, hermaphroditic broadcasters and hermaphroditic brooders. Two different processes contribute to the total amount of recruits. Internal recruitment from the simulated reef itself and external

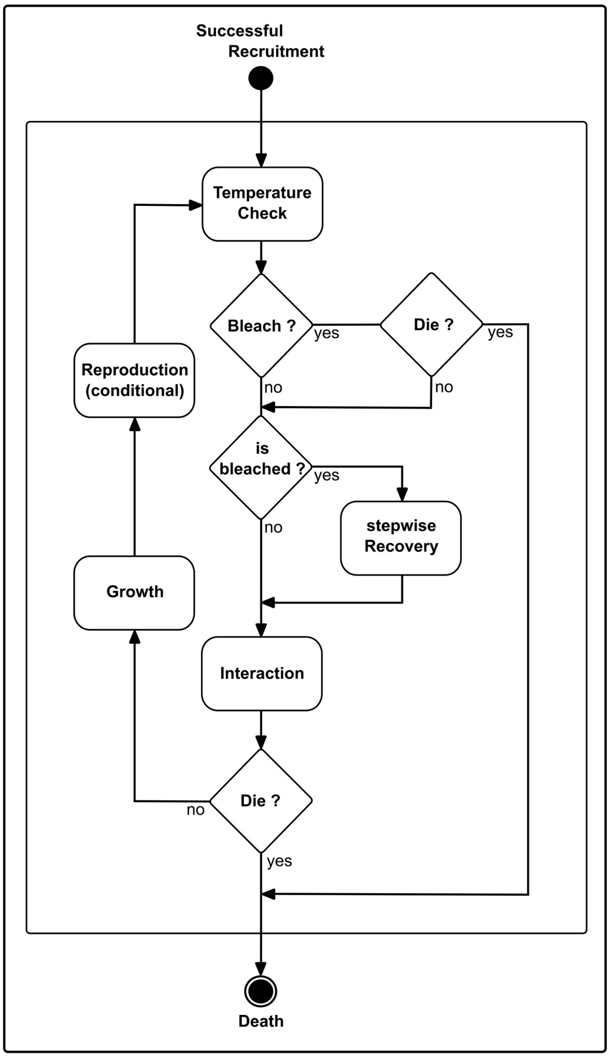

Fig. 2 **Flow chart of important processes of an individual coral colony.** If recruit settling is successful the coral colony enters its life-cycle. Within each iteration it checks the temperature upon which it decides if it will bleach or not. If it bleaches it can die or recover. In the next step it interacts with its neighbourhood and if it does not die, it grows. Reproduction only takes place when the reproductive cycle allows it.

recruitment from adjacent reef systems. Internal supply is estimated via a stock-recruitment relationship, where the larvae output per mature colony is calculated by multiplying the gametes or larvae per cm² with the surface area of massive and branching colonies, respectively. To estimate the surface area of a colony we multiply the hemispherical surface area (based on the average radius) of a respective colony, by the specific surface factor (see Tab. 2). The 'external supply' is divided into a basic rate (a fixed number of entering recruits per m² per recruitment event) and a variable amount, which is defined as a multiple of the internal stock-recruitment. Thus the focal reef patch can be considered statistically representative of the overall local situation and with a complementary connectivity factor to consider the distance to adjacent reef systems; i.e. a low value indicates low connectivity and *vice versa*. The amount of total recruit input for a species is then summed up from internal and external supplies and multiplied by a retention factor that integrates several factors, like (a) the reproductive mode, (b) the proportion of fertilized eggs, (c) predation, (d) the proportion of retained larvae and (e) early stage mortality. Settling larvae are distributed randomly on the simulation area. This approach allows for the depiction of a feedback process between the population density of a specific coral species and its number of recruits and simultaneously considers the relation to neighboring reefs.

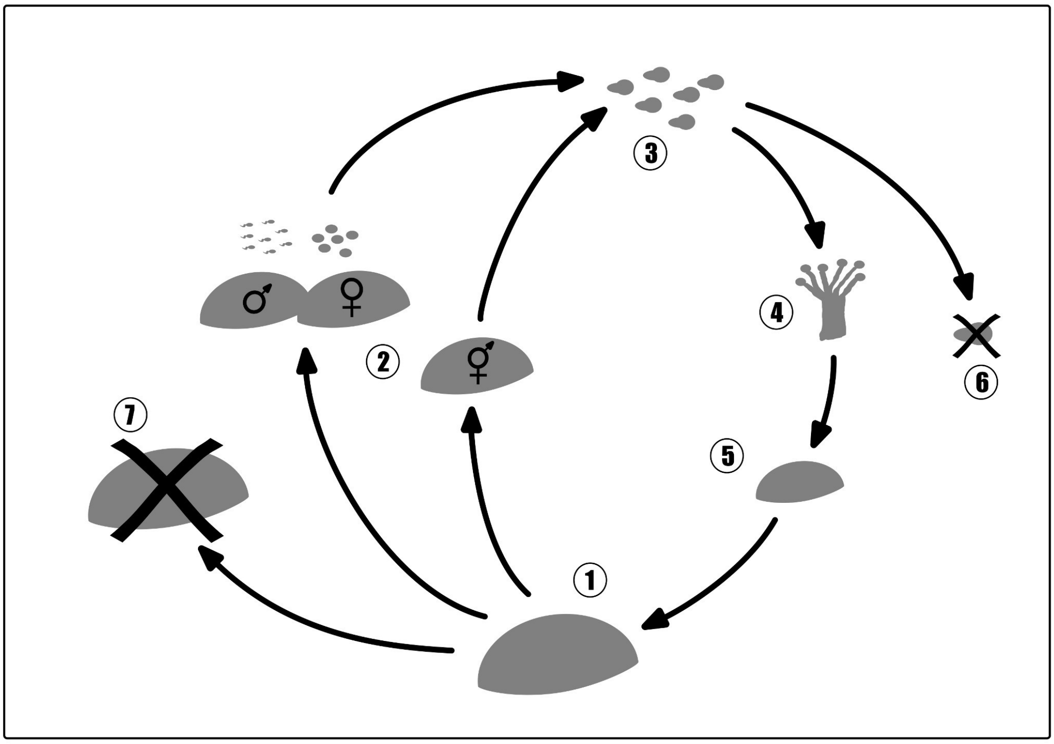

Fig. 3 The life-cycle of a virtual coral which applies for massive and branching groups. 1) A mature coral colony produces gametes. 2) Hermaphroditic brooders directly release planula larvae, colonies of hermaphroditic broadcasters release bundles of eggs and sperm, and gonochoric broadcasting species release eggs or sperm, respectively. In the latter two modes fertilization takes place in the water column and planulae develop. 3) The larva is distributed and settles randomly on the simulation area. If it settles on another living organism (6) it will die and is removed. A larva that recruits on unoccupied space develops (4 and 5) into a new colony. 7) Overgrowth, disturbance or bleaching can lead to the death of a coral colony, which is then removed from the simulation.

Tab. 1 Linear extension rates of the implemented coral species.

Species	Mean Lateral Extension Rate (mm/year)	Location	Source
Porites lobata	14.9	Ambon, Indonesia	[85]
	11.5	Cano Island, Costa Rica	[86]
	14.3	Java, Indonesia	[85]
	12.2	Lahaina, Maui, Hawaii	[87]
	11.0	Oahu, Hawaii	[88]
	6.4	Oahu, Hawaii	[89]
	7.8	Olosega, American Samoa	[90]
	14.7	Sulawesi, Indonesia	[86]
All Average	**11.6**		
Porites lutea	22.4	Abaiang Atoll, Kiribati	[91]
	5.7	Eilat, Gulf of Aqaba	[92]
	7.6	Enewetak, Marshall Islands	[93]
	19.4	Koh Phuket, South Thailand	[94]
	9.8	Kota Bontang, Indonesia	[95]
	11.0	Moorea, Society Islands	[96]
	16.7	Shikoku, Japan	[97]
All Average	**13.2**		
Acrpora muricata	123.3	Davies Reef, GBR	[98]
aka *A.formosa*	116.3	Hikkaduwa Nature Reserve, India	[99]
	62.6	Houtman Abrolhos, Western Australia	[100]
	34.2	Magnetic Island, Australia	[101]
	39.6	Magnetic Island, Australia	[102]
	86.4	Phuket, Thailand	[103]
All Average	**77.1**		
Pocillopora damicornis	32.2	Cano Island, Costa Rica	[85]
	50.2	Contadora Island, Panama	[104]
	25.0	Guam, Philippine Sea	[105]
	16.1	Lord Howe Island, GBR	[106]
	18.5	Oahu, Hawaii	[107]
	18.6	Oahu, Hawaii	[108]
	59.1	Pearl Islands, Panama	[109]
	18.0	Phuket, Thailand	[110]
	11.0	Rottnest Island, WA	[111]
	12.4	Solitary Islands, GBR	[85]
All Average	**26.1**		

Tab. 2 Reproduction parameters of the different coral species.

	Fix input (recruits cm^{-2} $event^{-1}$)	No. of Recruitment Events (events $year^{-1}$)	Spat size (mm)	Size at Maturity (diameter[cm])	Eggs/Larvae per cm^2 surface area	Polyps per cm^2 surface area	Eggs per polyp	Retention Factor	Surface Factor	Reproductive Mode
Porites lobata	0.01	1	1 [115]	8 [113]	1210 [112]	-	12 [118]	1.0E-8	1.5	gonochoric spawner [120-122]
Porites lutea	0.01	1	1 [115]	8 [113]	1375	19.1	72 [113]	1.0E-8	1	gonochoric spawner [120-122]
Acropora muricata (*formosa*)	0.01	1	1.2 [115]	4 – 7 [114]	109.5	15 [119]	7.2 [117]	4.5E-8	5	ermaphroditic spawner [120-12
Pocillopora damicornis	0.01	12	2 [115]	4 – 7 [114]	2.5 [116]	-	-	1.5E-7	3	hermaphroditic brooder [121]

CORALS – BLEACHING

Currently effects of temperature on corals focus on bleaching events. A model coral bleaches when a specific minimum bleaching temperature sum (see also Environmental Settings; Temperature) exceeds its threshold (see Tab. 3; values according to [51]; Fig. 3, transformed to 30-100% bleaching probability). In the case of bleaching, mortality occurs with a specified probability. Bleached corals, that do not die, will recover within the next 6 months with a reduced performance in growth and interaction strength during that phase. All affected rates (e.g. growth) increase linearly from 0% (full effect) to 100% (no effect) over this time span. Recruits settling on a bleached coral undergo a reciprocal survival probability, from 100 % on a fully bleached coral to 0% on fully recovered individuals.

Tab. 3 Miscellaneous parameters of the implemented coral species. The death temperature is calculated from above mentioned data to provide a continuous range upon which the probability for death at a specific temperature is determined once a coral is bleached.

Species	Mean Lateral Extension Rate (mm/year)	Maximum Radius (cm)	Minimum Bleaching Temperature (°C)	Temperature where all corals bleach (°C)	Minimum Death Temperature (°C)	Temperature where all corals die (°C)
Porites lobata	11.6	300	29.9	31	29.4	32
Porites lutea	13.2	300	29.9	31	29.4	32
Acropora muricata	77.1	50	29.4	31	28.2	32
Pocillopora damicornis	26.1	30	30	31	21.5	30.4

CORALS – MORTALITY

A coral colony can only die from a disturbance event, due to bleaching, or as a result of competitive interaction. Due to their hydrodynamic properties and the relatively small base of the colony, branching corals can break off if they are not sufficiently sheltered from surge and wave action. Virtual branching corals therefore are removed from the system with a 0.5% chance if they are not surrounded by two or more neighbors of at least the same size.

Macroalgae

The life-cycle of macroalgae, and hence algal patch dynamics, take place in much shorter time-spans than that of scleractinian corals, as algae grow faster and are generally subject to a higher frequency of trophic interactions. In the model algae are controlled by grazing where the intensity depends on algal density (see section 'Herbivory'). A virtual macroalga grows at first equally in vertical and horizontal orientation. As soon as it reaches its maximum allowed diameter, it only grows in height. The calculated diameter rather represents the alga's zone of influence towards other organisms. In contrast to corals, algae can die from old age and are removed from the simulation after reaching the maximum age.

Algae also disperse faster than corals. We simulate algal dispersal in two distinct processes: yearly recruitment and fragmenting as soon as a threshold height is exceeded. For each produced fragment a certain value is subtracted from its height. The fragment can then settle within the vicinity of the mother plant or is lost if it leaves the simulation area. To avoid edge effects (lower algal densities near simulation borders) we created a margin around the actual simulation area in which algae can reproduce and grow, but which is not used for any calculation (see boundary conditions).

Turf

All filamentous and encrusting algae are combined into turf which we simulate as a grid with quadratic cells (1 x 1 meters). In the model we currently consider turf as a component that hampers coral recruitment by occupying potential settling ground (see also Interaction). The implemented life history traits are simple. Rather than taking account of recruitment or mortality of these plants with a very high turn-over, the relative cover of all turf algae within one grid cell is taken as measure of their density. It increases by 20 % percent per month, or can be reduced by 50 % due to herbivory which is implemented as a stochastic process depending on herbivore density.

C) Interactions

In the model we put special emphasis on spatial interactions between different benthic organisms. Within an empty neighborhood corals grow unconstrained by interactions and expand into unoccupied space as long as they do not reach their maximum size. When a coral grows in the direction of another organism, its growth rate is reduced according to specified rules (Tab. 4) at the beginning of each time-step. Empirical studies revealed that some coral species are in principle competitively superior to others, i.e. if equal sized fragments of two species were placed in direct contact, one species overgrew the other one in most cases [52]. For this reason we applied a competition index, which together with the size of a colony determines the outcome of each competitive interaction. In all other cases, competitive success between members of the same growth morphology is only decided based upon individual size, location, and growth rate. We assume a slight competitive advantage for massive corals because they exhibit a more robust structure.

Tab. 4 **The effect of interaction on growth of individual colonies or organisms.** Focal individuals are listed in the rows and their respective competitor in the columns. As no literature values were available we made plausible assumptions for reactions on direct contact of corals.

	Massive Coral	**Branching Coral**	**Macroalga**
Massive Coral	if larger → grows 10% less if smaller → stops growing	if larger → no effect if smaller → grows 70% less	if larger → no effect if smaller → grows 30% less
Branching Coral	stops growing	if larger →grows 30% less if smaller → grows 70% less	if larger →no effect if smaller → grows 30% less
Macroalga	→ no effect on growth	→ no effect on growth	→ no effect on growth

A coral colony dies if more than a threshold amount (50 % for branching colonies and 75 % for massive colonies) of its size is overgrown by another organism. A coral recruit dies if it settles on space, which is already occupied by another organism. If it settles on turf, the mortality probability is reciprocal to the percentage cover of the turf algae. Macroalgae can overgrow smaller coral colonies and can be overgrown by larger colonies, whereupon the competitively inferior individual is removed from the simulation. Interspecific competition evokes death of a smaller alga if 50 % of space is shared with a larger conspecific.

D) Herbivory

We assume that the simulated reef patch is within a coral reef network with low fishing impact and free access for herbivores. In the current version we represent herbivory as a simple process that controls algal population densities, where grazing rates are determined with a basic logistic function [53,54]:

$$GP=\left(GP_{max}-GP_{min}\right)\cdot\left(1-\left(\frac{1}{1+\left(\frac{algalCP}{algalT}\right)^{z}}\right)\right)+GP_{min} \qquad (1)$$

where: GP Grazing Probability
GP_{max} maximal Grazing Probability

GP_{min}	minimal Grazing Probability
$algalT$	Critical Threshold of algal cover percent
z	Slope of the reaction
$algalCP$	Algal Cover (Percent density)

Parametrization

Standard parametrization

LOCATION
In the model we represent typical attributes of a coral reef system around Unguja, the main island of the Zanzibar Archipelago, Tanzania (6.18928° S, 39.34137° W) which is one important coral reef location within the Western Indian Ocean.

CORALS
We chose four typical scleractinian coral species for Zanzibar reef sites that represent important functional groups. *Porites lobata* and *Porites lutea* exhibit a massive colony shape while *Acropora muricata* (formerly aka *A. formosa* – see [55]) and *Pocillopora damicornis* feature branching growth patterns.

As no data on growth rates were available from Zanzibar, we applied average growth rates from literature (Tab. 1). *A. muricata* can reach a maximum radius of 50 cm and *P. damicornis* of 30 cm [56]. No data on the maximum size of massive corals was available, nevertheless we set a radius limit to 3m, because larger colonies of these species are rarely observed in reefs around Zanzibar.

The main reproductive traits are derived from a literature search and were calculated from other variables if no direct data entry was found for a certain species (see also Tab. 2).

Rinkevich and Sakai [52] found that *P. lutea* is competitively inferior to *P. lobata* if fragments of approximately the same size are located next to each other. Therefore we applied the rule that *P. lobata* has a higher competition index, and can still grow with 30% of its input growth rate if it touches a larger *P. lutea* colony whose diameter is less than 25% bigger than its own.

ALGAE
Macroalgae which are mainly parametrized with data from *Sargassum ilicifolium* [57,58] grow 30 cm per month, and can reach a maximum height of 60 cm and a maximum diameter of 45 cm. To account for the process of fragmenting we assumed that macroalgae fragment from a threshold height of 30 cm (a size at which surge can impact the alga) and for each produced fragment, their height is reduced by 5 cm. Algae recruit with a constant rate of 0.5 recruits m^{-2} once a year. All these values were tested prior to the experiments and the dynamics of virtual algae confirmed algal dynamics in Zanzibar reefs.

TEMPERATURE

The temperature data set used in this study originates from Chumbe Island, Zanzibar ([59], Muhando unpublished data). In March of 1998 we measured the highest temperature (approx 2 °C above average) coinciding with the 1998 El Niño mass bleaching event which caused severe coral bleaching and mortality. To simulate longer time spans, single years of this data set were concatenated in a stochastic order. As the 1998 temperature data trigger major bleaching events, the frequency of this year's occurrence can be set in the parameter list to simulate different scenarios of temperature extremes. To determine the strength of bleaching events sequential temperature sums were calculated over periods of 20 days. For each coral species the highest temperature sum in each month was compared to the respective bleaching threshold (Tab. 3) and used for determining the bleaching probability. For the parametrization of bleaching we used data from McClanahan [51] and adjusted our model to produce similar bleaching and mortality results as occurred when temperature reached levels of the hottest month of 1998 in East Africa. In order to gain a basis for calculation of a dynamic bleaching reaction and in accordance with field observations we decided on a maximum temperature value at which all corals of a respective species bleach. From the onset of bleaching and the maximum value we were then able to derive continuous specific bleaching probabilities. The same method was applied to assess specific coral mortality rates (see Tab. 3).

DISTURBANCE

Disturbance has strictly mechanical effects in the model and kills every organism within the affected area. Together with destructive fishing techniques [60–62], anchorage and boat contact have proven to have major destructive effects on scleractinian corals [13–15]. Therefore we chose two different disturbance intensities: a smaller one with 2-4 m in diameter – which represents, for example, direct anchor damage or a smaller boat hitting the coral reef at low tide – and a larger one with a diameter of 5-10 m representing, for example, damage by abrasion due to anchor chains, boat crashes or from fishing nets. Both intensity levels can occur alone or together within a simulation run and respective frequencies can be set for different scenarios.

HERBIVORY

In general algal densities in Zanzibar coral reefs are still very low. Therefore we set the algal density threshold (*algalT*) to 5 % cover. Herbivores are able to maintain this threshold and the initial probability of being grazed within one time step is set to 0.25 and can vary in the range between 0.2-0.3. The slope of the reaction is set to 2.0. The actual algal cover is then used to determine the grazing intensity or grazing probability for the next time step. The respective values were set and tested together with experts from the IMS, Zanzibar to represent macroalgal dynamics around Zanzibar best.

Simulation area and boundary conditions

For the simulations we defined a continuous area of 40 x 40 m on which we allow settlement of each organism group on unoccupied space. In order to minimize boundary effects we allowed macroalgal fragmenting to take place outside the actual simulation area within an additional 10 m margin that surrounds the field. Mechanical disturbance events were dealt with in an analogous way. The center of a disturbance is chosen randomly. In order to minimize edge effects (all individuals should have the same probability of being affected), the relevant area to determine the center of a disturbance extends the simulation area by the radius of the disturbance. Thus probabilities within the evaluated simulation area are equally distributed.

