How models can support ecosystem-based management of coral reefs

Weijerman, Mariska[a,b], Elizabeth A Fulton[c], Annette B.G. Janssen[d], Jan J. Kuiper[d], Rik Leemans[b], Barbara J. Robson[e], Ingrid A. van de Leemput[f], Wolf M. Mooij[d,f]

[a]Joint Institute for Marine and Atmospheric Research, University of Hawaii at Manoa, Honolulu, Hawaii 96822, [b]Environmental System Analysis Group, Wageningen University, PO Box 47, 6700 AA Wageningen, the Netherlands. mariska.weijerman@noaa.gov, +1 808 725-5468 (corresponding author)

[c]Division of Marine Research, Commonwealth Scientific and Industrial Research Organisation (CSIRO), Hobart, Tasmania, Australia

[d]Department of Aquatic Ecology, Netherlands Institute of Ecology (NIOO-KNAW), PO Box 50, 6700 AB Wageningen, the Netherlands

[e]Division of Land and Water, Commonwealth Scientific and Industrial Research Organisation (CSIRO), Black Mountain, Australia

[f]Aquatic Ecology and Water Quality Management Group, Department of Environmental Sciences, Wageningen University, PO Box 47, 6700 AA, Wageningen, the Netherlands

Abstract

Despite the importance of coral reef ecosystems to the social and economic welfare of coastal communities, the condition of these marine ecosystems have generally degraded over the past decades. With an increased knowledge of coral reef ecosystem processes and a rise in computer power, dynamic models are useful tools in assessing the synergistic effects of local and global stressors on ecosystem functions. We review representative approaches to model coral reef ecosystems and categorize these in minimal, intermediate and complex model applications. The categorization was based on the leading principle for model development and their level of realism and process details. This review aims to improve the knowledge of concurrent approaches in coral reef ecosystem modeling and highlights the importance of choosing an appropriate approach based on the type of question to be answered. We contend that minimal and intermediate models are generally valuable tools to get insight into the response of key states to main stressors and, hence, contribute to understanding ecological surprises. We argue that adaptive resource management requires integrated thinking and decision support which asks for a diversity of modeling approaches. Integration can be

achieved through complimentary use of models or through integrated models that combine many aspects of the system in one framework. In terms of the later, whole-of-system models can be useful tools for quantitative scenario evaluation. These models allow for a multidimensional view of the interactive effect of multiple stressors on various and potentially conflicting management objectives. All models are simplifications of reality and as such have their weaknesses. While minimal models lack multidimensionality, system models may be difficult to interpret as they require many efforts to decipher the numerous interactions and feedback loops that link input and output. Given the breadth of questions that must be tackled when dealing with coral reefs the best practice approach uses multiple model types and thus benefits from the strength of different model approaches in a given study.

1. Introduction

Coral reefs are extremely important as habitats for a range of marine species, natural buffers to severe wave actions, and sites for recreation and cultural practices. Additionally, they contribute to the national economy of countries with coral reef ecosystems. The economic annual net benefit of the world's coral reefs are estimated at US $29.8 billion from fisheries, tourism, coastal protection and biodiversity (Cesar et al. 2003). Moreover, coral reefs are important to the social and economic welfare of tropical coastal communities adjacent to reefs (Moberg and Folke 1999). Coral-reef related tourism and recreation account for $9.6 billion globally and have also shown to be important contributors to the economy of Pacific islands (Cesar et al. 2003, Van Beukering et al. 2007). However, the functioning of coral reef ecosystems and their biodiversity is deteriorating around the world (Hoegh-Guldberg et al. 2007). In recent reviews on the extinction risks of corals, the most important global threats to the survival of corals and coral reefs were human-induced ocean warming and ocean acidification (Brainard et al. 2011, Burke et al. 2011). While local governments are limited in their capacity to reduce greenhouse gas emissions worldwide and so reduce the on-going ocean warming and acidification, they can play a pivotal role in enhancing the corals' capability to recover from impacts of these global threats by reducing additional local stressors caused by land-based sources of pollution and fishing (Carilli et al. 2009, Hughes et al. 2010, Kennedy et al. 2013, McClanahan et al 2014).