Environmental settings and scenario conditions

In the standard parametrization (Tab. 2-3) a major bleaching event occurs every 15 years and small and large disturbance events every 12 and 60 months, respectively.

For the identification of long term community responses to particular environmental settings we ran several scenarios. Here we tested different frequencies of (1) extreme temperature events, occurring in 1 to 20 year intervals (2) two different intensities of mechanical disturbances (small: Ø 2-4 m; large: Ø 5-10 m) and (3) extreme temperature events under intermediate mechanical disturbance levels (small events every 12 and larger ones every 60 months) to assess the combined effect of the two perturbation types. All other parameters were kept constant. In the beginning of each simulation all coral species were distributed randomly over the simulation area with a respective coverage of 10 %. Macroalgae were initiated with 5%. Depending on the environmental settings it took about 50 to 100 years for the virtual reef to completely adapt to the specified condition. To eliminate any influences of the initial distribution we analyzed only the last 500 years from each 1000 year scenario. Data from 500 year simulations allowed to reduce the number of repetitions necessary to get consistent dynamics. The output from 10 repetitions was then combined for further analysis.

We concentrated our analysis on the dynamics of cover for each species. The total benthic cover is thereby the sum of the relative cover of all species. As corals can overgrow each other, the total sum may thus be over 100%.

Sensitivity analysis and validation

In order to assess the sensitivity of the model to parameter changes and to ensure the reliability of the application we conducted a detailed validation and sensitivity analysis (see Appendix). Here we show how the model reproduces observed dynamics of typical reefs in Zanzibar (Appendix, Fig. 2-4). The output is highly sensitive to alterations of the larvae retention factor (Appendix, Fig. 5), which combines many assumptions and cannot be approved with empirical data. Growth rates (Appendix, Fig. 6) and susceptibility to extreme temperatures (Appendix, Fig. 7) only produce considerable change if qualitative properties between species are affected and the variation of parameters relevant for herbivory, do not evoke any noteworthy changes under the given configuration (Appendix, Fig. 8).

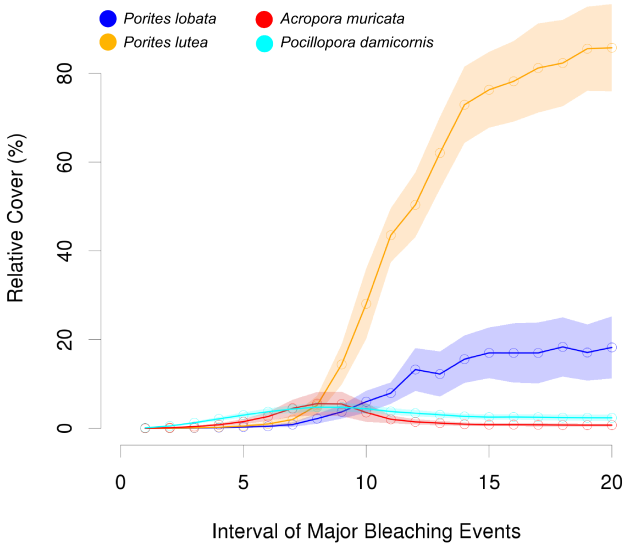

Fig. 4 **Variation of frequencies of major bleaching events without the influence of physical disturbances.** A clear shift in coral community structure can be observed when bleaching frequencies increase from 8-9 years.

2.3 Results

GENERAL PATTERN

At standard settings the massive *P. lutea* dominated, followed by the branching *A. muricata*. The other two species both leveled at around 5 % coverage. *A. muricata* exhibited the highest fluctuations in relative cover and *P. lobata* the lowest.

Surveyed exclusively, both perturbation modes triggered similar responses in the benthic community; not only changes in overall benthic coverage but also alterations in community composition. For low frequencies of rare events massive growth forms clearly dominated the system with high total benthic cover. Macroalgal cover is negligibly low. If perturbations occurred at intermediate frequencies overall cover decreased and space was nearly evenly distributed between the two different growth morphologies. At the highest perturbation levels the total benthic cover was very low, the relative fraction of algae increased strongly and massive species were displaced by branching ones.

Nevertheless, single effect testing of major bleaching events and mechanical disturbances revealed that both perturbation types triggered differential responses of the benthic community. These are discussed further below.

BLEACHING

Without the influence of mechanical disturbances, there was nearly no visible change in the total benthic cover (which was always ≥ 99 %), if major bleaching events occurred in intervals of 16 years or higher. The community was dominated by *P. lutea* with a relative coverage of ~ 80 % or more (Fig. 4), followed by *P. lobata* (~18 %). When extreme temperatures occurred every 10 to 15 years, major changes in relative cover arose mainly for *P. lutea* which decreased from 76.1 to 28.1 % coverage, and *P. lobata* which decreased from 17.0 to 6.0 % coverage. For the dominance of *P. lutea* we identified a threshold of 8-9 years between major bleaching events (Fig. 4).

At very high bleaching frequencies the total coral cover did not exceed 2 % coverage and macroalgae dominated the benthic community. Branching corals dominated, if bleaching events occurred every 8 years or more often. Within this range the cover of *P. damicornis* increased gradually and *A. muricata* only dominated if extreme temperature events happened between 7 and 9 year intervals.

DISTURBANCE

Without the influence of extreme temperature events both applied disturbance intensities trig-gered nearly the same community responses, although the frequency of the smaller size events had to be far higher for a similar effect (Fig. 5). Increasing disturbance frequencies abetted dominance shifts from massive to branching growth forms, resembling the pattern of the single effect of bleaching. The interface from the dominance of *P. lutea* to *A. muricata*, where the community featured the highest evenness, was restricted to a small range of configurations. At standard frequencies (i.e. for smaller intensities every 12, and for larger ones every 60 months) the total benthic cover was 117% (see section 2.3) where *P. lutea* clearly dominated, followed by *P. lobata,* the two branching coral species covered together ~ 3%, and macroalgae covered 0.5%. Under highest applied frequencies of mechanical disturbance events the total benthic cover amounted to 16.2%, and massive corals nearly disappeared altogether (< 0.1% cover) with only the faster growing branching corals still present in the system.

COMBINED EFFECTS OF BLEACHING AND DISTURBANCES

Under the regime of both applied perturbations, where different frequencies of bleaching events were tested under standard mechanical disturbance levels the effect of bleaching was amplified (Fig. 5). Similar to the single effect scenario the total coral cover was low and macroalgae dominated at very high frequencies of bleaching events. At 20 year intervals the total benthic cover did not exceed 63 %, and as in the assessment of the sole bleaching effect, *P. lutea* dominated the community, while all other species' coverage stayed below 10 %. *P. lobata* did not exceed 10% cover within all tested frequencies. Also contrasting is the behavior of *A. muricata*. It dominated the community at extreme temperature intervals between 8 and 14 years but its cover decreased tremendously at higher frequencies. *P. damicornis* again increased its relative cover gradually at high frequencies, but then stayed more or less constant at levels around 5% coverage if major bleaching occurred every 9 years or more seldom.

The ratio of massive and branching corals was nearly 4:5 at 15 year intervals for major bleaching, and the dominance threshold for *P. lutea* was shifted from 8-9 year intervals up to 14-15 year intervals in the combined perturbations scenarios.

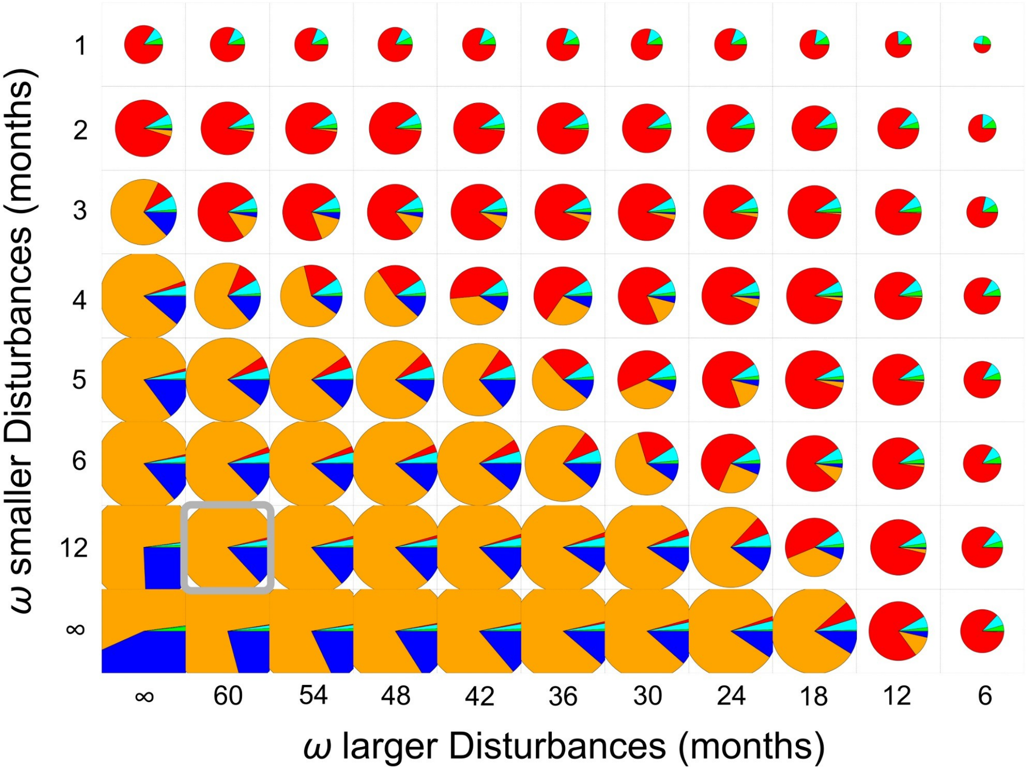

Fig. 5 Effect of different frequencies (months) of large (x-Axis) and small (y-Axis) disturbance events without the influence of major bleaching events. The size of a pie chart denotes the percentage of the total benthic cover and the chosen regime for standard settings of mechanical disturbances, with smaller intensities occurring every 12 and larger ones every 60 months, is indicated by the gray frame. The colours represent benthic organisms as follows: P. *lobata* in blue, P. *lutea* in orange, A. *muricata* in red, P. damicronis in cyan and macroalgae in green.

2.4 Discussion

The model outcome reflects findings of empirical studies in many regards and provides interesting insights on the influence of multiple perturbations on coral reef communities. Massive corals are generally slow growing but exhibit a strong physical structure. Provided their tissue is healthy and the defense intact, they are quite resistant to overgrowth by other organisms, like branching coral species or macroalgae which competitively mainly rely on their faster growth rates [63]. In addition, both of the observed massive species feature low susceptibilities to bleaching among the tested corals, and a low bleaching-induced mortality. The combination of slow growth and high endurance implies small fluctuations in relative coverage. As yet another consequence of the above mentioned properties, massive species outcompete their benthic opponents gradually if perturbation levels are low, where *P. lutea* overrules *P. lobata* and dominates the community due to its higher growth rate (see Fig. 4 and Fig. 5 at low perturbation levels). This effect is also pronounced by the applied stock-recruitment relationship which leads to a self-enhancing process; i.e. individual colonies grow fast, reach maturity earlier, and produce many propagules again resulting in a higher recruitment rate and new colonies.

The branching species *A. muricata* exhibits the highest fluctuations in population size and relative coverage. It has the fastest growth rate of all simulated species and, given there is enough space, can dominate the benthic community within a few years due to the self-accelerating process produced by the stock-recruitment relationship described above. On the other hand, its bleaching vulnerability to thermal stress is the highest within the tested community, which leads to considerable losses due to extreme temperature events. *Acropora* and *Pocillopora* are genera with many species which feature high susceptible to bleaching [64]. Accordingly, *A. muricata* is the only species in our model which shows bleaching responses in years when temperatures did not rise as high as

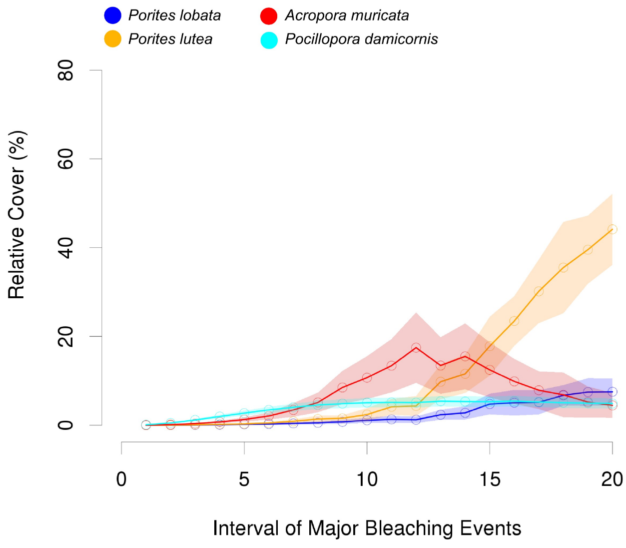

Fig. 6 **Variation of frequencies of major bleaching events at intermediate physical disturbance levels.** A clear shift in coral community structure can be observed when bleaching frequencies increase from 10 -15 years.

in 1998. For *P. damicornis* the situation is different. In our model, this species is the least susceptible of all tested species in terms of bleaching, but when a colony bleaches it nearly always dies. Therefore extreme weather events have nearly analogous effects on the mortality for both branching species. The long term survival of a species is hence strongly dependent on larval input from the outside and thence influenced by asynchronies on the regional and trans-regional scale.

The results show that different types and levels of perturbations can lead to very diverse community responses and thereby reef trajectories. In a mechanical disturbance event the only reason for an individual to be affected is if it is located at the wrong spot at the wrong time. At higher frequencies of these events the growth rate and recolonization speed of an organism decides winners and losers. Extreme temperature events feature a more selective pattern. Populations of higher susceptibility to thermally induced bleaching suffer the highest losses. Their lower abundance evokes a reduced reproductive output for the next spawning event which, in the long run, might constitute a disadvantage over less susceptible species. Generally, mechanical disturbances occur locally and do not affect the regional coral populations, so that neighboring reefs can serve as a source for new recruits and the local population can recover comparatively fast. An increase of the sea surface temperature is affecting populations at a larger spatial extent and evokes a regional effect. Conspecifics of a sensitive species are affected similarly region-wide if they are not protected from the high temperatures in some way. In such a scenario the larval support between reefs can be hampered tremendously and the risk of extinction increases [65].

Structural complexity of a coral reef is a very sensitive emergent property and high coral cover does not thoroughly imply high ecosystem function (e.g. provide 3-dimensional framework) [66]. Perturbations at too high or too low frequencies cause a loss of biodiversity and thereby structural complexity. Very low frequencies and/or intensities of mechanical disturbance events mostly lead to dominance of species with high competitiveness or endurance and it is just a matter of time until individuals of these species overgrow and displace inferior organisms. In our example massive corals dominate under very low disturbance regimes. They do not provide as much structure as branching corals, and so structural complexity is lost which might cause unfavorable conditions for other reef associated organisms which are deprived of hiding places. One example is Changuu reef, close to the city of Zanzibar, a very exploited site by the means of fishing and is under strong influence of waste water, and hence pollutants and nutrients from the town [67–69]. Muhando et al. [70] found that corallimorpharians covered 14% of the reef, mainly on the reef crest and flat. Here a large part of the (still persisting) coral cover is made up by Galaxea astreata and *Porites rus* [71], both of which seem to be quite resistant to environmental change and possess strong competitive traits over other taxa (e.g. corallimorpharians) but which facilitate scarce structure. Therefore this site exhibits low biodiversity of fish and other associated organisms.

Under very high physical disturbance levels the overall coral cover is generally very low. These conditions again disadvantage branching corals, because without shelter from surge or strong currents, they might break off. On the other hand, due to their high growth rates they play a crucial role in post-disturbance recolonization [72]. In this context, the principles of the intermediate disturbance hypothesis [73] are very well resembled by our model results and in line with previous studies [50,74].

In order to investigate the sole effects of perturbations on long term dynamics of a reef without the effect of extinctions, we made two major assumptions. First, we kept the grazing intensity on algae more or less constant, assuming that the herbivore community is completely independent of the structural complexity that the reef is providing. The general view is that the abundance of herbivorous fish and other associated reef organisms is directly influenced by the availability of sheltering places provided by the reef structure [19,75,76], and especially by the abundance of branching corals [66]. A loss of a reef's structural complexity therefore reduces herbivore abundance, macroalgae are not grazed efficiently and their populations can proliferate freely. Resulting stands of macroalgae decrease coral recruitment success [77,78] which can then produce a feedback in which macroalgae may take over a once coral dominated system. Secondly, we assume a constant larval supply from the outside, on top of the applied stock-recruitment relationship. According to McClanahan et al. [79] the extinction risk of all species tested here as a response to bleaching seems to be very low in the Western Indian Ocean region, with *Pocillopora* and *Acropora* showing a probability of 12 and 11 %, respectively, and the massive *Porites* of 7 %. In contrast to the observations that McClanahan et al. [80] made in Kenya, where they observed that *Pocillopora* was completely depleted at protected sites and close to gone from unprotected ones, *P. damicornis* survives in our simulations. This is due to our second assumption that nearby source reefs were not as much affected by high temperature influences as the focal reef, either because they are located in deeper waters where the heating effect is alleviated or by mixing of water masses.

These two assumptions implicate limitations for model extrapolations. To transfer the model to other sites, specific adaptations to the local conditions and to local species parameters have to be made. This also applies to the other explicit and implicit assumptions, underlying the model development, such as the 2-dimensional spatial configuration, the choice of reef components, and their rules of interaction and competition. Additionally, the applied parameter specifications, most of all the relative rates of growth, the reaction to bleaching and larval recruitment, are important for the model outcome.

Although there are many types of perturbations, in this article we concentrated on two of the main ones, which concern coral reefs and most probably will have increasing impact in the future. The framework of our model allows for the addition of other substantial threats, like ocean acidification, nutrient input (which hampers coral fitness but may have a positive effect on algae), coral diseases, and sedimentation, all of which will affect resource allocation in virtual corals and thereby decrease growth rates and/or competitive strength. Intensive fisheries constitute a fundamental problem for future coral reefs which should be treated with special attention. Enhanced fishing pressure depletes stocks, which most probably results in either higher effort (i.e. more fishing trips) and/or the utilization of more efficient fishing gear that often has destructive capacities. Both practices increase the risk of reef degradation (i.e. by more frequent anchorage and boat damage, or directly through fishing gear). In the longer run this might evoke a downward spiral.

While we are still far away from the point in which we can represent all features of these highly complex biota, our study extends model capabilities from former coral reef models. This extension is in terms of the accuracy of involved processes as well as on the spatial scale and resolution of the simulated reef system. The model reflects important coral reef dynamics and allows to test different scenarios relevant for resilience research. Its generic and modular structure and with the potential parametrization for different reef components and the respective species, as well as environmental influences it provides the possibility to adapting it to represent many reef sites worldwide. The model clearly shows that even when perturbation regimes are kept constant the system never reaches a stable state and stochasticity produces a continuously adapting and fluctuating community response. Pulse events can have a strong influence on ecosystem functioning, especially if they amplify each other's effects or stress the ecosystem in addition to a prevailing chronic disturbance [21] such as increasing nutrient loads or sedimentation. This may cause a shift of general system properties, and lead to, for example, a coral-algae phase shift [81].

Several studies that have quantified resilience with a small number of key parameters have already provided interesting insights [82–84]. Nevertheless, measuring resilience in such complex systems as coral reefs is hard to accomplish because the high number of site specific relations and components complicates generalization and extrapolation of specific findings considerably. However, management has a high interest in, and demand for, tools which aid in tracing and identifying distinct drivers for the decline of specific coral reefs. Only a clear recognition of drivers, mechanisms and causes makes it possible to establish or introduce adequate protection measures. Generic frameworks, like the model presented here, allows to for fairly easy integration of site specific features and may serve as the appropriate basis for management support tools.