The capacity of coral reef organisms and natural systems to 'bounce back' from disturbances can be degraded by sequential, chronic, and multiple disturbance events, physiological stress, and general environmental deterioration (Nyström et al. 2000) and through the reduction of large and diverse herbivorous fish populations (Bellwood et al. 2006, Pandolfi et al. 2003). These local stressors affect the coral-macroalgal dynamics and early life history development and survival of corals (Baskett et al. 2009, Gilmour et al. 2013) but these stressors can be mitigated by proper management (Graham et al. 2013, Micheli et al. 2012, Mumby et al. 2007b). Ecosystem models can help managers in system understanding and in visualizing projections of realistic future scenarios to enable decision making (Evans et al. 2013).

Large-scale regime or phase-shifts have been identified in pelagic systems (Hare and Mantua 2000, Weijerman et al. 2005) and on coral reefs (Hughes 1994) and have influenced a new understanding in ecosystem dynamics that includes multiple-equilibriums, nonlinearity, and threshold effects (e.g., Nyström et al. 2000, Mumby et al 2007a). As has been shown in the management of freshwater resources, insight in the conceptual relations between key states and their response to stressors can have profound impacts on the way natural resource managers think about their systems and the options they have for ecosystem recovery (Carpenter et al. 1999). The theory of alternative stable states implies, for example, that a stressed reef could not only fail to recover after a disturbance, but could shift into a new alternative stable state (e.g., algal-dominated state) due to destabilizing feedbacks, such as a change in abiotic or biotic conditions (Mumby et al. 2006, 2013). As a result, reversing undesirable states has become difficult for managers (Nyström et al. 2012, Hughes et al 2013), even when stressors are being lowered (also called hysteresis (Scheffer et al. 2001)).

The complexity of coral reef ecosystems with their myriad of processes acting across a broad range of spatial (e.g., larval connectivity versus benthic community interactions) and temporal (e.g., turnover time of microbes versus maturity of sea turtles) scales makes modeling coral reef ecosystems for predictive assessments very challenging. The modeler's dilemma is to choose an approach that meets the requirements for simplicity, realism and accuracy, and reaches the overlapping but not identical goals of understanding natural systems and projecting their responses to change (Levins 1966).

Leading principles for ecosystem model development vary and include:

1) To interpolate and fill data gaps, for instance to provide information regarding what is happening between two observations in time or to fill in the three-dimensional picture of a system from two-dimensional data;
2) To forecast or hindcast, i.e., to make predictions for operational management when a system is varying within historical bounds;

3) To evaluate scenarios for operational management;
4) To enhance systems understanding by quantification of a conceptual model (e.g., to calculate materials budgets) or to quantitatively test the plausibility of that conceptual model;
5) To develop ecological theory and generalizable ecological hypotheses;
6) Extrapolation and projection, i.e., to generate hypotheses regarding the function and likely responses of a particular system when perturbed beyond its previously observed state.

With regards to the identified leading principles, we believe that each circumstance is best suited by a different model approach (Table 1). Other authors who have considered the question of selecting an appropriate modelling approach to suit a particular purpose include Kelly et al. (2013), Fulton and Link (2014) and Robson (2014a). Robson (2014b) has further considered the implications of growing complexity in models of aquatic ecosystems.

Table 1. Leading principles for model development with a model approach suitable to reach the desired goal.

Leading principle	Suitable model approach
1) Interpolation	Data-driven (statistical) models Minimal models
2) Forecasting and hindcasting	Data-driven (statistical) models Physically-driven models
3) Operational scenario evaluation	Targeted/refined (intermediate) mechanistic models
4) Quantification of a conceptual model	Complex models or intermediate models
5) Hypothesis generation –theory development or testing	Simple conceptual models (minimal models)
6) Extrapolation and projection	Complex, process realistic models, which capture the feedback processes that dictate longer term evolution of dynamics