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Appendix

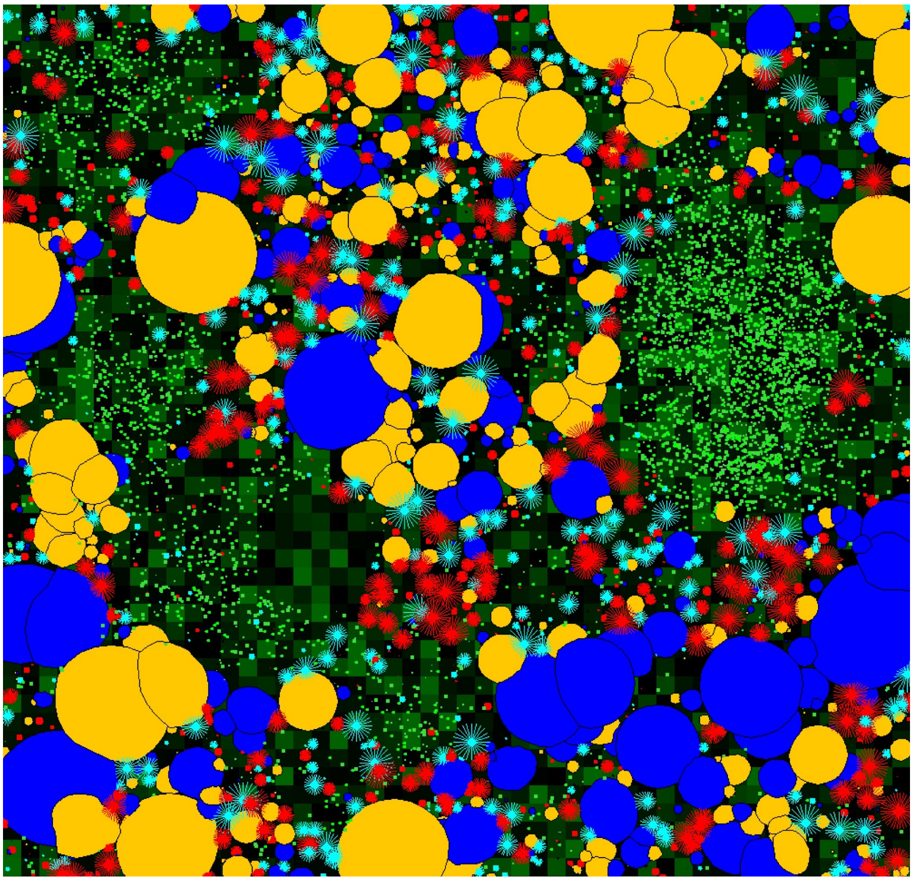

Fig. 1 Screen shot of the graphical user interface during a simulation. Colonies of the two massive species P. *lobata* (blue polygons) and P. *lutea* (orange polygons), and the two branching species A. *muricata* (red stars) and P. *damicornis* (cyan stars) compete for space with each other as well as with macroalgae (green dots) and algal turf (green squares). The free space which is largely covered by macroalgae and turf indicates post-disturbed areas.

Sensitivity analysis and validation

In order to ensure correctness of model properties and provide information on model reliability, we applied different techniques which may be subsumed under the broad and overlapping term of 'validation':

1. The comparison of model processes, dynamics and results with available data and current knowledge on the reef dynamics

2. A sensitivity analysis to investigate which parameters or combinations of parameters lead to relevant changes in model outcomes.

These techniques aim at specific aspects of model correctness which will be elaborated in the following sections. For individual-based models calibration and parameter fitting are comparatively less demanding as the applied parameters are very near to biological processes and empirical data, which leads to a narrow and clearly definable specific range of plausible values [1].

Model comparison with field data and observations

IBM requires a specific approach for validation [1] as they represent complex ecological situations, often with a large number of components and many varying relationships. In this situation a standard statistical approach [2] to model validation by simply comparing model results with a specific data set is not meaningful enough.

The detailed level of representation of organismic processes in IBMs allows for a different approach of model validation which is followed here. The accuracy of model processes and outcomes is checked at different integration levels comprising the range from individual life-histories to community dynamics. Here a 'hierarchically structured validation' [3] investigates to what extent model mechanisms reproduce the proposed characteristics of the studied ecological context that is known from expert knowledge and that is described by the conceptual model. In this case the model should not only reproduce the observed system dynamics on different levels but should also reflect the processes and causal level in which the real system operates to generate this behavior [4]. As model dynamics result from self-organization processes a correct representation of key processes on lower hierarchical organization levels increases the probability that the system behavior has been represented correctly, and that the results are trustworthy within the specified conditions and the implemented conceptual system.

Individual level

The individual level is very close to the implemented model processes. The main task on this level is to check the accuracy of implementation and the consistency of sequence in life-cycles and with current knowledge. In our analysis on this level we focus on the development of individual corals and their interaction with other corals. The reaction to neighbors is an important process in a model which emphasizes the representation of spatial interaction and competition. The outcome of the competition depends on factors, like local density, the individual growth rate and rules which determine interaction (see also section 2.1 c). As defined by the rules, growth is clearly restricted in direction of neighboring individuals and the common irregular shapes arise (Fig. 2).

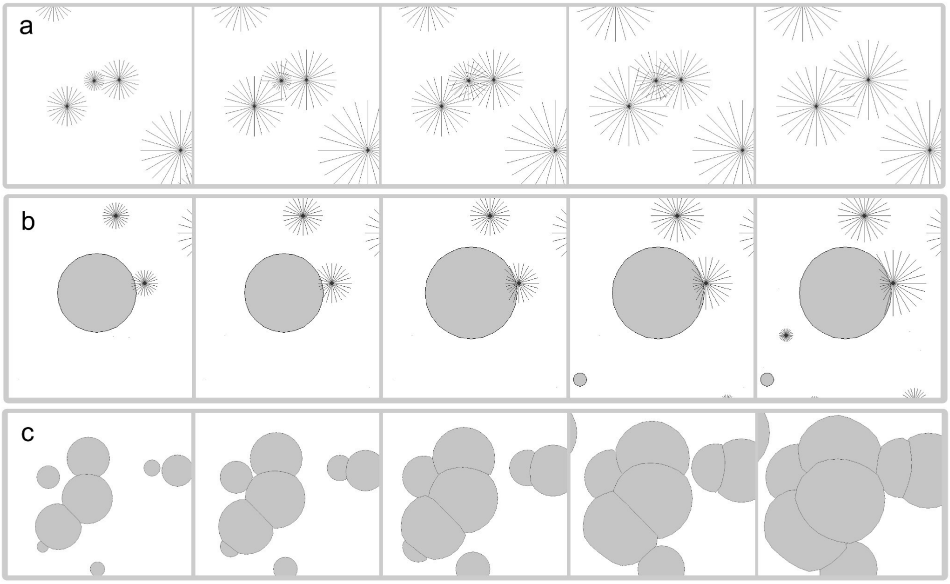

Fig. 2 Interaction between different neighboring coral colonies. Different growth forms interact in different ways which is shown for (a) branching colonies, (b) massive with branching colonies and (c) massive colonies, respectively. Growth is clearly restricted in direction of neighboring individuals and thus the common irregular shapes arise.

Population level

The population level constitutes an important integration level to control and evaluate the implementation and the effects of individual parameters. The results on this level are based on the interactions of the individuals in their respective interaction ranges. The overall results on this level thus emerge as a self-organized process.

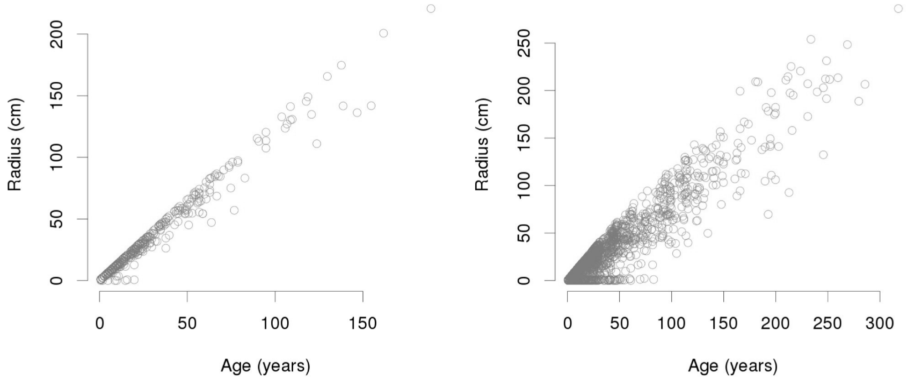

Fig. 3 The population's growth performance of *Porites lutea* under different disturbance levels and crowding regimes; high disturbance levels, which imply low crowding (left), and low disturbance levels which imply high crowding (right), respectively.

Coral growth has been described as linear extension rates which are influenced by neighboring corals and by the state of each coral. Thus it can be expected that the age-dependent size distribution (Fig. 3) of a coral population differs clearly from the linear relationship which we would get without any influences. Furthermore it should vary according to the different development phases of the population, the overall community density and external influences.

Community level

In principle on this level the same conditions apply as on the population level, but with an additional consideration of inter-species interactions. During the 1998 major bleaching event in the Western Indian Ocean region many reefs showed tremendous declines in coral cover. At Chumbe Island reserve the total hard coral cover decreased from >50% to about 20-25% (Fig. 4 a), which is also confirmed by Muhando and Mohammad [5]. In particular the cover of *Acropora* species decreased from about 25 to 10%. The model which was parametrized with bleaching data of the 1998 bleaching event from Kenya [6] represents these characteristics quite well (Fig. 4 b). Here the total coral cover is reduced

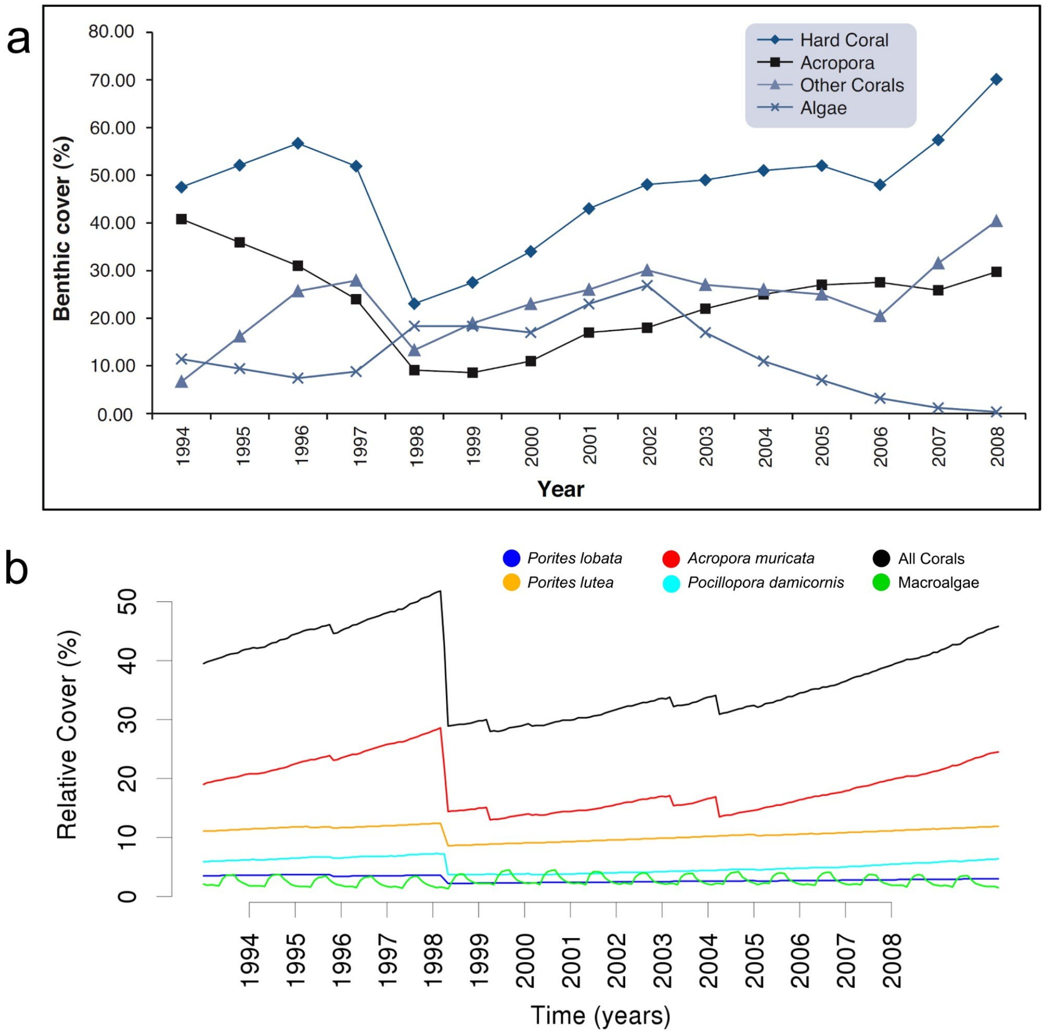

Fig. 4 **Validation of the community response to a major bleaching event.** In the upper part the relative benthic cover of Chumbe Island MPA is shown before and after the 1998 bleaching event. Taken from Muthiga *et al.* [7]. The lower chart shows a time line of the model output that represents the impact of the 1998 bleaching event.

from >50% to ~30% and that of *A. muricata* from about 25% to 10%. The regrowth of the reef seems to be quicker in the Chumbe reef site which might be explained by a higher variety of coral species, of which several may exhibit higher growth rates than those represented in the model.

Sensitivity analysis

The sensitivity analysis provides information on how specific parameter values influence model results. Those parameters, which cause large effects on overall results upon small variations of values should receive high attention during parametrization with the aim of minimizing uncertainty. In this way it can be determined whether parameters with a potentially high uncertainty have a critical influence on the model output.

For our analysis we concentrated on parameters which related directly to properties of the coral species, and are thought to likely alter the model's behavior tremendously upon small changes of values. Among these parameters we tested growth and reproduction of corals, the bleaching reaction to temperature, and the impact of herbivory on coral abundances, and varied these parameters in a biologically plausible range:

- Growth rates as well as larvae retention factors for all coral species were varied by ± 10% of their standard value and tested in all possible combinations to estimate their influence on the population's growth performance, relative abundance, and population age structure.
- The temperature threshold at which a coral starts to bleach was varied for each species within a range of ± 0.4 °C. This might have a strong impact on the community composition of the observed system, as soon as qualitative differences between species arise. We chose 0.4 °C because the threshold temperature for *A. muricata* is just that much higher than the long term average temperature from which the temperature sums are calculated (Tab. 3).
- In the equation for herbivory, the input grazing probability and the algal threshold are variables which were estimated, and the influence of their variation therefore needs special attention; both parameters were changed by ± 10% and tested in all possible combinations.

Standard configuration

In the standard configuration, where major bleaching events occurred every 15 years, and small and large mechanical disturbances occurred yearly and every 5 years, respectively, the total benthic cover amounted to ~44% and the community was partitioned as follows:

P. lutea made up the largest fraction with 41%, followed by *A. muricata* with 29%, the two other coral species had each a 12% share, and algae ~ 6%.

Retention factors

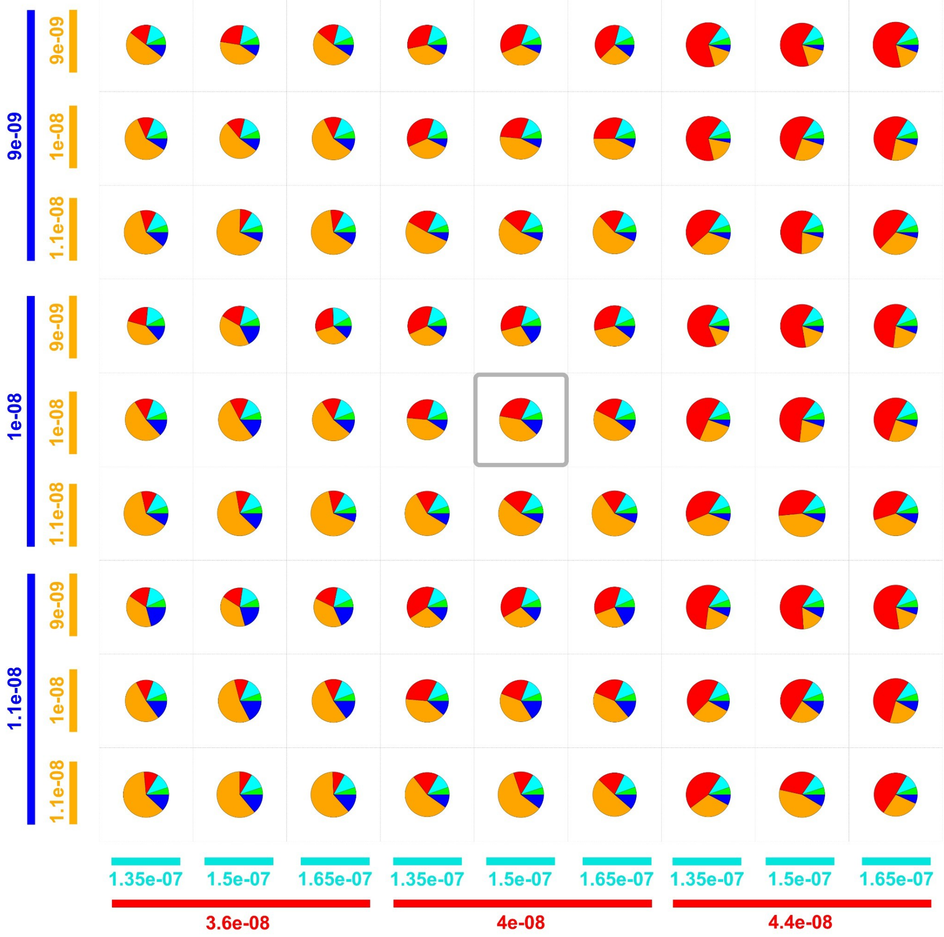

Fig. 5 **Retention factors of all coral species were varied by ± 10% of their standard value and respective community responses plotted for each setting.** Vertically the retention rates of the two massive species (*P. lobata* in blue and *P. lutea* in orange) are varied and horizontally the ones of the two branching species (*A. muricata* in red and *P. damicornis* in cyan). The size of the pie chart indicates the total benthic cover and the gray box indicates the standard values.

Varying retention rates produced highest rates of change for the dominant species in each growth morphology group, namely *P. lutea* and *A. muricata* (Fig. 5). At highest levels, *A. muricata* almost always dominated the community. *P. lutea* dominated in all other cases if its retention rate was at intermediate or highest levels. In contrast to all other sensitivity analyzes the total benthic cover was affected little by changing configurations.

The retention of coral larvae is a critical parameter for the outcome of the model and, hence, has to be determined with great care.

Growth rates

The variation of growth rates had an effect on the overall benthic cover and on the community structure (Fig. 6). If *P. lutea* grew at its maximum level it always clearly dominated the community. At the highest applied growth rate *P. lobata* dominated, if *P. lutea* was growing at lowest or intermediate levels. *A. muricata* only dominated if both of the massive species were growing at their lowest or intermediate levels and with increasing covered area the variance also increased. *P. damicornis* was affected the least by varying growth rates.

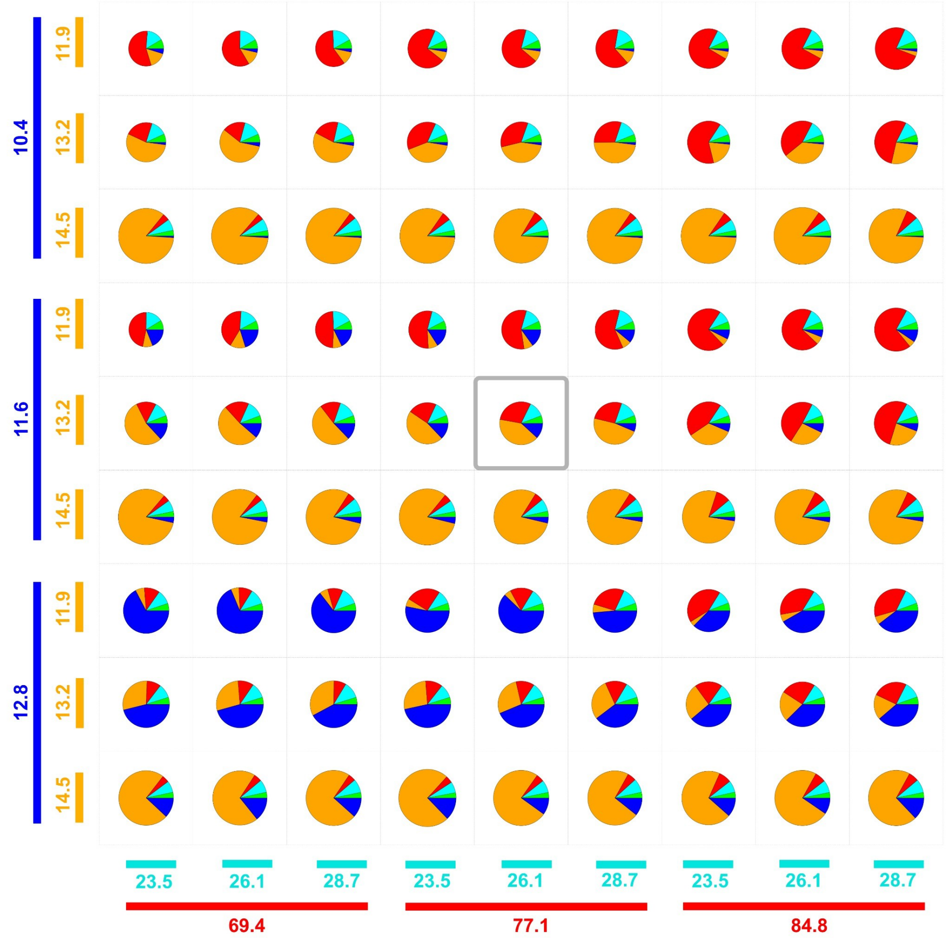

Fig. 6 **Growth rates of all coral species were varied by ± 10% of their standard value and respective community responses plotted for each setting.** Vertically the growth rates of the two massive species (*P. lobata* in blue and *P. lutea* in orange) are varied and horizontally the ones of the two branching species (*A. muricata* in red and *P. damicornis* in cyan). The gray box indicates the standard values.