For coral reef managers, who need to define management strategies for the entire coral reef ecosystem, interactions among system components and management sectors as well as cumulative impacts of disturbances to the system need to be considered (Ban et al 2014, Kroeker et al 2013, Rosenberg and McLeod 2005). Ecosystem understanding should include the human component in terms of their social and economic dependencies on these marine resources (Nyström et al. 2012, Plagányi et al. 2013, Lui 2001). Management scenarios that enhance the biological state might be unfavorable for the local economy, especially on short time scales. Responses of slow-reacting systems, such as coral reefs, could diminish community support for effective management. Still, they also give managers an opportunity to act before a new, less favorable, condition has established itself (Hughes et al. 2013). To date, few tools have been available that evaluate the socio-economic and socio-ecological tradeoffs of management scenarios of an ecosystem-based approach to coral reef management. Coral reef ecosystem models that do include the human component are mostly focused on fisheries management with socio-economic impacts presented as changes in catches or landings (Gibble 2003, McClanahan 1995, Tsehaye and Nagelkerke 2008). Few models dynamically couple ecological dynamics to socio-economic drivers and these models also focus on fisheries management (Kramer 2007, Melbourne-Thomas et al. 2011, Schafer 2007).

The modeling approach most suitable to reach specific goals for ecosystem-based management depends on the type of governance (e.g., existing laws and enforcement), time and space scales under consideration and data availability (e.g., data quantity, quality and accessibility; Tallis et al. 2010) as well as the maturity of scientific understanding of the system under consideration and the time and resources available for model refinement and validation (Kelley et al. 2013). The concepts encompassed by Management Strategy Evaluation (MSE) or Decision Support System (DSS) tools are a useful way of exploring management issues that can be applied to many model types. MSE involves simulation testing of the implications for both the resource and the stakeholders of alternative combinations of monitoring data, analytical procedures and decision rules, and can be used for evaluating the tradeoffs between socioeconomic and biological objectives (Smith et al. 2007). In situations when neither data nor time is a limiting factor for model development and one aims to simulate site-specific management scenarios, ‘end-to-end’ or ‘whole-of-system’ models can be developed for the MSE. In more data-poor or time-limited situations or when one aims to simulate less-specific scenarios with processes that are easily traced back, ‘minimum realistic’ models can be used as a basis of the MSE (e.g., Plagányi et al 2013). Alternatively simple, even qualitative, models can be used to shed light on ecological (or other system) concepts, helping stakeholders to think about topics important in defining effective management strategies (Tallis et al. 2010) or these simpler models can be used as the logical basis of the MSE in their own right, as per Smith et al (2004).

Drawing in all models of reef systems would be intractable, especially given the number of conceptual models that exist in the mainstream and grey literature. Consequently, here we review the strengths and limitations of ‘dynamic’ coral reef ecosystem modeling approaches in their application to management scenario analyses. We define a ‘dynamic’ model of a given system as a set of mathematical formulations of the underlying processes in time and/or space with outputs for each time step over a specified period. With such a model, the development of the system in time and space can be simulated by means of numerical integration of the process formulations. We put particular emphasis on their usefulness to evaluate the ecological implications of model applications for MSE. This review is not an exhaustive comparison of all dynamic coral reef ecosystem models but we have selected studies that employ oft-used or exemplar approaches that represent model types categorized as ‘minimal’, ‘intermediate’, and ‘complex’ models. These classifications were based on a scoring system that combined (1) their level of realism (determined by the conceptualism of space, time and structure) and (2) the process details incorporated into the model (Table 2). Additionally, we looked at the leading principle for development of each model (Mooij et al 2010). We contend that the leading principle of minimal dynamic models is understanding the type and shape of the response curve of ecosystems to disturbances. The leading principle of complex dynamic models is to predict the response of ecosystems to disturbances under different management regimes given the many feedbacks in the system. Intermediate dynamic models try to balance between these two objectives. They do so by expanding parts of the system to the full detail while deliberately keeping other components simple. In this way they can capture some key feedbacks while maintaining the tractability of simple models, meaning they can make use of analytical and formal fitting procedures (Plagányi et al. 2014). We highlight the differences between the model approaches, discuss their main goals, and outline the approach to take the strength of the different modeling types to obtain clarity and predictive capabilities in a model.

2. Categorization of Three Coral Reef Model Types: Minimal, Intermediate, and Complex

The rationale for any model is the desire to capture the essence and to remove or reduce the redundant aspects of the system under study. What is essential and what is redundant and, thereby, what level of reduction is required, to a large degree depends on the questions being asked, the available information to base conceptualizations on and the way in which abstractions are formulated. The result is a 'model' that is realistic to varying degrees. It is not a clear cut recipe book approach as modelers need to make a tradeoff between the levels of resolution of time, space, taxonomy and model structure, as well as model detail, i.e., between comprehensiveness and complexity. Using 26 published studies we felt were representative of reef models in the literature we classified the dynamic coral reef models along an axis of model type (Table 2, 3) to get a greater understanding of how differently sized models can be used in coral reef ecosystem management, particularly in the context of MSE. We first classified models primarily on basis of their leading principle. However, while categorizing models in terms of all of these facets separately is possible it is difficult to think in such hyper dimensional spaces, so to facilitate comparisons we then mapped models to a simple continuum of simple to complex via a scoring system (Table 2; for scoring results see Appendix A).

Table 2. Complexity scoring of various criteria to classify models or model applications.

Criteria/Score	1	2	3	4	Comments
Conceptualization of structure					
# plankton grps	0	1-2	3	> 3	groups can be individual species or aggregated species groups
# benthic grps	1	2	3-4	> 4	
# invertebrate grps	0	1-2	3-4	> 4	
# vertebrate grps	0	1-2	3-5	> 5	
Conceptualization of space					
	non-spatial	lumped	grid or cell based		lumped has a single output of entire modelled area; grid or cell based represents uniform or non-uniform grid or vectors
Process Details					
trophic interactions					
inter/intra species competition					
age structure					
biogeochemistry					

hydrodynamics

2.1 Minimal models

With few mathematical equations, minimal dynamic models are often used as a toolkit for the development of ecological theory. Minimal models have proven to be a helpful tool in gaining fundamental insight into the complex dynamics of a specific system (i.e., chaos, cycles, regime shifts, etc.). In coral reefs, for example, they have played an important role in conceptualizing and understanding observed regime shifts (Hughes 1994, Mumby et al. 2013). Generally, people do not intuitively consider nonlinear responses, i.e., we often assume that a small change in environmental conditions will lead to a small (or at least consistently proportional) change in the ecosystem. Minimal models have been used to show what kind of surprises could arise when nonlinear interactions between system variables (e.g. feedback mechanisms) are taken into consideration (#1 in Table 3). Using minimal models to simulate coral reef dynamics, one can thus gain fundamental insight into thresholds (#1), primary drivers of system dynamics (#2 and #3), the type of system response to changing conditions, and the effect of hysteresis (#4 and Mumby et al. 2013) Recently, the interaction between ocean acidification and warming, and coral growth/cover has been examined with minimal models (#5). Some minimal models also incorporate local environmental changes (e.g., nutrient input, hurricanes, and fishing) to study coral cover response and are able to forewarn whether current levels are precautionary or whether new challenges are coming (#6). Early minimal models examined the main drivers of reef accretion and erosion processes (#7–9). Gaining insight in these important aspects of a system's response to current or future perturbations can help managers to understand observed surprising dynamics, focus on the most relevant (sensitive) variables, and to conservatively move away from tipping-point thresholds by increasing reef resilience. While there is currently no published MSE using a simple reef model as a basis (to the author's knowledge), the response curves derived from such models could be used as the basis of a qualitative MSE of the form undertaken in a temperate system by Smith et al (2004).

One advantage of minimal models is that one is able to thoroughly explore the behavior of the model in a multidimensional parameter space by using analytical or numerical methods. This way, one can easily trace back the relative importance of specific processes or interactions. However, minimal models ignore other potentially important phenomena that affect a system's behavior (Scheffer and Beets 1994). Moreover, they often assume spatial homogenous conditions and constant environments. Reefs have patchy distributions of corals and fish, often determined by environmental factors (Franklin et al. 2013), so including spatial dimensions explicitly in the model can greatly improve the realism of reef dynamics. However, explicit spatial representation is not automatically required, so long as careful thought is given to how to implicitly represent the spatial influences. Because minimal models lack the link between all trophic groups and the response of multiple stressors, they can be less suitable in a multispecies or multidisciplinary decision-making context. Minimal models have paved the way for the theory on generic early warning signals of tipping points (Scheffer et al. 2009). While minimal models themselves are likely to be too simplistic to precisely predict future behavior in systems that are not already well understood, generic early warning signals may be an important additional tool for ecosystem managers.