The model reacted sensitively to growth rate alterations if qualitative changes arose (i.e. species A, which normally grew slower than species B, grew faster than species B after an alteration); and mainly within populations of the massive coral species. Therefore, we suggest that coral growth rates should be accurately determined for the investigated site.

Bleaching temperature threshold

The variation of minimum bleaching temperatures of the two massive species caused the highest alterations in overall benthic cover (Fig. 7). Low sensitivity levels for *P. lutea* generally implied the highest overall benthic cover, and *P. lutea* always held the largest frac-

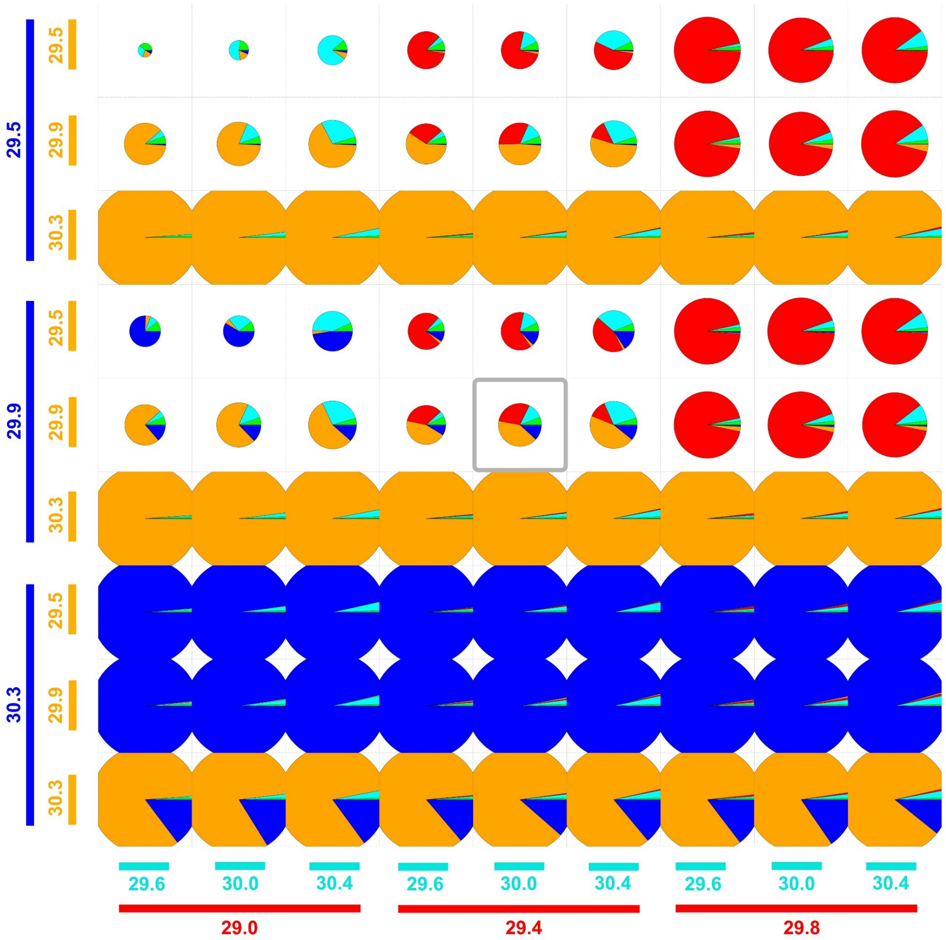

Fig. 7 **The minimum bleaching temperature for each coral species was varied by ± 0.4°C of its respective standard value and the community response was plotted for each setting.** Vertically the growth rates of the two massive species (*P. lobata* in blue and *P. lutea* in orange) are varied and horizontally the ones of the two branching species (*A. muricata* in red and *P. damicornis* in cyan). The size of the pie chart indicates the total benthic cover and the gray box indicates the standard values.

tion of the community (> 50%). On the highest tested value of the minimum bleaching temperature *P. lobata* showed similar but not as pronounced effects on the overall outcome. If the bleaching susceptibility of *P. lutea* was at its highest or intermediate and that of *P. lobata* was at lowest levels, the overall benthic cover increased and was dominated by *P. lobata*. Analogous to the sensitivity tests for growth rates, massive corals were only influenced by branching corals at intermediate and highest bleaching sensitivities.

Within the branching coral species, *P. damicornis* dominated only in scenarios where it was least or intermediately susceptible and all other species at their most susceptible. In these cases the total benthic cover was lowest. *A. muricata* disappeared completely from all simulations if its minimum bleaching temperature was set directly to the long term mean temperature, but dominated at lowest susceptibility if massive corals were at their highest and standard levels.

The reaction to bleaching reveals that small changes in susceptibilities to extreme temperatures lead to large changes in species composition and overall benthic cover. The parametrization of respective bleaching properties is very sensitive, has to be done with great care, and is of particular relevance for any alterations of temperature. We emphasize the need for more detailed studies to be conducted to reduce uncertainty in this point.

Herbivory impact

A change in the herbivory parameters led to surprisingly small changes in on overall model outcomes (Fig. 8). Algal cover increases slightly with an increase of the algal threshold and the total benthic cover stays approximately the same over all treatments.

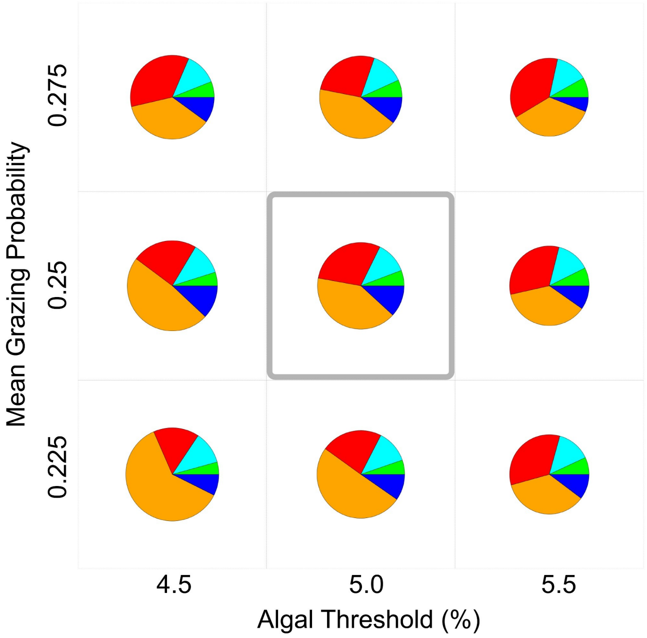

Fig. 8 Variation of key parameters for herbivory (± 10%) shows no decisive effect on coverage and community composition. The colours represent benthic organisms as follows: *P. lobata* in blue, *P. lutea* in orange, *A. muricata* in red, *P.* damicronis in cyan and macroalgae in green.

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Chapter 3

Multiple feedbacks in coral reefs – Source of stability or mutual disorder?

Andreas Kubicek, Hauke Reuter

In preparation

Multiple feedbacks in coral reefs
- Source of stability or mutual disorder? -

Andreas Kubicek, Hauke Reuter

Leibniz Center for Tropical Marine Ecology, Bremen, Germany

Abstract

With their extraordinary biodiversity coral reefs feature numerous interrelations and feedback processes, which span over several hierarchical levels and keep the whole subtly balanced system within its bearings. Reef communities are subject to extraordinary alterations as a consequence of global climate change and many sites have already undergone a coral-algae phase shift, which can occur if chronic stress is superimposed by an extreme pulse event.

In this study a spatially explicit individual-based model – in which coral reef dynamics with multiple coral species and macroalgae can be simulated – is utilized to analyse relationships and processes within three major feedback systems in a coral reef: (i) rugosity – herbivory – algal densities, (ii) larval connectivity/larval input – coral population sizes – densities of macroalgae that hinder coral recruits from settling, and (iii) fishing pressure, which is assumed to increase if rugosity, and with it fish densities fall below a specified threshold.

Simulation results show that changes in one parameter and a resulting unbalance in one of these feedback systems can disorder the whole interplay of regulating processes. This highlights the necessity for a holistic analysis of the reef, in order to grasp all ecosystem consequences. Additionally, the importance of an intact herbivore fauna and recruitment success of corals, both of which regulate reef dynamics in favour of a diverse and resilient coral community, are reconfirmed by the presented findings.

Keywords: feedback loops, coral reef benthic community, interactions, herbivory, recruitment, disturbances, bleaching.

3.1 Introduction

Coral reefs feature extraordinary biodiversity, and thus a highly complex structure of interconnections between organisms and their environment, which creates a large number of feedback loops within as well as among hierarchical levels (Mumby and Steneck 2008, Nyström *et al.* 2012). These feedbacks are vital for the subtly balanced functioning of an intact reef system and their respective relationships have to be considered when the effects of varying environmental factors on coral reef systems are investigated. We focus our study on three main loops (Fig. 4) which in themselves contain several feedback processes:

1) The **herbivory loop** includes the (i) grazing intensity, treated here interchangeably with herbivore density, (ii) algal density which is partly determined by the grazing intensity and – in a situation with low larval connectivity to other reef sites or limited herbivore densities – (iii) reef rugosity, which again influences the herbivore densities (Hixon and Beets 1993).

2) The **recruitment loop** consists of (i) a stock-recruitment relationship for coral populations, (ii) the larval connectivity to other reef sites, which influences the external larval input into the focal reef (Almany *et al.* 2009, Botsford *et al.* 2009) and, as a touching point to the herbivory loop, of (iii) algal density, which is a decisive factor for coral recruitment success (Birrell *et al.* 2008) and in the longer run coral abundance and thus also reef rugosity.

3) The **fishing loop** includes the (i) density of herbivorous fish, which is directly influenced by reef rugosity, and (ii) fishing, which affects the frequency of (iii) mechanical disturbance events. It is assumed here, that if the density of herbivorous fish falls below a threshold, the destruction due to fishing increases. In order to maintain a minimum catch in overfished habitats (Jennings and Polunin 1996, Mangi *et al.* 2007) fishermen frequent the site more often or intensify their fishing effort, often in combination with destructive techniques (NOAA 2007, Hlavacs 2008).

Subtly balanced processes and the above mentioned feedback loops maintain the existence of a coral reef with its manifold and highly diverse organisms inhabitants. Sustaining this balance, or the persistence and regeneration potential of an ecosystem is also termed resilience (Holling 1973). Within a coral reef it is provided by species diversity (Loreau *et al.* 2003), functional redundancy (Nyström *et al.* 2008), life history of reef participants (Vermeij *et al.* 2007) and the fact that species act on different spatial and temporal scales (Hobson 1973, Burkepile and Hay 2010). Within this network of traits the loss of one specific function may be buffered by others but multiple deficiencies can decrease resilience.

Coral reefs around the world are increasingly under pressure. Global climate change (Hughes *et al.* 2003, 2007b), ocean acidification (Hoegh-Guldberg *et al.* 2007), coral disease (Brandt and McManus 2009, Williams *et al.* 2010) and over-exploitation (Muhando 1999, Mumby 2006) are just a few among many threats that impact on these unique ecosystems at all possible levels (Riegl *et al.* 2009). If reef resilience is already hampered due to chronic disturbances, additional perturbations can induce system alterations which may lead to a phase-shift from coral dominated habitats to the domination of other life forms (Hughes *et al.* 2003, McManus and Polsenberg 2004, Bellwood *et al.* 2004, Norström *et al.* 2009, but see Bruno *et al.* 2009, Zychaluk *et al.* 2012). Such an alternative state of an ecosystem may evoke self-enhancing feedback processes, that lock the system in ”unfavourable” conditions (Nyström *et al.* 2012). In many cases a phase shift is related to the above mentioned feedback processes. If herbivore densities are depleted and grazing intensity reduced, macroalgae can proliferate freely and hinder coral larvae from successful settlement, which in the long run depletes coral populations, and thus habitat for herbivores.

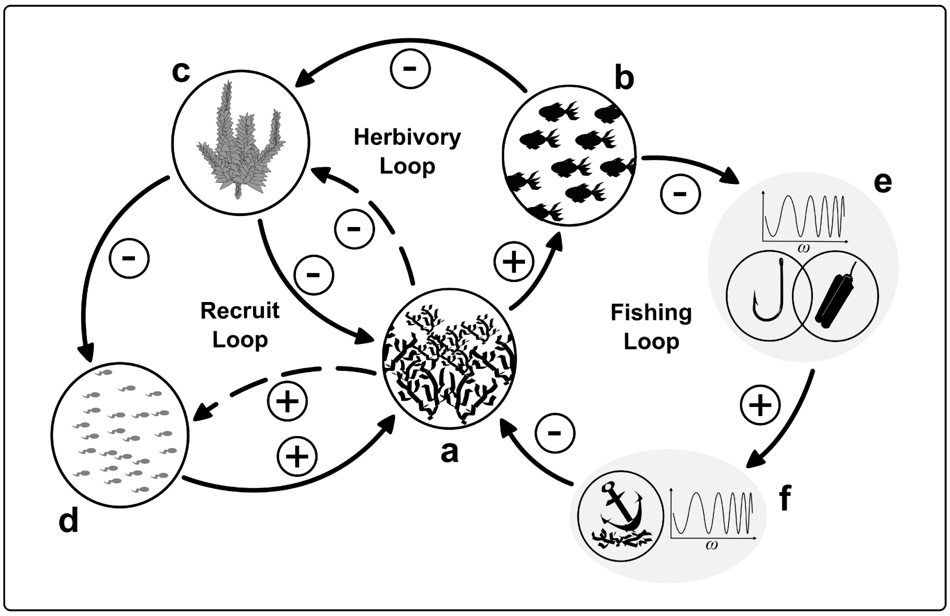

Fig. 1 The three major feedback loops and important relationships analysed in the model. In the herbivory loop rugosity (a) determines fish abundance (b), which regulates macroalgal densities (c). Macroalgae hamper recruitment success (d) of corals in the recruit loop and overgrow small corals. Recruitment (d) is also strongly dependent on larval connectivity (not displayed here). The fishing loop only takes effect, if the fish density (b) falls below a threshold, which then leads to an increased fishing effort (e) and respectively, higher mechanical disturbances (f).

In this article we explore the influence of interacting key processes on the resilience of a typical coral reef in the Western Indian Ocean with an individual-based model. We analyse important feedback loops and investigate how alterations of single processes can affect the reef's functioning and resistance to perturbations. We survey (i) which effects the coupling of rugosity and herbivore density has on community dynamics, (ii) how larval connectivity and recruitment success influence reaction to changed environmental conditions and (iii) how single species perform during unfavourable conditions. Finally, (v) we want to investigate how a possible recovery takes course, and identify potential winners and losers after different durations of unfavourable conditions.

3.2 Material & Methods

Model description and standard settings

General

We developed a spatially explicit, individual-based model of a typical coral reef in the Western Indian Ocean region (Kubicek *et al.* submitted). In monthly iterations the model simulates dynamics of a benthic reef community in which different corals and algae compete for space. The modelled area is 40 x 40 m in size and the substratum allows settling for all defined organism types over the whole simulation area. Coral colonies and macroalgae are represented as individuals, which feature situational reactions to neighbouring individuals and environmental conditions in accordance with their respective life history. Turf algae are represented by a grid with a cell size of 1 x 1 m and their density is measured as percentage cover.

The model was validated on three hierarchical levels, the organism, the population and the community, and its sensitivity to the variation of several parameters was tested. Here we found that larval retention, growth rates and bleaching susceptibilities of the different species have to be parameterized with greatest care in order to achieve meaningful results (see Kubicek *et al.* submitted).

Corals

We use four different coral species with contrasting life histories and differing responses to external influences (Tab. 1). *Porites lobata* and *Porites lutea* are massive corals which grow relatively slow, feature a low susceptibility to bleaching and high spatial competitiveness against other organisms. *Acropora muricata* and *Pocillopora damicornis* are branching corals with relatively fast growth rates, higher susceptibilities to bleaching and lower spatial competitiveness compared to the two massive coral species. In terms of reproductive properties *P. damicornis* is a hermaphroditic brooder and spawns monthly which leads to the highest larval input into the focal reef. All other species are broadcasters and spawning takes place once a year. Among these *A. muricata* is hermaphroditic and has therefore higher recruit input numbers than the two massive species which are gonochoric.

Algae

Macroalgae are parameterised with data from *Sargassum* spp. (Ateweberhan *et al.* 2005, 2009). They are specified to grow 30 cm month^{-1}, can reach a maximum height of 60 cm and a maximum diameter of 45 cm. The threshold height for fragmenting is set to 30 cm and for each produced fragment the height is reduced by 5 cm. Macroalgae recruit with a constant rate of 0.5 recruits m^{-2} once a year. If a macroalga is grazed on, it is removed from the ongoing simulation. The percentage cover of turf algae patches increases by 20 % every month until it reaches 100 %. If the patch is grazed, its cover decreases by 50 %.

Interactions

In reef systems spatial interactions are important processes determining the community composition and survival of specific populations. In the model, the extension of a coral colony in a particular direction depends on the species, its growth form, its own fitness and on the species, growth form and fitness of the competing organism (Tab. 2).

A coral colony dies if a fraction of its covered space is overgrown by a larger colony or, when small, by a macroalga; i.e. if 50 % or 75 % are overgrown for branching and massive colonies, respectively. A recruit dies if it settles on another organism and if it settles on algal turf its mortality probability is reciprocal to the percentage cover of the turf cell. Macroalgae can be overgrown by corals or, if they share more than 50 % of their space with a conspecific, the smaller individual dies.

Environmental conditions

The virtual coral reef is subject to external influences like temperature and physical damage. Temperature data are taken from long-term observations (1997-2010) from Chumbe Island near Zanzibar (Muhando unpublished/Kubicek *et al. submitted).* In order to simulate longer time spans we concatenate yearly data sets in random order. Within the data set 1998 is treated as an extreme year because during that period an El Niño event struck the East African coast and observations of large scale bleaching were numerous (Muhando and Francis 2000, Muhando 2002, McClanahan *et al.* 2007b). Thus, the data set of 1998 is separated from the other yearly data sets and can be set to reoccur in designated intervals. In the model extreme increases of the sea surface temperature (1998) occur every 15 years. If the temperature exceeds a specific threshold, a colony will bleach with a certain probability and can eventually die in the course.

During a physical damage event all organisms within the affected area die. Physical damage is specified with two different intensities which represent different modes of anthropogenic disturbances (e.g. fishing gear, anchor/boat damage, use of dynamite, etc.). In the standard settings smaller disturbances affect an area of 2-4 m in diameter and occur every year and larger disturbances affect areas of 5-10 m in diameter and occur every 5 years.

For a more detailed description of interactions and model parameters see Kubicek *et al.* (submitted).

Tab. 1 Key parameters for the four chosen coral species. For a full description of parameters see Kubicek *et al.* (submitted). Upper and lower values for bleaching and death temperatures determine the range, from which the dynamic bleaching and death probabilities are calculated.