Based on the leading principle defined for minimal models, 10 models could be classified as minimal models developed to enhance understanding of the type and shape of the response curve of ecosystems to disturbances (#1–9). According to our scoring system, the overall complexity score based on the mean score of model structure, representation of space, and process details varied between 2.3 and 4.4 with a mean score of 3.3 (Appendix A). The box model (#7, 8) had an overall score of 4.4 and could therefore also be placed in the intermediate category, whose overall score was between 3.0 and 5.0 with a mean of 4.1.

2.2 Intermediate models

Intermediate models are more focused than typical whole-of-system models; they try to marry the strengths of simple models (in terms of tractability) with a broader system perspective to selectively link the key drivers of the system. These models simulate species-specific behavior and age or size structure with a set of mathematical formulas, capturing the population dynamics of key functional groups, and potentially their spatial heterogeneity if spatially explicit (Plagányi 2007). These kinds of models typically include at least one key ecological process (e.g., a link to lower trophic levels, interspecific interactions or habitat use) and potentially some representation of how the modelled components are affected by physical and anthropogenic drivers (Plagányi et al. 2014).

The leading principal for this type of model was defined as trying to find a balance between system understanding and predictive capabilities by expanding parts of the system to the full detail while deliberately keeping other components simple. For example, by including more details on process dynamics but limiting the functional groups (#15, #18), a greater understanding was reached into the population dynamics and perturbations (fishery [#15] or environmental factors [#18]) of that specific group. This more realistic and heterogeneous system representation provides information about a system that is not available from a minimal model. In pointing to a representative example of an intermediate complexity reef model there are a number of potential candidates. Two clear classes of questions have been tackled with these kinds of models. The first is around using multispecies or trophic models to explore the coral reef ecosystem impacts of fishing (Table 3, #10–16, 19) and the second uses models, often individual or agent-based models (Grimm et al. 2006), to consider how competing habitat defining groups respond to changing conditions (#17, 18, 20, 21).

The Ecopath and Ecosim (EwE) modeling platforms (Polovina 1984, Walters et al. 1997, Pauly et al 2000) is one of the most commonly used models for exploring trophic connections and responses to fishing pressure. Although the suite of EwE models can be considered complex based on our criteria (Table 2), the application of EwE models in the selected studies has been mostly to look at just one disturbance (fisheries) through expansion of that part of the model components while leaving the rest simple (e.g., few functional groups, no inclusion of Ecospace or life cycle (age structured) processes) and, hence, the leading principle fits with our classification of 'intermediate'. Similarly while some agent-based models can be considered complex in terms of the elaboration of particular ecological mechanisms, in the context of their use in coral reef systems they have often been used as intermediate complexity models. When EwE is used to explore reef dynamics it can give insight into a system's 'state' based on changes in energy flows as a response to perturbation (#10, 12 and 13), and multiple positive or negative feedback loops can be included with this model approach (#17, 21 and 22). The classification of EwE models also illustrates that modelling platforms often do not simply slot into one or other category but can be simple, intermediate or complex depending on the details of a particular application. For example, one application of EwE, for examining fishery scenarios for Indonesian reef systems, included 98 tropic groups and 3 of the 5 selected process dynamics (# 14) and was used for evaluating management scenarios. Thus it was categorized as complex (Table 3) as its overall complexity score of 6.0 sits within the span of scores (5.3 to 6.8, mean 5.9; Appendix A) of complex models.