	Porites lobata	***Porites lutea***	***Acropora muricata***	***Pocillopora damicorins***
Mean lateral extension rate (mm year^{-1})	11.6	13.2	77.1	26.1
Surface factor	1.5	1	5	3
Bleaching				
Min. bleaching temperature	29.9	29.9	29.4	30
Temp. where all corals bleach	31	31	31	31
Min. death temperature	29.4	29.4	28.2	21.5
Temp. where all corals die	32	32	32	30.4
Reproduction				
Reproductive Mode	gonochoric spawner	gonochoric spawner	hermaphroditic spawner	hermaphroditic broadcaster
Propagules cm^{-2}	1210	1375	109.5	2.5
Retention factor	2.00E-008	2.00E-008	4.50E-008	1.59E-006

Model implementation of feedback loops

Herbivory loop

In the model the grazing intensity is dependent on algal densities (Equation (1)). For standard conditions we assume that the focal reef patch is situated in a well connected reef network and fishes and other herbivores can freely enter and leave the system depending on the abundance of algae; i.e. the higher the algal density, the higher the grazing rate and *vice versa*. Therefore we employed a sigmoid function which adjusts algae dynamics as known of reefs around Zanzibar.

$$(1) \qquad gR = (gR_{max} - gR_{min}) \cdot \left(1 - \left(\frac{1}{1 + \left(\frac{algalCP}{algalT}\right)^{z}}\right)\right) + gR_{min}$$

where:		
	gR	grazing rate ($\%_{\text{algae}}$ month^{-1})
	gR_{max}	maximal grazing rate ($\%_{\text{algae}}$ month^{-1})
	gR_{min}	minimal grazing rate ($\%_{\text{algae}}$ month^{-1})
	$algalT$	critical threshold of algal cover (%)
	z	slope of the reaction
	$algalCP$	algal cover (%)

If a key herbivore species is depleted or the connectivity of the reef is reduced and less herbivores frequent the patch, the grazing intensity does not only depend on algal densities, but also on the rugosity of the reef (Equation 2-4); in the following this situation is termed as **coupled conditions**. Rugosity, the structural complexity of a coral reef strongly increases the availability of habitat and hiding places for various organisms. Therefore it has a significant influence on the abundance of herbivorous organisms because they can avoid encounters with potential predators. Empirically determined values for reef rugosity start at 1 (for no structure) and rarely exceed 3.0, at structurally complex sites (Alvarez-Filip *et al.* 2009). Nevertheless, in Mikindani Bay at the Tanzanian coast Davies (2006) measured a value of 3.5 for Naumbu reef, the maximum value in his study, which was also correlated to the highest density of butterflyfish over all studied sites. In contrast to the classical measure of rugosity (Risk 1972), in the model we first determined the 2-dimensional rugosity of the simulation area. The hemispherical surface area of all colonies of a species was added up and multiplied by a species-specific surface factor (Tab. 1). The specific surface areas were then added up for the whole coral community and divided by the total area of the reef. The square root of that value was then comparable to the linear rugosity value, attained by the chain transect measurement method used in the field (Risk 1972). The model's absolute maximum areal rugosity value of 12.25 (3.5 in linear rugosity) was achieved, if the whole area was covered only by *Acropora muricata* – the species with the highest surface factor. This value corresponds to the *in situ* measured value of Davies (2006) for Naumbu in Mikindani Bay. For the simulations we nevertheless chose to use a maximum value of 3.0 for the linear rugosity, because this value is rarely exceeded in nature. The maximum grazing rate the herbivores feature under coupled conditions can only be reached if the maximum rugosity is provided.

$$R_{areal} = \frac{\sum_{i=1}^{n} SurfaceArea_i \cdot sf_i}{ReefArea} \quad ; \quad n = 4 \tag{2}$$

where	R_{areal}	the areal rugosity coefficient
	$SurfaceArea_i$	surface area of all coral colonies together (m^2)
	sf_i	specific surface factor
	n	number of species
	$ReefArea$	the two-dimensional reef area (m^2)

$$R_{linear} = \sqrt{R_{areal}} \tag{3}$$

where	R_{linear}:	the linear rugosity coefficient

$$gR_{actual} = \frac{R_{actual} \cdot gR_{max}}{R_{max}} \tag{4}$$

where	gR_{max}	maximum grazing rate ($\%_{algae}$ $month^{-1}$)
	gR_{actual}	the momentary grazing rate ($\%_{algae}$ $month^{-1}$)
	R_{max}	maximum rugosity
	R_{actual}	the momentary rugosity

Recruitment loop

Recruitment is a vital process for the persistence of a coral population, faced with numerous perturbations. In the model we introduced larval connectivity as a dimensionless constant which was used to determine the larval input into the focal reef. The stock-recruitment relationship determines the number of larvae which are produced within the focal reef. The reproductive output for a species is the amount of released eggs or larvae cm^{-2} times the surface area for a species, which was estimated as above for the rugosity, and multiplied by the species-specific retention factor (Tab. 1). The external larval supply is then the product of this on-site produced larval input multiplied by the connectivity factor to simulate different distances to neighbouring coral reefs. In the standard settings the larval connectivity value is set to 1.0 so that the external larval supply is as high as the internal supply produced by stock-recruitment.

Tab. 2 **The effect of interaction on growth of individual colonies or organisms.** Focal individuals are listed in the rows and their respective competitor in the columns. Taken from Kubicek *et al.* (submitted).

	Massive Coral	Branching Coral	Macroalga
Massive Coral	if larger → grows 10% less	if larger → no effect	if larger → no effect
	if smaller → stops growing	if smaller → grows 70% less	if smaller → grows 30% less
Branching Coral	stops growing	if larger →grows 30% less	if larger →no effect
		if smaller → grows 70% less	if smaller → grows 30% less
Macroalga	→ no effect on growth	→ no effect on growth	→ no effect on growth

Fishing loop

In many tropical regions, especially where human populations have been growing rapidly during the last decades, the destructive impact of fisheries increases if the abundance of target fish decreases (NOAA 2007, Hlavacs 2008, Burke *et al.* 2011). Among the used fishing techniques some have a high potential for mechanical destruction, like dynamite fishing, and the usage of anchors to indent cavities in order to drive fishes out of their refuges. In some of the analysed simulations we take this situation into account to analyse the according change in the specified feedback loops (Fig 1). If the rugosity falls below a threshold, the fish abundance is so low that sufficient catches can only be maintained with intensified fishing pressure. Under these conditions the frequencies of large (Ø 5-10 m, every 5 years) and small (Ø 2-4 m, annually) mechanical disturbance modes increase by 10 % every year, as long as the rugosity is below the assigned threshold. In case that the threshold is exceeded again the disturbance intensities return to the original values.

Scenarios

In the following we establish different scenarios for testing the respective influence of various key states and processes on reef dynamics. The framework of the above described feedback systems will be used as guidelines.

S1 Connectivity/Recruitment scenarios

These scenarios were used as a control to analyse reef dynamics with a (independent) mean grazing rate under different regimes of larval input into the focal reef. In order to alter external larval input the connectivity factor was varied between 0 - 2 in 0.1 intervals.

S2 Herbivory scenarios

In these scenarios the grazing rate becomes a function of the reef rugosity after a specified time span. For the first 50 years herbivory is independent of the reef rugosity and only depends on algal densities (like in S1). Hereafter the system switches into the coupled conditions, meaning that the herbivory rate is not only regulated by algal density but also by the reef rugosity (see Equation 4). These conditions either (a) prevail for the rest of a simulation run or (b) return to “standard” conditions, like in S1 after another 50 years.

S3 Fishing scenarios

The fishing scenarios base on the scenarios described in S2a) and b). In these simulations yet another dependency in the feedback loops was added. If the overall rugosity value falls below the assigned threshold of 1.7 (determined as suitable in preliminary tests) the frequency of the two modes of mechanical disturbance increase by 10 % every year.

S4 Duration of coupled conditions

In order to investigate the recovery potential of a reef and to analyse which species may go extinct, or might even “profit” from a phase-shift, we varied the duration of unfavourable conditions from 0-100 years in 10 year intervals. In these scenarios we tested the effect of herbivory as a function of rugosity without (as in S2 b) and with (like S3 b) additional increases of disturbance frequencies. The data for the analyses were taken 10 years after the initial conditions had been re-established to allow a short post-disturbance recovery period.

3.3 Simulations

At the beginning of a simulation run the coral species were distributed randomly to cover about 10 % of the total area. The initial mean grazing rate was set to 0.15, a value where macroalgae were kept between a relative cover of 5-10 %. Each parameter combination was run over 150 years (for S4 accordingly longer) and replicated 50 times. For the analysis of simulation results the means and standard deviations of the relative cover for each coral species and for macroalgae were calculated and plotted, using R statistical software (R Core Team 2012)

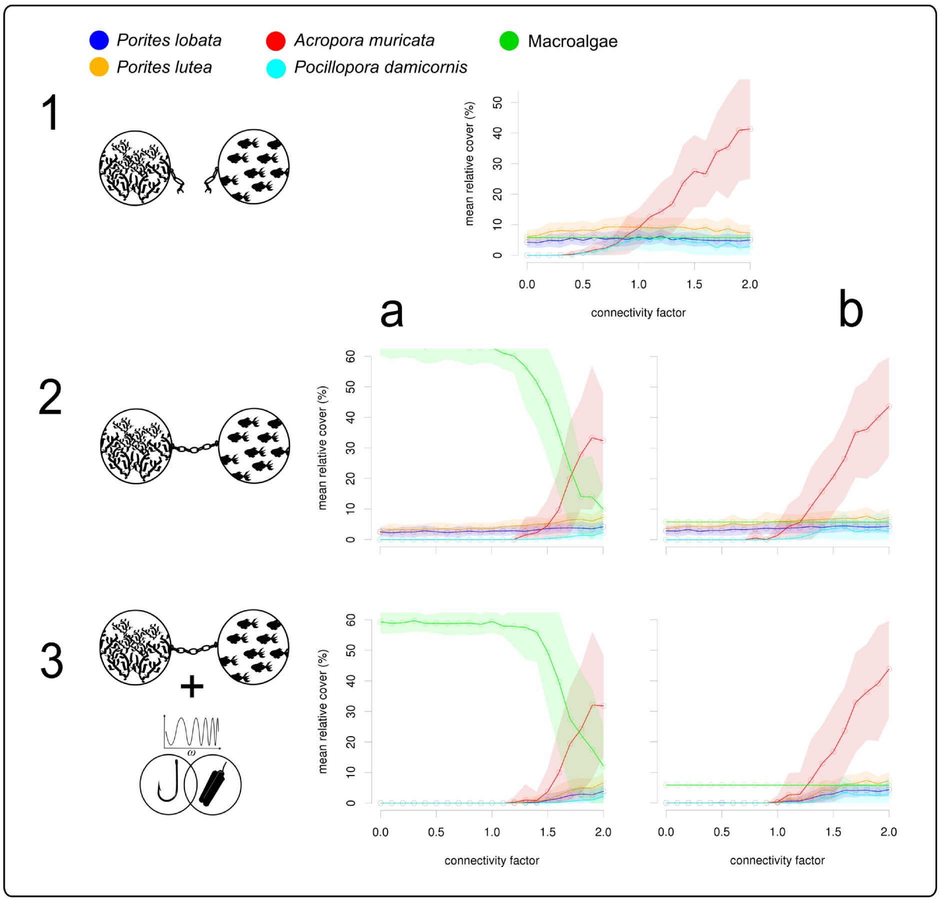

Fig. 2 Mean relative cover (± SD) of different coral species and macroalgae versus the connectivity factor for different scenarios. The top figure (1) displays the situation where herbivory depends only on algae density (S1). In the middle row rugosity and herbivory are coupled (S2) and in the lowest row the disturbance frequency increases as well (S3), if (a) the coupled situation prevails until the end of the simulation or (b) the system returns to "normal" conditions after another 50 years.

3.4 Results

Under standard conditions (Fig. 2, 1) if the connectivity factor was at 1.0, each coral species covered more than 5 % of the total area, the total coral cover amounted to 30-35 % and was evenly distributed between massive and branching growth forms. The cover of massive corals was independent from connectivity levels, and the cover of the faster growing *P. lutea* was generally higher than that of *P. lobata*. This pattern held also for the coupled scenarios (Fig. 2, 2 a and b). The combination of coupled conditions and threshold dependent increases of disturbance frequencies (Fig. 2, 3) allowed coral survival only for connectivity levels equal to, or larger than standard settings, and lead to extinctions after a few decades (Fig. 2, 3; Fig. 3; Fig. 1 d).

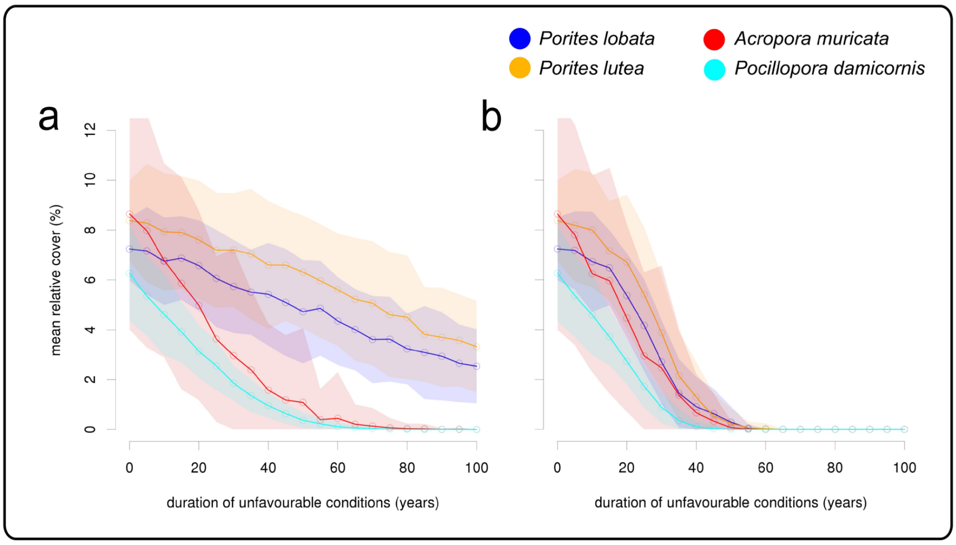

Fig. 3 **Relative cover (± SD) of the different coral species 10 years after normal conditions have been re-established.** The community was either subject to (a) coupled conditions alone or to (b) coupled conditions and increasing disturbance frequencies.

Different levels of larval connectivity lead to diverse results. Under low and intermediate connectivity regimes (0-1.0) massive corals persisted throughout the 50 year-period of unfavourable conditions, while both of the branching coral species went extinct (Fig. 2, 2). The recovering reef was therefore just populated by the two massive *Porites* species (Fig. 1 b). The relative cover of branching corals was far more dependent on larval recruitment rates. Highest applied connectivity levels, and thus high larval input particularly favoured the fast growing *A. muricata* (Fig. 1 c). Even under coupled conditions, the rugosity was always high enough to facilitate sufficient herbivore densities and grazing rates, to keep algal cover low. In the long run A. *muricata* dominated the coral community and slowly displaced the other species – a pattern, which held for all different scenarios (Fig. 2).

The minimum larval connectivity value, and thus larval input to sustain the survival of both branching coral species had to increase under higher levels of environmental pressure. If no coupling occurred, branching corals still survived at low connectivity levels ($cf = 0.4$). Under coupled conditions the minimum necessary connectivity factor, to ensure survival increased from 0.4 to 0.8 or 1.3 if coupled conditions returned to standard conditions or remained for the rest of the simulation, respectively.

Massive corals survived, even though coupled conditions prevailed for 100 years, if fishing pressure did not increase (Fig. 3 a). Nevertheless, their cover was very low after such a long period. Without increased fishing pressure, *A. muricata* was able to survive up to 80 years of unfavourable conditions, but then featured less than 1 % coverage. If fishing pressure increased all coral species went extinct if unfavourable conditions lasted for 60 years or longer.

3.5 Discussion

The simulations show clearly, that pulse events, which can be buffered by the reef under standard conditions, can become harmful by small changes of one or more external factors. Standard background disturbances (major bleaching events every 15 years; smaller and larger mechanical disturbance events annually and every 5 years, respectively) facilitated a total coral cover of > 30 % and even fractions for massive and branching growth forms. Single bleaching events reduced coral cover on the patch, but recovery was possible, because potential settling ground for new recruits was always guaranteed by sufficient grazing.

The coupling of rugosity and herbivory altered the coral community composition as soon as the first larger bleaching events occurred, and a two-step rugosity decline commenced. (i) Branching coral species, which are highly susceptible to bleaching in the Indo-Pacific Region (Brown 1997, Fitt *et al.* 2009), suffer first from these effects. Their population sizes declined heavily during a bleaching event decreasing their reproductive output, and thus evoking a reduced next-generation larval input into the reef. In an intact reef, the rugosity is given by a balance of fast growth and breakage of branching corals (Glynn 1997). Dead skeletons of branching corals, though, erode relatively quick (Glynn 1997, Sheppard *et al.* 2005) decreasing reef rugosity. Hiding places and as a consequence herbivorous fish disappear (Risk 1972, Luckhurst and Luckhurst 1978, Gratwicke and Speight 2005), and the resulting grazing intensity often does not guarantee controlled algal densities (Mumby *et al.* 2007, Mumby and Hastings 2008). (ii) The second step proceeds

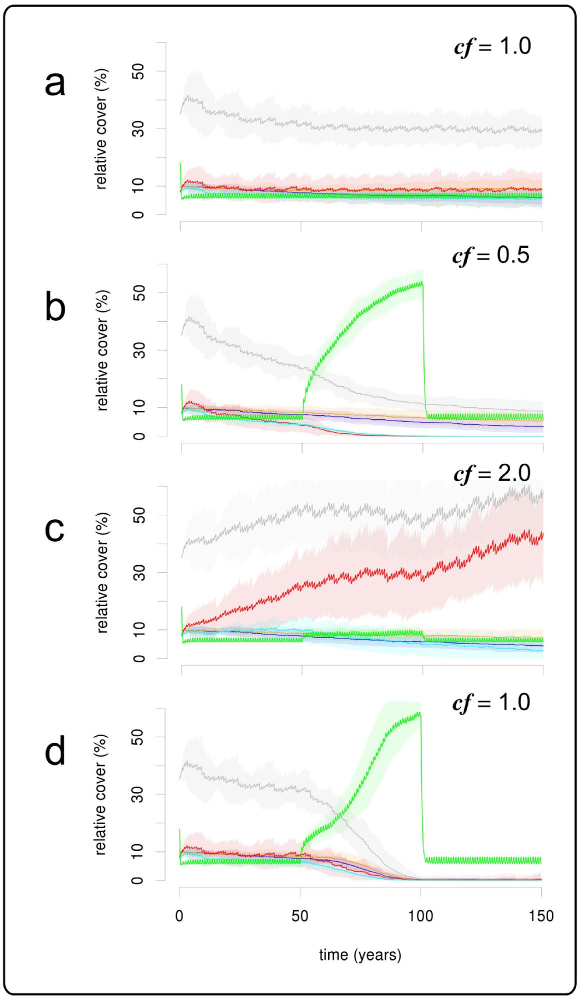

Fig. 4 Mean relative cover (± SD) for the different species over time with different connectivity factors (cf), (a) if initial scenario settings remain at standard connectivity level throughout the whole run, and (b-d) with coupled conditions after 50 years, which return to standard settings after another 50 years. The charts (b) and (c) show the temporal development at low and high connectivity levels, respectively, and (d) shows the temporal development at standard connectivity (1.0), if the fishing pressure increases as the rugosity value falls below its threshold.

slower. Massive corals are less susceptible to bleaching and can persist longer during unfavourable conditions (Loya *et al.* 2001, McClanahan *et al.* 2007a, McCowan *et al.* 2012). Macroalgae occupy potential settling ground for coral recruits and impede their successful settlement (Birrell *et al.* 2008, Diaz-Pulido *et al.* 2009) and although the reproductive output of massive corals stays high, recruits have low chances for successful settlement.

Under unchanged background disturbances the reef might already be doomed, when the first step of degradation is accomplished. Coral populations cannot recover, because older colonies are destroyed by mechanical disturbances or bleaching and no new colonies can establish due to a lack of settling ground. Additional coral cover is lost, accelerating the downward spiral which in the long run locks the ecosystem in these self-propagating unfavourable conditions (Nyström *et al.* 2012). These patterns were observed in the field and can also be seen in our simulation results, where the extinction of branching corals reduces the rugosity so much, that grazing rates become insufficient to guarantee low cover of algae, which grow quicker than corals, proliferate undisturbed and occupy all emerging free space. New coral recruits are thereby hindered from settling and disappearing massive colonies cannot be replaced by younger ones.

Larval connectivity plays an important role for the survival of coral species, and hence the persistence of a coral reef (Pineda *et al.* 2007, Cowen *et al.* 2007, Ritson-Williams *et al.* 2009). The simulations reveal that different levels of larval input can evoke diverging coral community responses. At low connectivity levels, branching corals went extinct, while massive corals persisted under all applied parameter settings. Intermediate levels facilitated an even community composition with nearly the same fractions of massive and branching corals. At highest connectivity levels *A. muricata* always dominated the system and mostly displaces all other coral species. The rugosity stayed high and algae did not stand any chance to increase their density. Here a decrease of the original grazing community hardly had any effect on the total coral cover, because lost corals were quickly replaced by the high amount of incoming recruits. The simulation runs showed that a species with the properties of *A. muricata* reacts the most sensitive to changes of larval connectivity among all tested species; it goes extinct at low levels and totally rules at highest.

A further aspect is that duration matters: the longer the duration of unfavourable conditions lasts, the lower is the overall survival chance of corals. Branching coral species went extinct first in all tested scenarios, while massive species persisted longer. If sufficient recruitment is guaranteed, though, the faster growing branching species will dominate a recovering reef. The longer unfavourable conditions lasted, the lower was the survival of branching species and more persistent massive corals dominated a recovering system. These findings are in line with van Woesik *et al.* (2011), where the authors found that short-term winners also win in the long run.

What do the results tell us?

Feedback loops play an important role in coral reef functioning and small changes in parameters can evoke tremendous ecosystem changes if the interplay of involved feedback loops is shifted or disrupted.

Herbivory is an important process for coral reef resilience. An intact herbivore fauna can control algal densities even though other parameters, like nutrient concentrations or water temperature might promote macroalgae in direct competition with corals (Smith *et al.* 2010), and nutrient enrichment may even enhance herbivore activity locally (Boyer *et al.* 2004). Many studies have shown that the loss of key herbivores, like the mass mortality of *Diadema antillarium* in 1983 in the Caribbean (Lessios *et al.* 1984), strongly decrease herbivory performance on a coral reef. As soon as herbivore densities or diversity decreases, algae may take over in already stressed coral systems, if additional changes happen (McCook 1999, Szmant 2002). In our simulations these patterns can also emerge, as soon as the first bleaching events occur under coupled conditions.

A reef, which is dominated by branching corals may have less resilience (Côté and Darling 2010) than one with a higher diversity of growth forms, because these branching corals are generally more susceptible to extreme temperatures (Loya *et al.* 2001, McClanahan *et al.* 2007a). If such a reef is struck by an extreme temperature event, like the 1998 El Niño, the whole coral population will decrease so much that reproductive output cannot support the survival of the species. Within a short time the calcium carbonate structures will be eroded and rugosity diminishes, kicking the afore mentioned downward spiral into gear. High diversity reefs, with different growth forms and susceptibilities to various threats, may cope better with change. Here some sort of insurance is provided, which always guarantees a minimum rugosity, and hence habitat for herbivores. If not overfished, such a reef generally features a sufficient grazing intensity, which prevents algal takeover. It is therefore important that coral cover is seen diversified and not as a whole. The functional composition of a coral community can have a strong influence on the trajectory of a site, especially when faced with a combination of perturbations (Kubicek *et al.* submitted). Since a change of one parameter can disorder the whole interplay of feedback processes, it is important to understand the whole network of interconnections rather than to anticipate one reaction to one stimulus.

Model assumptions and limitations

While typical growth forms and life histories of coral species and important reef dynamics and processes were considered in the simulations, the community may respond in different ways, if all species associated with a reef would be included. (Bellwood *et al.* (2006) showed, for example, that common grazers on a reef were not able to reverse an algal phase-shift, but a batfish, which was not recognized as an important grazer before, was. This example shows that you can always miss some important properties of a system, especially if these properties only become visible in special situations.

In the model corals, which are bleached and die in the course, are directly removed from the simulation. In reality the calcium carbonate structure of a dead coral colony persists for a certain time, before it erodes, which nevertheless can happen quickly. However it is proven that bleaching among other climate change related threats decreases live coral cover and structural complexity, which then reduces the species richness and the functional groups within a reef (Graham *et al.* 2006).

Interesting work on connectivity in coral reefs (Gawarkiewicz *et al.* 2007, Hedgehock *et al.* 2007, Cowen *et al.* 2007, Sale *et al.* 2010) has been done, so far, but the scaling of larval connectivity is still hard to accomplish. Therefore just a few model applications have been introduced during the last decade, and most of them are biophysical ones, in which larvae are treated as neutrally buoyant particles (Cowen *et al.* 2006). Recently, the biology of marine larvae is also included (Cowen and Sponaugle 2009, Melbourne-Thomas *et al.* 2011a, 2011b), which increases the ecological relevance. In the presented work, however, larval connectivity is treated as a dimensionless multiplier because here we are mainly interested in the amount of incoming larvae and which influence these have on the observed feedback processes.

We simulated herbivory with a density-dependent grazing rate in order to reproduce algal dynamics for typical reefs in the Western Indian Ocean. This assumption may not hold for all locations. However, grazing intensity is hard to measure and just a low number of quantitative studies exists. One priority in future extensions for the reef model will, therefore be the inclusion of additional components of a trophic network.

All in all, the simulations showed that the assumptions used in this study were sufficient for a general analysis of the feedback systems in focus. For an application at a specific reef site, with the goal to aid management decisions, a coupling of the presented application with e.g. one of the before mentioned connectivity models and a careful parameterization of herbivory parameters would most definitely improve the predictive value and allow for meaningful recommendations.

Conclusions

It is very important to understand feedback processes – both, self-enhancing and self-regulating – within an ecosystem to assess which drivers cause which responses. The presented model helps to disentangle interacting environmental factors and feedback processes. In that way they can be studied one by one and their influence on related processes can be assessed more clearly. A prospective coupling of the presented application with other modelling systems that focus on larger scale dynamics, will enhance the overall informative power and may constitute promising management decision tools. Our results are in line with previous findings and confirm that herbivory and larval connectivity are key processes for sustaining reef resilience and may release once coral dominated systems from their algal burden (Hughes *et al.* 2007a, Riegl *et al.* 2009, Selig and Bruno 2010), unless these systems are not impaired by excessively long-reigning unfavourable conditions.

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Chapter 4

Hierarchically structured validation of individual-based models: How to consider qualitative, compositional and quantitative implications

Andreas Kubicek, Fred Jopp, Broder Breckling, Christoph Lange, Hauke Reuter

Submitted to Ecological Modelling

Hierarchically structured validation of individual-based models: How to consider qualitative, compositional and quantitative implications

Andreas Kubicek[1], Fred Jopp[2,3], Broder Breckling[4,5], Christoph Lange[6], Hauke Reuter[1]

[1]Leibniz Center for Tropical Marine Ecology (ZMT), 28359 Bremen, Germany
[2]IFZ, Dept. of Animal Ecology, Justus Liebig University, 35392 Giessen, Germany
[3]Department of Biology, University of Miami, P. O. Box 249118, Coral Gables, FL 33124
[4]Center for Environmental Research and Sustainable Technology, Dept. General and Theoretical Ecology, University of Bremen, 28359 Bremen, Germany
[4,5]Landscape Ecology, University of Vechta, 49377 Vechta, Germany
[6]Bruker Daltonik GmbH, 28359 Bremen, Germanny

Abstract

Validation constitutes a vital process in model development and application, as it ensures that the model can be applied for the intended purposes and that the results are trustworthy within the range of model assumptions. The commonly used approach for validation is to compare independent empirical data sets statistically with the generated model results. For models which operate on single hierarchical levels, such as most equation-based models, this constitutes an adequate approach. However, as individual-based models (IBMs) can operate on different organisation levels synchronously and have an inherent variable interaction structure it is for many applications sufficient to compare plain functional congruity. A more comprehensive assessment of model validity can require additional investigations which encompass also qualitative and structural relationships.

Here we describe a hierarchically structured approach which organises the validation process in close relation to the different hierarchical levels which are covered in the model. This organisation protocol for validation includes the following steps: (1) assessing the different model levels separately, then, (2) applying a set of different techniques such as visual inspection, statistical comparison, involvement of experts, aggregation of data on higher integration levels, and experimental validation.

The outlined approach accounts for the specificity of individual-based models – i.e. the dynamic self-organisation of model outcomes from individual interactions without an inherent determination of properties on higher hierarchical levels – and extends the potential of the validation process qualitatively as it allows to assess structural and causal relations and multi-level feedback processes of the developed models.

Keywords:
Validation, Calibration, Parameterisation, Individual-based model, Agent-based model, Hierarchically structured validation

4.1 Introduction

Validation is an essential part of model development because it ensures applicability of the model for the intended purpose and assesses how robust and reliable model results are. Validation assesses the extent to which a model is rational and fulfils its objectives (Hamilton 1991) and, furthermore, validation should provide information on both, the model's range of validity and its specific applications or parameter combinations. In a strict sense, validation constitutes the last step in securing the correctness and applicability of a model which is then followed by the application to its intended purposes.

A broad spectrum of validation approaches are available and have been described in the literature with respect to ecological modelling. Most of them have been tailored to equation-based models (Power 1993, Rykiel 1996) or describe general aspects of quality assurance (Oreskes *et al.* 1994, Janssen & Heuberger 1995, Sargent 1998, Troitzsch 2004, Jakeman *et al.* 2006, Marks 2007).

Validation for most equation-based models constitutes a single level problem because processes are generally described on the same hierarchical level as the results. For example, Lotka-Volterra equations describe population growth and population interaction (predator-prey in its basic form) to simulate population dynamics. Validation processes in this case can only take place on the same integration level of the population. However, this procedure is not transferable to other modelling approaches for which this relation between described model processes and model generated output is not valid. A good example for this case are individual-based models (IBMs) which do have specific characteristics and, therefore, require specifically designed, extended approaches for validation.

Inherent to the approach, individual-based models can have a hierarchy of model processes for which model results emerge in a self-organised mode from interactions of the specified components on lower integration levels. Thus, model processes often span over several integration levels (e.g. individual life-history, population dynamics and community development) and exhibit across-level feedbacks requiring a specific validation on each of the levels. The fact that modelled processes and components are relatively close to the represented biological processes facilitates additional methods of model testing. It further enables a direct assessment of the causal relationships implemented in the model and allows for potential conclusions on the natural system.

Therefore, it is necessary to extend validation procedures for IBMs and include structural aspects, multi-level analyses and feedback processes between different model levels to cope for inherent variability in model structures. This approach requires a qualitative extension of the validation processes and not only a quantity supplement in the sense of a more sophisticated statistic based comparison with empirical data.

Currently, in publications on individual-based models in ecology, validation is often handled as a negligible aspect. A survey of models using an individual-based approach published during the last 5 years (2007-2011) in the journal Ecological Modelling[1] revealed that validation procedures were applied for a minority of publications. Out of 124 publications which met the search criteria of implementing an IBM type of model, only 22 (less than 18 %) had an extended paragraph on validation (independently if actually a validation analysis was given or just the conditions under which a validation would be possible were stated). Sixty-three percent of the publications did not mention the term 'validation' at all and more than 43 % neither mention 'validation' nor 'sensitivity analysis'. This overview indicates that validation of model results is a deficit in many ecological IBMs.

A reason might be that specific validation approaches for individual-based models in ecology are limited up to now. Compared to ecological IBMs, agent-based model (ABM) validation in the social sciences, is more advanced. Here the discussion on validation is an ongoing issue (Moss 2008), where different approaches for validation and checking the accuracy of model representations are discussed for their context and appropriateness (e.g. Windrum *et al.* 2007, Qudrat-Ullah 2005, Küppers & Lenhard 2005). ABM and IBM are quite similar approaches because they are based on similar modelling paradigms (Reuter *et al.* 2008). Troitzsch (2004) distinguishes between different types of model validity relating to replication (how well the model matches data), prediction (model matches data before they are acquired) and structure (reflects the way the observed systems produces its dynamics). Moss (2008) differentiates ABM validation approaches in two ways; those

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[1] Search in SciVerse (Elsevier) for publications in the journal 'Ecological Modelling' in the five years 2007-2011 which encompass at least one of the following combination of key words: "individual based model*" or "agent-based model" or "multi agent system" or "multi agent model" or "multi agent simulation" or "pattern oriented model*". Publications with an obvious review character or that did not focus on ecological topics were excluded.

that closely relate empirical procedures in data generation, and to those which depict processes as they are perceived by participating stake-holders.

To provide a set of different approaches for validation of IBM, we review and systematise potential strategies and possibilities of validating individual-based models in ecology. The different approaches are evaluated with respect to their potentials and drawbacks the validation of models is outlined as a multi-level problem in ecology using a hierarchical approach. The presented validation approach thus extends the standard approach qualitatively.

4.2 Steps of assessing model correctness

Several distinct steps are necessary to assess the adequateness and correctness of model results. As the distinction of steps and the used terms vary in literature and additionally depend on the different modelling approaches, the specific aims of a model application and also on the different (disciplinary) background of the modellers, these steps have to be defined clearly. Figure 1 gives an overview of the different steps for the general assessment of correctness of model results. Limitations may already become obvious in early stages of model development, for example, restricted data availability may necessitate restructuring of the general outline. The process of parameterisation and sensitivity analysis often confirms this, and can require returning to previous steps of the model development because essential conditions could not be met.

Precondition for validation procedures

Evaluation of the appropriateness of underlying assumptions

The first step in considering model validity is to assess how the investigated ecological context conforms to what the applied modelling approach can actually represent and, furthermore, if the conceptual model meets requirements of the investigation and is reasonable (Sargent 1998). Three basic questions arise when assessing the quality of an ecological model: (1) What are the underlying assumptions of the model, (2) How do these assumptions relate to the model results in the specific case, and (3) Do the boundary conditions hold (Reuter *et al.* 2011)? This requires a recurrent process in which these questions have to be answered at the beginning of the concept development, but also as part of the evaluation process.

Technical and mathematical correctness of programme code

The precondition to assessing the applicability of a model is to assure the technical and mathematical correctness of its implementation; a process sometimes referred to as 'verification' of a model (Sargent 2003, Mitro 2001). For further considerations we assume a technically correct implementation of programme code and a fully developed, executable model. However, it should be recognised that the mathematical correctness of the executed simulation cannot be mathematically proven (Hawking 1988, Oreskes *et al.* 1994), which is particularly relevant to differential equation models as these are more prone to propagation of infinitesimal small errors. As with other modelling techniques, plausibility analysis is also important to IBMs because it estimates the reliability of the model. This should comprise a consideration of expected model dynamics for critical phases such as extremely rapid changes in values, higher order non-linearities and hints for the existence of inherent chaotic dynamics.

Setting and testing parameters

Any data set which is used in the testing and validation process of an ecological model must be independent from the measurements which were used for the model specification and development. Otherwise, it would restrict conclusions on the reliability of the model. This can constitute a problem when data availability is limited and the situation can be even more difficult if a return to earlier stages of model development was necessary which increases the number of necessary data sets.

Calibration (parameter identification)

The process of calibration (also called 'parameter identification') denotes the choice of parameter values to minimise the deviation between model results and a specific set of measured values. Thus a target, consisting of e.g. an empirical data set, an observed pattern, an index or sequence of events, is needed to define the output which the model should generate in case of an optimal fit. Parameter values are varied systematically, applied to the model and then the outcome is evaluated with respect to its fit to the target values. In an iterative process new sets of parameter values are derived on the basis of the previous values and the direction and extent of change expressing the quality of fit is analysed quantitatively (Janssen & Heuberger 1995). This constitutes an optimisation process for which different techniques are available for IBM (Pereira *et al.* 2008).

For individual-based models it has to be considered that the number of parameters is usually high, as model components and sequences often closely resemble biological processes. This reduces the applicability of brute force optimisation techniques and makes more sophisticated approaches necessary (Manson 2003). However, for complex ecological situations it is interesting to see, that the degree of freedom for parameter values is limited considerably. As parameters in IBMs mostly depict real processes, their values are constrained to a biologically plausible range. Experience shows that this often leads to reasonable results without extended fine-tuning. The relative robustness of processes on the level of single organisms is a reason for this situation. If an organism was constricted by very narrowly defined behavioural and physiological reactions to environmental conditions this would result in a high probability for extinction. On the other hand, the occurrence of extreme sensitivities frequently indicates that highly aggregated process descriptions were used. The forest fire model by Ratz (1995) is an example for this situation. He revealed that model assumptions may be unrealistic if results depend on very small changes of parameters. Adding non-linear components considerably reduced parameter sensitivity and made the model more realistic. It is often the case that unrealistic results are obtained outside the limits of plausibility of biological parameters and when using unrealistic structural assumptions.

Sensitivity analysis

Sensitivity analyses provide information on how model results depend on specific parameters and how varying parameter values influence model results. Thus it is methodologically very close to parameter calibration, but focuses on the effects of parameter variation rather than on finding the ideal fit parameters. It is sometimes presented as part of the model results depicting changes to external settings.

The general intention is to get an overview on the parameter space and identify parameters where changes of values implicate significant changes of model results. These have to be handled accordingly, i.e. eliminate parameters which induce no or little change or pay high attention to those which lead to drastic changes in model behaviour. Of additional interest is the identification of parameter ranges which encompass a threshold and might lead to a qualitatively different model behaviour (i.e. phase transition). Any parameters within this range will also have to be treated with extreme care because they can be statistically regarded as coming from different sample sets.

To perform a sensitivity analysis the simulation runs are repeated successively with one of the parameters changed by a small amount (e.g. 10 %) around the standard value identified in the parameter calibration. To obtain a coherent view of model sensitivity implies performing a systematic combination and variation of parameters. It has to be emphasised that the sensitivity to a given parameter variation constitutes an inherent property of the model and that the results are only valid for the given situation and the tested combination of parameters. As sensitivity analysis is a model inherent process it is much easier to perform than validation which requires external data.

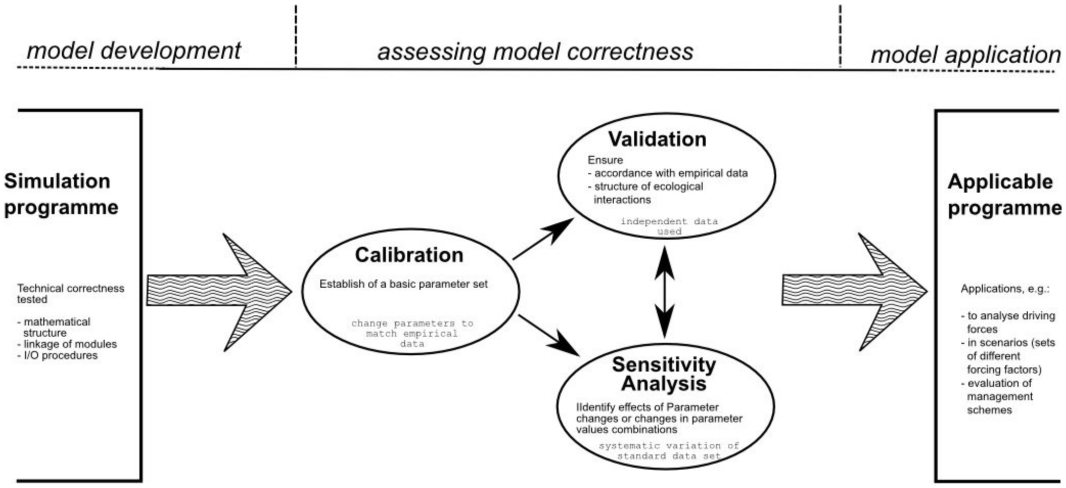

Fig. 1 **Basic steps to assess model accuracy.** Assuming a technically approved model the next step is the calibration and establishment of a standard parameter set. Before application the model should undergo a process of analysing effects of parameters (sensitivity analysis) and assessing relationship to empirical determined data and knowledge (validation). The order of all steps in assuring model correctness is interchangeable and depends on available data and model goals.

For model testing in specific fields different approaches have been developed (e.g. different multivariate approaches, Klepper 1997; spatial aspects of sensitivity analysis, Jager & King 2004), besides the standard statistical procedures. Multi-parameter approaches are important to cope with context specific parameter changes and for analysing the mutual influence of parameter combinations (e.g. van Griensven *et al.* 2006, Makler-Pick *et al.* 2010).