A disadvantage of intermediate models is that the software code often consists of linked models, which complicates the interpretation of results (Lorek and Sonnenschein 1999). Additionally, because of the need for more parameters, variables and model formulations, each with their own uncertainties, model output becomes less certain or robust

(Pascual et al. 1997) and validation and sensitivity analyses are more cumbersome (Rykiel Jr 1996). Nevertheless these models are still simple enough that good use can be made of formal statistical estimation procedures originally developed for simpler models (Plagányi et al 2014).

Management applications of intermediate models include the ability to inform managers where a system is on a gradient from 'pristine' to degraded/disturbed so that effective action can be identified and implemented (Kramer 2007, McClanahan 1995). Additionally, especially with respect to the suit of EwE models that have been used for fishery management strategy evaluation, this model approach gives valuable insight in ecosystem impacts of alternative fishery scenarios. However, spatial factors, nutrient dynamics, benthic processes and extrinsic forcing functions are not always included in intermediate models but can be important for projecting the effects of some perturbations on ecosystems (Robinson and Frid 2003).

2.3 Complex models

What we categorized as complex models are often called end-to-end models or whole-of-system models. These models typically include a food web spanning set of trophic groups: detritus, primary producers, zooplankton ranging from small (μm) to large (m) animals, forage fish, invertebrates and apex predators, including humans. They also often explicitly simulate biogeochemical dynamics. For coral reefs that are surrounded by oligotrophic water, nutrients play a key role in ecosystem dynamics. Including biogeochemical processes in a coral reef ecosystem model is, therefore, essential to simulate these processes, especially since land-based sources of pollution have played an important role in the demise of many reef systems in the Caribbean (Lapointe 1997) and on the Great Barrier Reef (De'ath et al. 2012). In comparison with the other two model types, additional key ecosystem processes (e.g., trophodynamics and feedback loops) are represented to more comprehensively simulate a system's behavior. These complex models aim to provide quantitative projections of system changes in response to a set of changing abiotic and biotic conditions taking into account key components and their spatial heterogeneity (in some cases from microbes to whales and humans, and from sediment bioturbation to physical oceanography). Simplicity is sacrificed as these models are simultaneously complex in many dimensions (process details, number of functional groups, nutrients, spatial and temporal dimensions, see Table 3 #23–26). That is not to say every component or aspect is resolved in fine detail, such an approach does not lead to useful outcomes; tradeoffs between the dimensions are nearly always required so as the scope, or the number of scales extends sacrifices are likely required in other facets (such as using growth terms rather than very finely resolved physiological representations of each ecological process for each modelled group).

Representing a system in this way can be advantageous for capturing trophic cascades and synergistic effects of perturbations, as the model implementation explicit includes (1) key functional groups at each trophic level (Mitra and Davis 2010) and (2) model complexity varies with details where needed in terms of number of functional groups and compatibility between lower and upper trophic level formulations (Fulton et al. 2005). These models can represent the myriad of nonlinear, two-way interactions that simple or intermediate models do not represent. Humans are an integral component of most complex models, both as users of ecosystem services and as drivers influencing ecosystem processes (Levin et al. 2009).

The major drawback of these model types is similar to that of intermediate models: the addition of complexity does not guarantee an improvement in the simulated output as uncertainty and error associated with the added components will be introduced to the model and can potentially degrade its performance. Uncertainty arises both from assumptions made in the model structure and from uncertainty around the values of parameters, amongst other sources (Draper 1995, Renard et al. 2010).

The difficulties of properly understanding the implementation of ecological and socio-economic processes in a complex model hamper straightforward validation and could lead to less reliable projections. To improve the performance of complex ecosystem models, studies have looked into the effects of trophic aggregations (Fulton 2001, Gardner et al. 1982), model structure (Sebastián and McClanahan 2013), physiological detail (Fulton et al. 2004, Allen and Pollimene, 2011), spatial representation (Fulton et al. 2004), and predator-prey relationships including age-structure (Botsford et al. 2011) and inter-predator competition (Walters and Christensen 2007). Best practice guidelines for developing complex models have been formulated (Fulton et al. 2004, Flynn 2005, FAO 2007, Travers et al. 2007). Some of these recommendations are (1) the inclusion of functional groups at low trophic levels and species of higher trophic levels with an appropriate spatial dimension to represent organism dynamics more accurately; (2) inclusion of abiotic processes to simulate important drivers in structuring ecosystem communities; (3) the integration of physical and biological processes at different scales (relevant to the scales of key processes) to more realistically simulate those dynamics; (4) evaluating the model in terms of its ability to reproduce expected patterns from ecological theory and in terms of the degree to which it accords with current biophysical understanding of the system; and (5) two-way interactions between ecosystem components to allow dynamic feedback and nonlinear dynamics to emerge.

Most complex coral reef models are developed to assess the synergistic effects of climate change and fishing on ecosystem dynamics (#25 and 26) and the resilience of coral reefs under simulated management scenarios (model #23 and 24). Through the inclusion of the breadth of the food web and many alternative interaction pathways, non-intuitive (and, therefore, unanticipated) outcomes in community structure can present themselves. It should be noted that unexpected, chaotic and non-linear system dynamics can be exhibited by simple models, again simply including more components does not guarantee revelations outside the purview of other approaches. Not only the number of groups represented, but also the number and types of interactions between them is important (Baird, 2010, Takimoto et al., 2012). The important consideration is the inclusion of mechanisms of achieving alternative outcomes – multiple reaction pathways that can reach alternative stable states. The same logic is behind why the inclusion of humans and their activities in model simulations facilitates further evaluation of tradeoffs between ecosystem services and management goals. This information can then support the identification of policies and methods that have the potential to meet *a priori* stated objectives (Levin et al. 2009).

Table 3. Selected dynamic coral reef ecosystem models and model applications categorized as minimal, intermediate, and complex based on their system conceptualization and process detail (Table 2). BBN is Bayesian belief network. EwE is Ecopath with Ecosim. ODE is ordinary differential equation. CORSET is Coral Reef Scenario Evaluation Tool. CAFFEE is Coral-Algae-Fish-Fisheries Ecosystem Energetics. For overall complexity score calculations, see Appendix A.

#	Model	Source	Reef area	Leading principal	Suitable for MSE	Category based on leading principal	Overall Score
1	Caribbean reef model	Mumby et al. 2007a	Caribbean fore-reef	System understanding of coral-algae dynamics	Insight in benthic dynamics	Minimal	2.3
2	BBN model	Renken and Mumby 2009	Caribbean fore reef	System understanding of macroalgal dynamics	Insight in benthic dynamics	Minimal	3.3
3	HOME model	Wolanski et al. 2003	Great Barrier Reef & Guam	System understanding of coral-algal dynamics	Insight in benthic dynamics	Minimal	4.3

#	Model	Source	Reef area	Leading principal	Suitable for MSE	Category based on leading principal	Overall Score
4	Community model	Żychaluk et al. 2012	Kenya, Caribbean, Great Barrier Reef	System understanding of occurrence of alternative ecosystem states	Insight in benthic dynamics	Minimal	2.8
5	Community model	Anthony et al. 2011	Caribbean	System understanding in benthic dynamics under climate change	Insight in benthic dynamics	Minimal	3.4
6	Determinis-tic model	Blackwood et al. 2011	Caribbean	System understanding of coral-algal dynamics including reef complexity	Insight in reef resilience in relation to fishery	Minimal	2.9
7	Box model	Eakin 1996	25,308 m^2 Uva Island, Panama	System understanding of reef accretion/ erosion processes	Insight in reef complexity	Minimal	4.4
8	Box model	Eakin 2001	25,308 m^2 Uva Island, Panama	System understanding of reef accretion/ erosion processes	Insight in reef complexity	Minimal	4.4
9	ReefHab	Kleypas 1997	Generic reef (parameter-rized for Mesobarrier reef Caribbean)	System understanding of reef accretion/erosion processes	Insight in environmental factors limiting reef habitat	Minimal	2.6
10	Energy-based model	McClanahan 1995	Generic local reef (parameter-ized for Kenyan reef)	System understanding of effect of fishing on ecosystem structure and fishery yield	Insight in trade-offs of alternative fishery scenarios	Minimal/ Intermediate	5.0
11	EwE model	Tsehaye and Nagelkerke 2008	6000 km^2 Red Sea	Fisheries effects on ecosystem - change in fishery scenarios	Insight in ecosystem impacts of alternative fishery scenarios	Intermediate	4.1
12	EwE model	Weijerman et al. 2013	Hawaii	Identify indicators for fishery for management - change in fishing intensity	Insight in ecosystem impacts of increased fishing	Intermediate	4.5
13	EwE model	Arias-González et al. 2004	Mexico	Fisheries effects on ecosystem - change in fishery scenarios	Insight in ecosystem impacts of alternative fishery scenarios	Intermediate	3.9
14	EwE model	Ainsworth et al. 2008	Indonesia	Fisheries effects on ecosystem - change in fishery scenarios	Insight in ecosystem impacts of alternative fishery scenarios)	Complex	6.0