In individual-based models the number of parameter combinations often exceeds the amount which can be handled in reasonable time. In complex models the duration of simulations may also hinder testing all combinations. In these cases a substantiated selection of parameters for evaluation procedures is necessary. Criteria include the inaccuracy and uncertainty of parameters, not directly measurable parameters, the relevance for model processes, and the assumed influence on model outcomes. Experience obtained in the development process of a specific model allows to estimate the potential effects of parameter variation and gives substantiated hints on relevant parameters for testing. Furthermore it is necessary to employ technical approaches to reduce the number of required model runs and replicates.

In an IBM dynamics are frequently determined by the inherent rules rather than by external parameters. Therefore it is important to note that the concept of a sensitivity analysis can be extended and may also include the variation of rules. In case of representing the interactions of individuals a slight behavioural variation may lead to a different model outcome or could also affect the structure of the model itself (Jakeman *et al.* 2006).

Validation of model results

Validation constitutes the final step of checking correctness and applicability of any model. According to most literature on model development (e.g. Gardner & Urban 2003, Janssen & Heuberger 1995, Sargent 1998) the basic procedure implies a direct comparison of model results with an independent data set. Independent data sets are necessary to test the model and secure the possibility to transfer the model to further situations.

For this purpose standard statistical procedures are available which have led to a long history in the validation of differential equation-based models (e.g. Power 1993). For IBMs this validation procedure has to be extended to include the structural difference of this approach.

4.3 Validating individual-based models

A reason for the necessity of a specific approach for IBMs is the structurally broader extent of the applied mathematical repertoire. The object-oriented design of autonomously acting agents is the predominant concept and in addition to equation-based modules, extended rule-based decisions are possible which relate to different hierarchical levels. Thus, as in IBM the structure of relationships of model entities can be modified during run time execution, classical validation approaches do not cover all aspects which should be tested.

Depending on the specific aims of a model different elements of potential validation approaches will be more important to evaluate the correctness and the applicability to the respective research questions. It is not possible to define a generally applicable validation procedure which will deliver satisfactory results for all different model goals and situations. However, it is possible to outline different elements which can be composed to design a specific evaluation procedure to fit the projected model goals.

In IBMs and ABMs the detailed level of representation of organismic processes allows to follow a clearly organised process of validation relating to the different hierarchical levels of the model (e.g. Auman 2007, Caron-Lormier *et al.* 2009). The basic scheme of comparing model results with independent goal conditions (data, processes, structure etc.) stays the same. However, we additionally advocate to evaluate the accuracy of specific model processes and outcomes on each of the model levels separately, ranging from the lowest to the highest level. Typically (see examples at the end of this section) this could comprise the level of individual life-histories, population development and community dynamics. As the model dynamics in IBMs emerge from self-organisation processes a correct representation and functioning of lower level processes emphasises the assumption of accurate results on corresponding higher levels.

With such a '*Hierarchically Structured Validation*' approach it is thus possible to investigate how far the implemented model mechanisms reproduce the characteristics of the studied ecological context. The IBM should not simply reproduce the observed system dynamics but also reflect the causal mechanisms, interaction structures and processes operating in the real system to generate its behaviour (Troitzsch 2004). Such a consistency check for key processes and dynamics on different hierarchical levels increases the probability of a correct representation of the system behaviour and that the results are reliable within the applied conceptual system.

Depending on the model aims, the empirical background and the availability of data, structural validation can include different procedures which are explained in the following. We emphasise combining several of these procedures to reach a high level of confidence in the correctness of model results.

Visual inspection of results (plot results)

The visual inspection constitutes an immediate, fast approach to get a first impression of the model results and has already been proposed for many years (Anscombe 1973). It consists of comparing single data points, time series, spatial structures (patterns), and thresholds with expected values or data and diagrams derived from empirical studies. It can also include a test for extremes resulting from the range of biological plausible parameter values. Even if the results are not precise and do not have a statistical relevance, in many cases a visual inspection allows to get a reasonable overview of the model performance. Therefore, we list it here as the first step to assess model results. Usually, it is performed by most modellers during model development to evaluate the effect of parameter changes or changes in model structure. However, depending on the model goals we can also find a visual inspection or pattern comparison as the final method in many model studies. In the publications from the Journal 'Ecological Modelling' surveyed with respect to their validation approaches (see Introduction) approx. 50 % of those with an explicit paragraph on validation refer to this as the main or only method. This method is often applied when empirical data are not reliable enough to perform a statistical comparison or when the goal of the investigation is more on the theoretical side focusing on the general feasibility of implemented model processes.

An example for the visual inspection method, applied without referring to the term 'validation', is the IBM of Railsback & Johnson (2011) representing the foraging of migratory birds on a pest insect (the coffee berry borer, cbb) in Jamaican coffee farms. The model represents a grid based habitat structure consisting of different tree vegetation types and shade intensities. Bird food resources (bugs and cbb) undergo a fixed seasonal dynamic (bugs) or change depending on previous values (cbb). An important feature of the habitat is the amount of forest-like vegetation which provides food resources when pest densities are low. The implemented birds feed on both resources and apply a different behavioural strategy as a reaction to the depletion of local food resources. The authors tested visually and graphically if the generated patterns (functional reactions of birds) match the patterns that were determined empirically. It thus constitutes an example for visual inspection following the "pattern-oriented modelling" approach of Grimm *et al.* (2005). Further examples are the models of Rupp & Rupp (2010) who analysed the movement and distribution of elks and tested the visual accordance of spatio-temporal patterns of habitat use between model and observation on different organisation levels, and Larocque *et al.* (2011) who extended the forest gap ZELIG model by Urban (1999) and visually compared growth rate time series of different trees and stand densities over time. Visual inspection proofed to be applicable in many situations in which the distinction of a good fit between model and real world information was easy to estimate.

Statistical validation – comparison of model results with independent data sets

Analysing statistical coherence of model results in relationship to independent empirical data can be seen as the standard procedure of model validation for which a wide set of literature and examples are available (Power 1993, Rykiel 1996). In the context of a hierarchically structured validation approach it constitutes a specific methodology which allows to test model results against data on the same aggregation level. In this context a model can be viewed as a 'data-generating machine' where the range of possible distributions of data is restricted by the model ('the machine') itself, while the actual distribution is normally influenced by parametrization. Statistics allow to estimate the relevance of differences between the model generated and empirical data sets and to make *generalized* statements about the functioning of the system that the model is based upon.

Testing the model using the *same* data for parametrization and validation would only show, that the model was optimized to generate such distributions. But that does not tell anything about the validity of the model in general: to be able to test for generalisation, one has to use different empirical data sets (collected data) for parametrization and statistical evaluation of the model. Independent data sets may be collected or constructed by splitting data sets or by applying cross validation techniques. By providing those kinds of independent data sets one rules out a direct connection via parametrization data.

For the validation it is necessary to prove that there is a connection between the data collected in the biological system and data generated by the model. Here the substantial question of statistics applies whether two samples derive from the same data set (have the same statistical properties). However, it is also necessary to keep in mind that all potential pitfalls of statistical analysis apply as well.

One important thing is that many biological data sets do not fulfil basic assumptions of classical, so called 'parametric' tests, which is the reason for a wide-spread use of 'distribution-free'[2], non-parametric tests. But generally, the question to test is, whether there is a relevant difference between collected data and those produced by the model. Thereby 'relevant' or 'significant' is always in the eyes of the researcher, and *not* naturally given by *any* statistical value as the p-value. And even when using statistical values for thresholds of accepting or rejecting equality of modelled and collected data distributions, most statistical tests will report a difference as sufficiently reliable, regardless of the size of the difference, as long as the difference is consistent. So, whether a model fits the collected data appropriately can never be decided from the results of statistical tests alone.

Validation with expert knowledge

A further potential component in evaluating model results is to make use of expert knowledge. This should be considered either in situations where data are scarce, have a high degree of uncertainty, or when a direct and intensive exchange with model users is helpful and desirable. The choice of experts depends on the required knowledge, e.g. on theoretical concepts, specific ecological processes or organism groups, or the management of resources. Thus experts may have either a strong disciplinary background or might be stakeholders and come from a group with indigenous knowledge on effects of intervening into specific ecological processes. In this respect validation with expert knowledge can be considered as a specific case of visual interpretation of the results (see part 3.1). When the direct participation of stakeholders is desired, an exceptional care in the processing and visualisation of model handling and model results will have to be taken in order to enhance the communication of model processes and results.

The evaluation of model results by experts can be done for their consistency by checking the correct relation between model processes, input data and the corresponding results. To estimate the plausibility of scenario investigations or to test the extrapolation of model processes can also yield interesting insights. This also includes the structure and internal realisation of model processes.

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[2] But by no means 'assumption-free'!

A more formalised approach would be to perform a 'Turing Test' (Turing 1950) in a generalised form where the experts have to decide if the results derive from simulations or from real data. The explicit involvement of experts in the evaluation of model results thus extends what should be considered as the normal situation of a close cooperation with experts from the field. For the evaluation of the correctness of habitat use of European Robins, Reuter and Breckling (1999) constructed an artificial map and compared the model results with experts opinion on the potential use of this map by the Robins. In the social science context Moss (2008) discussed validation aspects for the companion modelling approach which involves stake-holders in a feedback process of model development and evaluation of model processes and results.

Statistical properties on higher integration levels

Most validation approaches evaluate model output directly with an ecological data set on the same integration level (e.g. in a model on population dynamics of bullhead fish comparison of age classes with according field measurement (Charles *et al.* 2008) and in a model on a small mammalian carnivore the number of territorial animals (simulation) with abundances in the field, Popp *et al.* 2007). In some cases, however it is useful to apply a conceptual or more indirect analysis which focuses on the implications which the model has on higher integration levels. This allows to extend the range of validation. A reason to consider and apply this focus is the dependence of many ecological situations on very specific local situations which make it difficult to reproduce dynamics exactly.

In ecology we often have the situation that only a very limited number of replicates are available or even that data sets are unique either due to limited resources, high inherent variability or singularity of the event or the investigated processes. It is possible to use knowledge and data derived from these cases for model development, however this creates specific problems for the validation of the model: a) Fitting the model dynamics to exactly represent the investigated system would constitute an example of a single case parameterisation with a generalisation and wider applicability of the results being highly questionable and b) in most cases the independent data for the validation process will be missing.

A typical example for the described situation would be pronounced spatial heterogeneous distributions which are amplified or modified through organismic activities or interactions (e.g. feedback processes in coral reefs between algae and coral recruitment, Nyström *et al.* 2000). Other examples are models of plankton dynamics where it is difficult to simulate specific local dynamics as this would require to know and include all responses for the conditions which influence patch dynamics (e.g Petroviskii & Petrovskaya 2012).

In cases, where a direct validation of a comparable integration level is not applicable, it is however, possible to assess the quality of a model by analysing and comparing model results on higher integration levels. This could for instance comprise the comparison of frequencies of certain situations in an extended time span (e.g. extinction events, population oscillations (Huitu *et al.* 2003) or maxima in the occurrence of a particular species. It should also be analysed whether a change in the random seed of the model or a slight variation in model input parameters lead to comparable distributions. This approach is closely related to the problem of choosing the right scale of investigation in ecology (Reuter *et al.* 2010) to get correct, reliable and generalisable statements.

The oscillation of rodent populations (Krebs 1996, Stenseth 1999, Huitu *et al.* 2003, Sundell *et al.* 2004) is an example for this situation. Because of the complex relationships of a large number of involved species and trophic levels and the diverse driving factors an attempt to exactly represent the population dynamics in a specific location over time is doomed to fail. An analysis of aggregated properties on higher levels e.g. indexes focusing on the oscillations may however very well capture the basic properties of these dynamics. In this case a cyclicity index (Henttonen *et al.* 1985) can be used as a reasonable comparator for validation (Reuter 2005). Thus the type of oscillations with respect to structure (shape, amplitude) and periodicity may be represented correctly even if specific patterns of population dynamics are highly variable. In case of models generating spatial patterns, their characteristics on higher levels (e.g. area-boundary relations, clumping, fractal dimension) could be used to compare model results with the characteristics of the empirical studies.

With this approach of assessing characteristics on higher integration levels it is thus possible to include complex situations in the model evaluation for which the direct validation on levels comparable to the available data are not possible. It may not be possible to directly describe a particular dynamic but, nevertheless to capture and formalise certain relevant characteristics.

Experimental validation of model generated hypotheses

With this validation approach the standard temporal sequence of generating field data and knowledge which is then followed by the model development and parameterisation is turned around. Here experiments follow the analysis of model processes and the generation of model results. It is appropriate if no according data was available at the time of model development or to test additional aspects for which only educated guesses could be made. This constitutes a very interesting approach as it allows to substantiate predictions or extrapolations which are generated by the model thus extending the chain from empirical work to the model development by a feedback to empirical work.

Besides explicitly generated new experiments this approach also includes cases of retrospective analysis in which model sequences give hints for a re-analysis of already existing data from a new perspective. The latter case occurred in the model on the reproduction phase of European robins (Reuter & Breckling 1999) which provides a detailed calculation of time and energy expenditure to calculate energy demands and reproduction events. This model showed a distinct increase of individual weight during the day followed by a considerable weight loss in long and cold nights. This feature was not explicitly programmed but resulted as an implicit property of temporal sequences of feeding and diurnal patterns in energy expenditure. A reciprocal analysis of catch data during different intervals after sunrise gave a very similar pattern (Grajetzky 2000) which thus strengthened trust in a correct implementation of the underlying time-energy budgets.

Examples for a hierarchically structured validation approach

The model of Kubicek *et al.* (submitted) on spatial competition in coral reefs shows an example of a *hierarchically structured validation*. It aims to analyse key processes of coral reef functioning in order to increase the understanding of reef resilience and to advance management measures for these unique ecosystems. Different functional coral species and algae are represented with a very detailed life history and interact with their environment as well as with their direct neighbours (e.g. compete for space). Environmental impact such as changes in temperature or mechanical disturbances influence growth and mortality of the displayed organisms. Generally, the model reproduces dynamics of a coral reefs realistically and allows to simulate system responses to various drivers. The multitude of parameters and the high stochasticity within a coral reef system which induces non-linear dynamics, complicates the validation of the model by comparing properties of single datasets which should be reflected by the simulations.

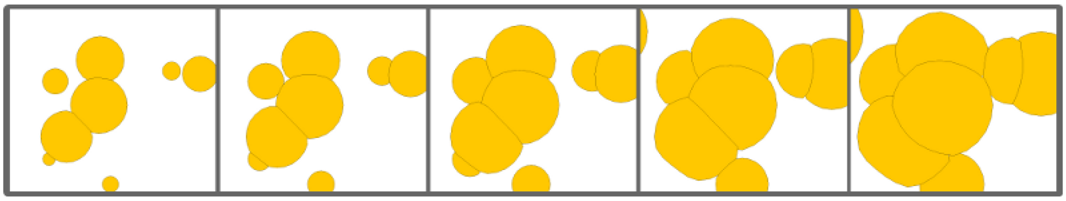

Fig. 2 The growth pattern of massive coral colonies as an example of the competition between individual entities. Individuals reduce growth in the direction of direct contact with neighbouring corals and die if overgrown to a large extent (Kubicek *et al.* submitted).

On this account, the validation was accomplished with the analysis of processes on three different integration levels, (i) the individual, (ii) the population, and (iii) the community. Virtual individuals were observed visually through time to assess how they react on directly neighbouring, contacting organisms; e.g. smaller coral colonies stopped growing towards the direction of a larger neighbour (Fig. 2) and to ensure that implement rules are followed correctly. In the model all coral species had specific linear radial growth rates, which were used as a base for the validation on the population level. The size of all individuals of a species was related to their age which allowed to evaluate the population's growth performance. A linear fitting of that relation would represent the assigned growth rate if all individuals were able to grow without density dependent limitations. Through this method it became visible that high local densities (i.e. the abundance of neighbouring organisms that competed for space) decreased the population's growth performance by hampering the expansion of individual colonies (Fig. 3). Finally, in order to evaluate the community response to rare events, data of a major bleaching event in the Western Indian Ocean region in 1998 were compared to model results.

Here the results of the model reflected the empirical data very well (Fig. 4). The overall coral cover declines dramatically after a bleaching event in 1998 and led to a subsequent change in community structure. This decline and the following slow recovery is depicted well.

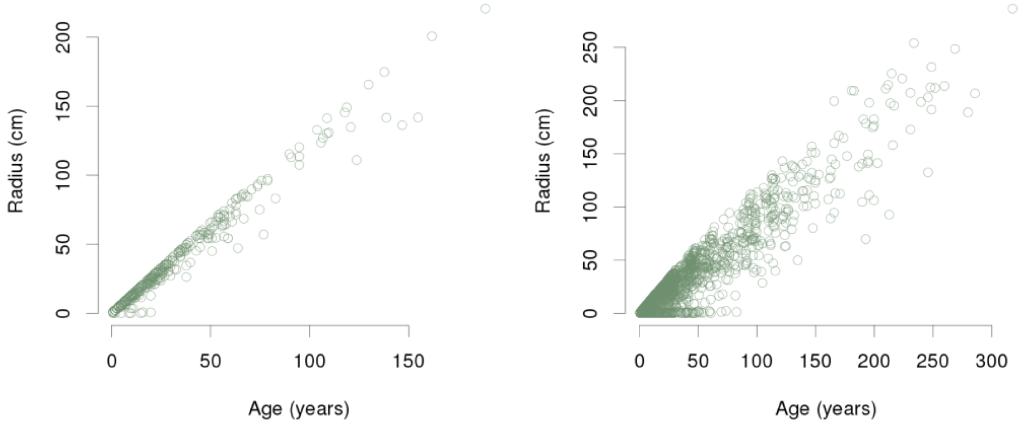

Fig. 3 **Population age-structure in relation to size for *Porites lutea*.** For high disturbance frequencies (low density situation, left) the age-size relationship corresponds closely to the maximum growth rates. In contrast, in simulations with low disturbance frequencies (high densities) the age-size relationship indicates much lower average growth rates due to spatial competition (Kubicek et al. submitted).

Laperrier *et al.* (2009) present a further example for a structural validation in a model of plague spread. Despite extended knowledge on the role of different elements of the infection system and the dynamics and processes which lead to local disease outbreaks, data availability for the case study on the island of Madagascar was limited. To cope with these conditions the authors did not attempt to test model results with empirical data with a direct comparison, but applied a conceptual approach by linking scenarios of e.g. prevalence levels in recipients with model results and a then comparing sufficiently general characteristics of the natural system on higher integration levels.

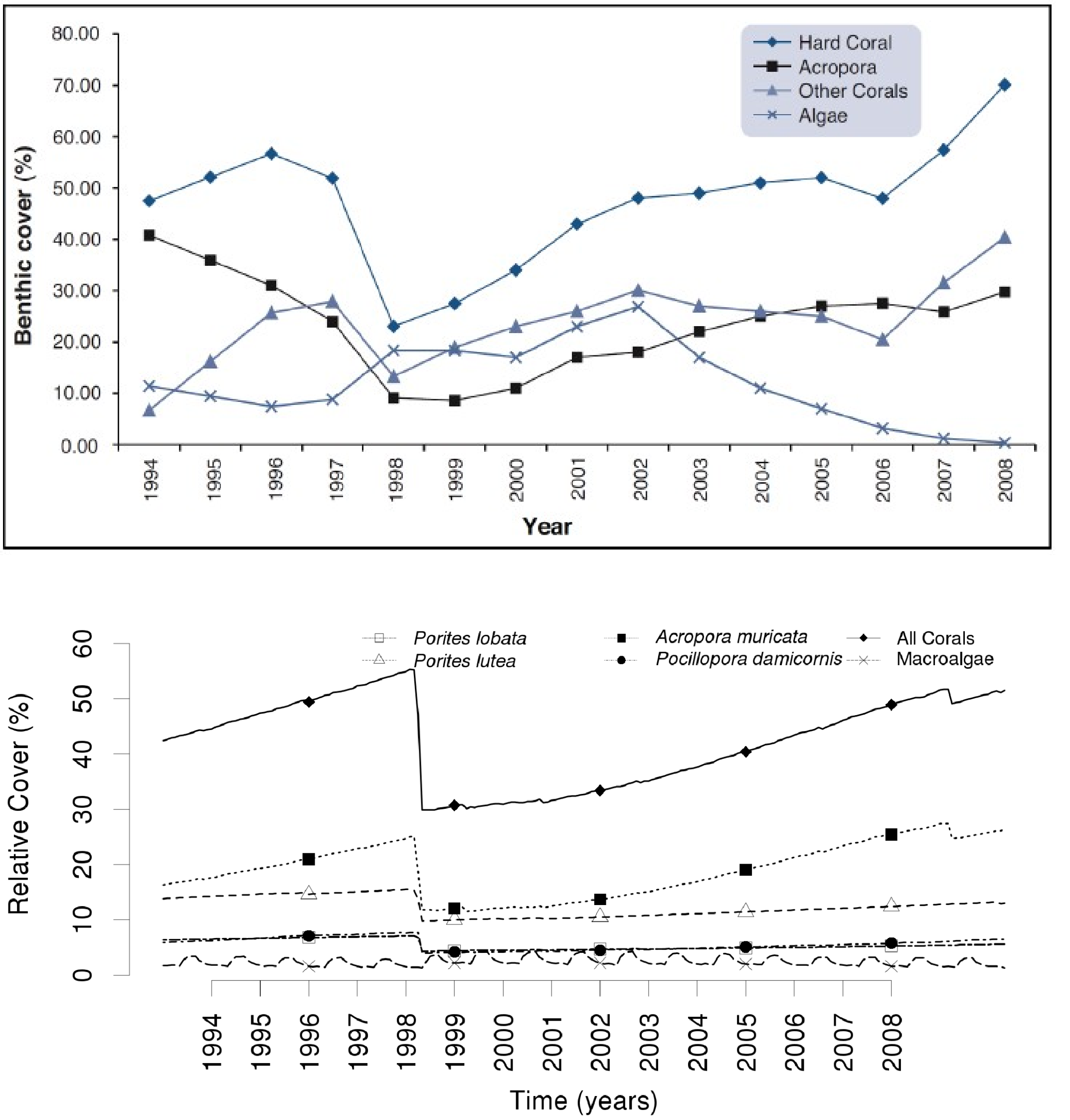

Fig. 4 **Comparison of model results on the community level** (bottom, Kubicek *et al.* submitted.) with data from the 1998 bleaching event in Zanzibar (top, Muthiga *et al.* 2008).

4.4 Limits of validation

Models are a formal construct to represent analysed systems and to investigate complex interrelationships. They are used as an instrument to reduce complexity of the system with respect to a given problem to be solved and as an abstraction process of the reality, never giving a complete picture of real processes (Wainwright and Mulligan 2004; Tedeschi 2006, Müller *et al.* 2011). Therefore an important task in the evaluation of every model is to assess what degree of accordance can be expected and where the limits of the model are.

Assessing the validity range of a model is closely related to the validation procedure and sensitivity analysis. These should be explicitly applied to estimate the range of accuracy for the model. In order to determine the range of potential valid statements it is also ne-

Table 1.: Overview of potential components of a hierarchically structured validation process

	Procedure to test model accuracy	**Conditions of applicability**	**Pros & Cons**
Visual inspection	Check accordance of model results with empirical data, dynamics and patterns by eye. Simple test of reasonability	Availability of knowledge on plausible dynamics	+ fast intuitive approach - no quantitative data - not statistical reliable statements
Statistical comparison	Apply statistical procedures to compare model results with data derived from empirical work.	Availability of sufficient empirical values and patterns to be compared with model results, comparison of data and model results on the same level (single level approach)	+ statistical reliable statements + quantitative data of model evaluation - often no information on causal relationships
Expert knowledge	Confront experts with model structure and model results.	Limited availability of data, intention to involve stake-holders	+ inclusion of user knowledge + test of qualitative knowledge - quantification is problematic
Higher-level properties	Comparison of aggregated model results with ecological characteristics on higher integration level	Singularity or uncertainty of empirical data	+ extension of validation possibilities - no information on causal relationships
Experimental validation	Generation of hypothesis and prediction which are subsequently tested empirically.	Empirical testability of model generated results	+ strong interlinking between model and empirical work - time delay in validation

cessary to refer to the model assumptions and the underlying theory as these are crucial for the interpretation and validation of the results (see part 2.1). Explicit assumptions made during the development of the conceptual model can be directly referred to when analysing model implications and results and they constitute the boundary of model applications. However, very often a model has considerably more inherent assumptions resulting from model concepts, modelling approaches (technical limitations, restrictions), and from aggregation processes in which specific processes are omitted in order to simplify representation. In equation-based population models it is often implicitly assumed that structuring a population e.g. into size or age classes or representing spatial interactions is not relevant for the intended results. In IBM the situation is often more sophisticated as model processes are more biologically realistic. The leading questions here are which components have been omitted and if their influence is really negligible. As parameters usually have a clear biological meaning and thus a defined range of plausibility in IBM calibration of model is simplified and straightforward. This also helps to identify whether a process has been represented incorrectly or has been aggregated too much i.e. if correct results can only be obtained with parameters outside a biologically plausible range.

Ecological models are often developed for a specific situation. One aspect of the validity range thus implicates answering the question whether it is possible to transfer the model to another setting without violating the explicit or implicit assumptions of model development and to which degree a model application is generalisable (see e.g. Rykiel 1996). Transferability can relate to the general settings of the model (usually environmental factors influencing species life-histories and interaction) or how general the descriptions of organisms, their physiology or interactions are. It should also relate to the question of adaptability to other species. As organisms adapt to changes in their environment with a multitude of potential changes in behaviour or physiology this has to be evaluated against the inherent *ceteri paribus* conditions of the model. IBMs have a high potential of transferability and adaptability through the potential to distinguish between inherent model processes and environmental forcing. DeAngelis *et al*. (1993) and Nisbet *et al.* (1997) showed this with comparative modelling studies on age-structured and spatially structured populations.

However, often it is not possible to define sharp boundaries for a model's range of validity. Depending on the specified conditions (parameters and internal rules) it is more realistic to assume a gradual range of increasing uncertainty.

4.5 Conclusions and recommendations

In this contribution we have outlined how crucial it is to understand that the process of model development does not end with formulating and testing the mathematical code and correctness of rules and structure but necessitates a subsequent model evaluation. Securing biological adequateness and determining the range of high quality results includes calibration, sensitivity analysis and validation in which model performance and structure are compared to empirically determined data and causal relationships. This process includes the necessity to determine the limits of validity for the model and also the degree of uncertainty which is the precondition to discuss the model outcome adequately.

Here we have pointed out the specificity of IBM with respect to structure and representation of causal relationships which extends the range of processes and dynamics that can be represented in ecological modelling. This approach requires specific and advanced strategies for validation which allow to cope with the new structural qualities. The *hierarchically structured validation* adds a specific approach to general validation procedures applicable for individual- and agent-based models. It focuses on analysing the different hierarchical levels separately, and thus creates additional possibilities for proofing the functionality of the model. This approach strongly increases the probability that the behaviour and causal structure of the investigated system has been represented correctly and results are reliable within the explicated assumptions on system functioning.

From the validation process the validity range of the model is derived. Applying the model within this range will usually lead to high quality results. However, when models aim at predicting developments with new combinations of parameters (e.g scenarios of environmental change) applications often leave the range of validated model configurations. The evaluation of such scenario simulations therefore has to be carried out with great care and it always has to be kept in mind that model results will remain uncertain to a high extent. We therefore state that models inform more about potential outcomes under the specified model assumptions and scenario conditions (extrapolation) rather than providing a strict prognosis. However, it remains difficult to foresee whether the implemented structure and relationships as well as parameters are actually the most appropriate description for the given investigation. In this regard, model validation elaborates the potential to answer the investigated questions and to explore the contribution of a model to expand ecological knowledge.

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Synthesis

Major findings and advancements for coral reef science

Ecological modelling constitutes an important tool for the analysis of complexity, both to handle the sheer amount of different entities and interactions, and also if these components are interconnected and feature mutual feedback relationships. Especially in ecology, where processes of interest are often interlinked on many different spatial and temporal scales, models demonstrated their potential for integrative system analysis (Hastings 1990, DeAngelis *et al.* 1998, Reuter 2005, Breckling *et al.* 2006, Jopp *et al.* 2010).

As we see in Chapter 1, the choice of the right modelling technique with a suitable level of detail is no trivial task and the temporal and spatial scale of the investigated system need to be considered carefully. It might be appropriate to treat the reef as a whole, without the consideration of space, if the consequences of different fishing regimes on reef communities are estimated (Chapter 2, 17.2). The simulation of ecological patterns of an individual alga, though, needs more detailed information as input, to produce meaningful results (Chapter 2, 17.4). Mumby (2006a) highlighted the importance to apply a higher degree of detail to the analysis of coral reef dynamics because these extraordinarily diverse ecosystems can create quite different responses to particular changes of state variables. Although space was not represented continuously and the representation of organisms was constrained to massive coral colonies and algae, the application of Mumby (2006a) proved, that its results could not have been achieved by simple methods, because abiotic and biotic processes were highly interdependent and often influenced each other.

The presented IBM offers a diversified representation of the coral community in a generic framework to simulate and analyse coral reef dynamics. An arbitrary number of different coral species with massive or branching growth patterns can be specified according to their relevant life history traits and interaction patterns. In the represented community, algae play an important role as primary competitors for all coral species, and can influence reef trajectories decisively. Each of the implemented coral species reacts differently to its neighbourhood and its external conditions and therefore the community composition may change completely with only small changes in overall conditions (see Chapter 2 and 3).

In this way the various community responses to changing species properties or external conditions can be analysed more realistically compared to applications in which the reef is treated as a 'black box', only adjusting its overall coral cover upon change. What is most important, though, is that community outcomes to particular types of perturbations (e.g.

bleaching or mechanical disturbances) in the IBM simulations and respective regrowth patterns can be examined diversified as well and may give insight on the recovery potential of a particular reef site. Such observations are not possible with aggregated 'black box' methods. They may be appropriate to estimate the amount of resulting coral cover after a certain perturbation, but cannot give any insight in how far the resilience of a reef is affected. In the presented work the resulting community could not only be analysed in total (cover) but also with respect to the post-disturbance diversity of species, growth forms, and population- and community structure, which thus allows to draw conclusions on the overall system stability and resilience.

Three examples of reef sites close to Zanzibar Island with high coral cover, two of which feature (partially) low diversity, may help to exemplify the patterns, which can be observed with the diversified analysis in the model. (i) Changuu reef, close to the city of Zanzibar, is a good example for a site with high coral cover (~ 50 %) and a high persistence towards mechanical perturbations, but with low 'functional value'. It is a heavily used and exploited site by the means of fishing and is strongly affected by waste water, and hence pollutants and nutrients from the town (Bjork et al. 1995, DeGeorges et al. 2010, Rushingisha 2012). Muhando et al. (2002) found that corallimorpharians covered 14 % of the reef, mainly on its crest and flat. Here a large part of the (still persisting) coral cover is made up by Galaxea astreata and *Porites rus* (Muhando and Lanshammar 2008), both of which seem to be quite resistant to environmental change and possess strong competitive traits over other taxa (e.g. corallimorpharians) but facilitate scarce structure. Therefore this site exhibits a low biodiversity of fish and other associated organisms. Territorial damselfish foster gardens of epiphytic turf algae for their own foraging (Lobel 1980) and cast out larger herbivores like parrotfish, which might in the long run also lead to a phase shift to larger macrophytes if they cannot be maintained in low abundances due to a loss of herbivory (Ceccarelli et al. 2005). (ii) Ukombe Reef (), in large parts dominated by branching Acropora, is quite pristine and unfished, compared to many other non-MPAs around Zanzibar. It provides high 'functional value', insofar that it can host many different herbivores, which guarantee low algal densities. An extreme temperature event, like El Niño, though, may kill large parts of the coral community and subsequent storms might eradicate all structural complexity at the site. Free space would be taken over by faster colonizing macroalgae. (iii) Chumbe Reef, a Marine Protected Area (MPA), located 12 km South of Zanzibar town, can be seen as a very small but resilient coral reef site. Here different coral species of various growth forms are represented and each features alternative life histories. A thermal pulse event might kill parts of the branching coral community but some structural complexity and herbivore activity would be maintained, to allow a subsequent recolonization of branching coral species. But, as surrounding reefs are under high pressure, the larval input and the abundance of herbivores, which rely on other types of habitats, might also decrease for such a pristine site in the future (Chapter 3). All of these contrasting outcomes can be represented and simulated with the introduced modelling framework, which also allows to analyse respective dynamics of reef degradation and recovery. Within the coral community massive coral species dominate under low perturbation levels, but are displaced by branching species if disturbance events occur in high frequencies, while intermediate disturbance levels promote the highest evenness. Without adequate grazing intensities the system generally shifts to macroalgal dominance, but if the fishing pressure is moderate high larval connectivity levels always guarantee high coral cover, sufficient structural complexity, and thus adequate herbivore densities to keep macroalgal densities low.

As already mentioned for adaptive systems with non-linear dynamics (Preface, Resilience stability and phase shifts), the virtual reef never levels into a steady state – except from total extinctions – but usually fluctuates around a basin of attraction. The relative cover of respective coral species can vary considerably over time although conditions are kept constant. Such variation can arise from stochastic processes or circumstances, e.g. that one of the last large colonies of a coral species is destroyed in a disturbance event and thereby the reproductive output, and thus the larval input are diminished. This may have incisive effects on the recovery or persistence of a population. Stochasticity complicates the prediction of trajectories or fates for ecosystems, likewise in the field and in the theoretical analysis, and impedes their comparison with each other. One possible improvement on that account could be the investigation of larger spatial arrangements which not only incorporate coral reefs but also adjacent habitats like seagrass beds and mangrove systems.

The presented model allows to examine specific impacts of perturbations separately for each type, -intensity, or -frequency or in combination as applied and discussed in Chapter 2. Complex community/ecosystem responses can thus be backtracked to specific triggers. Additionally, several interfaces for coupling with other modelling systems are provided, and the resulting tools may aid in directing management measures.

Model validation constitutes an important part in model conception and development. It tests the accurateness of the implemented model processes as well as the behaviour and interactions of components by comparing model results to field data. The iterative development of a model can thus often improve the understanding of the study system, before simulations are run, because ambiguities in model behaviour may point out gaps in system apprehension.

Potential future developments

The presented model application provides a completely new and realistic representation of relevant processes in coral reefs. It incorporates current knowledge and is the first tool that permits a high-resolution (temporal and spatial), diversified analysis of benthic community dynamics. Of course, some aggregations and assumptions had to be made and the model results have to be interpreted with these preconditions in mind. Nevertheless, it provides the possibility to (a) incorporate modifications to meet the conditions of particular sites, and (b) new biological and ecological insights with little effort, because all processes and components can be equipped with additional modules.

In the current version macroalgae are only implemented with one representative group. But coral responses to different macroalgae are diverse (Jompa and McCook 2003), and thus it is highly important to consider algal properties, such as being vectors for coral diseases, physical abrasion and chemical cues, all of which can be decisive components of competitive interactions, worth being included in future versions. The group of turf algae, which combines many different species and morphologies, is only considered as hindering coral settlement. A diversification within this group is indispensable to increase the validity of represented recruitment patterns. For example, crustose coralline algae can be important components for the attraction and transformation of coral larvae (Heyward and Negri 1999), or some turfing filamentous specimen (e.g. *Corallophila huysmansii*) might be quite harmful for living coral tissue (Jompa and McCook 2003) or capture sediments and suffocate corals thereunder (Nugues and Roberts 2003). In the model such properties can be implemented with different layers for 'good' and 'bad' turfing algae, which either enhance or reduce coral performance.

Corallimorpharia are taxonomically located between anemones and scleractinian corals (Daly *et al.* 2003). They can cope particularly well with climate change related alterations, such as increased CO_2-levels and temperatures (Medina *et al.* 2006, Kuguru *et al.* 2007, 2008). Corallimorpharia can become a threat to reefs because they can even attack and kill living corals under certain preconditions (Chadwick 1991, Rushingisha 2012), and thus can invade and outcompete intact or recovering benthic communities (Tkachenko *et al.* 2007, Work *et al.* 2008), like at some reefs around Zanzibar Island (Muhando *et al.* 2002, Kuguru *et al.* 2004). The consideration of these organisms is of major interest for the risk assessment of WIO coral reef sites, but complicated, because just a few predators (Annett and Pierotti 1984) including humans (Ates 1991) are documented, and so far alternative control mechanisms for corallimorpharian dispersal are unknown. In already disturbed reefs diseases play an important role for coral health (Page 2009) and reef resilience and may decide over life or death upon the occurrence of perturbations. Their potential risk was already assessed in several models (Brandt and McManus 2009, Williams *et al.* 2010).

Connectivity to adjacent ecosystems is crucial for recruitment and has an important influence on herbivory. In the current version both processes are parametrized with rather course estimations. Indeed, herbivore communities are well studied in coral reefs but they consist of are normally made up by many different species and quantitative studies of respective grazing impacts – which would allow to exchange the density dependent process in the model with a more realistic representation – are still scarce. The implementation of recruitment patterns for specific reef sites as a function of connectivity may be further improved by coupling the model with other applications, which operate on different spatial scales (e.g. Melbourne-Thomas *et al.* 2011).

Quantitative studies on ocean acidification are also still scarce and it is hard to disentangle involved processes. It is not yet fully understood, how a low pH alters organismic physiology, in particular calcification (Feely *et al.* 2004, Pandolfi *et al.* 2011), or how much calcium carbonate is degraded at which pH if sheltered by living tissue. Therefore a direct implementation does not make much sense, but should be kept in mind as future improvement.

Although the third dimension is considered in some of the processes of the virtual coral reef, it would be interesting to fully make use of a 3-dimensional representation in a further version. The topographic properties of a coral reef could be included into the model. The orientation, namely whether a coral is located on the reef flat, in a lagoon or at the slope, might have decisive consequences for its fate. Such representations then would need a coupling with high resolution Regional Oceanographic Modelling Systems (ROMS) – already utilized in larval connectivity studies (Baums *et al.* 2006, Paris *et al.* 2007) – for an adequate representation of physical properties, like currents, eddies, and surge.

Several questions are still unsolved and will remain hard to clarify in the near future, but the potential for filling these gaps is high. We still cannot completely understand the total extent of coral reef resilience. Many important components, processes, and functions, which supported the resilience of coral reefs in the past may have disappeared, before we even knew them, or their influence may have diminished already, so that they are out of consideration in today's studies. Nevertheless, the opportunities and tools to cope with complexity do exist. The here introduced framework constitutes an important step forward. It can handle the high number of organisms and processes, but also the interactions and feedback relationships, all of which are important components for coral reef functioning and hence for the understanding of resilience.

Outlook

Individual-based models have a high potential to be used as management tools, which may aid the involvement of local communities, because they allow a straightforward communication with all stakeholders. Species interactions can be implemented with a low degree of abstraction and a simulation of additional organism groups can be realised with small programming effort. It is intended to couple the model with other modelling systems, that function on different spatial and temporal scales. In combination such applications will allow to identify potential trajectories for particular reef sites with high informative power. The here introduced application will be put open-source for everyone to use, and opens the possibility to advance the performance together with reef scientists all over the world. This may give rise to a global comparison of reef sites in different hotspot regions and give insight on which threats are globally relevant or which are specific for a particular region. Model results can then aid in pointing out, which knowledge gaps have to be filled with empirical information to increase the understanding of coral reef dynamics, and aid the decision for appropriate measures in local management regimes.

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Presentations

Kubicek A., Reuter H.: Analysis of coral reef resilience – A generic modelling tool. Talk at the "International Coral Reef Symposium 2012", 09. - 13.07.2012, Cairns, Australia

Kubicek A.: Modelling Coral Reef Dynamics of Zanzibar – Application of an Individual-based Model. Talk at the "7th Western Indian Ocean Marine Science Association (WIOMSA) Scientific Symposium", 24. - 29.10.2011, Mombasa, Kenya

Kubicek A.: Life history traits influence resilience in a virtual reef system. Poster at the "Gesellschaft für Ökologie – 41st Annual Meeting", 05. - 09.09.2011, Oldenburg, Germany

Kubicek A.: Spatial Interaction in Coral Reef Communities – An Individual Based Modelling Approach. Talk at "The 7th European Conference on Ecological Modelling", 30.5. - 02.06.2011, Riva del Garda, Italy

Kubicek A.: Individual Based Modelling of Coral Reef System Dynamics. Poster at the "Gesellschaft für Ökologie – 40th Anniversary Conference", 30.08. - 03.09.2010, Gießen, Germany

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Eidesstattliche Erklärung

(Gem. § 6(5) Nr. 1-3 PromO)

Hiermit versichere ich, dass ich die vorliegende Arbeit:

1. ohne unerlaubte Hilfe angefertigt habe.
2. keine anderen, als die von mir im Text angegebenen Quellen und Hilfsmittel benutzt habe.
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Bremen, 07. September 2012

Andreas Kubicek