#	Model	Source	Reef area	Leading principal	Suitable for MSE	Category based on leading principal	Overall Score
15	ELFSim	Little et al. 2007	Great Barrier Reef	Understanding of population dynamics of single species under alternative fishery scenarios	Evaluate trade-offs on population dynamics of 1 species under alternative fishery scenarios	Intermediate	3.0
16	Individual-based model	Edwards et al. 2011	Caribbean mid-depth fore-reef	System understanding of disturbance impacts under alternative fishery scenarios	Insight in resilience of benthic community from disturbances under different fishery scenarios	Intermediate	4.6
17	Individual-based model	Wakeford et al. 2007	32 m^2 Lizard Island, Great Barrier Reef	System understanding (coral community dynamics after perturbations) and projected trajectory under future disturbances	Insight in reef resilience in relation to disturbances	Intermediate	3.8
18	SPREAD (individual-based)	Yñiguez et al. 2008	Florida, 3-D cells of 1x1 cm	System understanding (macroalgal growth and morphology)	Insight in environmental factors influencing macroalgal dynamics	Intermediate	4.4
19	Lotka-Volterra model ~ adaptive behavior model	Kramer 2007	Generic Caribbean reef	Understanding in coupling between biological and fishery dynamics	Effects of fishery on ecosystem state and vice versa	Intermediate	5.0
20	Cellular automaton model	Langmead and Sheppard 2004	Caribbean	System understanding (coral community restructuring processes after disturbance)	Insight in reef resilience in relation to disturbances	Intermediate	4.1
21	Biogeochemical ~ hydrodynamic model	Faure et al. 2010	2066 km^2 lagoon, New Caledonia	System understanding (ecosystem variability under environmental disturbances)	Insight in biogeochemical response under different scenarios	Intermediate	3.4
22	ODE-based model	Riegl and Purkis 2009	Generic (parameterized for Arabian/Persian Gulf)	System understanding of coral community structure and recovery after multiple bleaching events)	Insight in coral community structure after repeated disturbances	Intermediate	3.8

#	Model	Source	Reef area	Leading principal	Suitable for MSE	Category based on leading principal	Overall Score
23	CORSET (based on Fung 2009)	Melbourne -Thomas et al. 2011	1342 km^2 (5-20 m depth) Generic reef	Decision support tool with simulations based on 'what if' scenarios	Projecting reef futures under different scenarios	Complex	6.8
24	ODE-based model	Fung 2009	Generic local reef	System understanding (key ecological processes responsible for reef degradation) and scenario testing	Projecting reef futures under different scenarios	Complex	5.3
25	Integrated agent-based model (based on Fung 2009)	Gao and Hailu 2011	~6000 km^2, Ningaloo Marine Park, Australia	Decision support tool with simulations based on 'what if' scenarios	Site closure strategy analyses	Complex	5.4
26	CAFFEE	Sebastián and McClanahan 2013	Kenya	Model structure understanding, calibration methods	Insight in reef resilience in relation to fishery closure and environmental disturbance	Complex	6.1
27	eReefs	Schiller et al., 2013; Wild-Allen et al., 2013; Mongin & Baird, 2014	300000 km^2, Great Barrier Reef, Australia	Support tool for both rapid response and slow response management and system understanding	Projecting reef futures under different land management scenarios	Complex	6.8

Although there is a continuous scale from minimal to complex model approaches, we differentiated between three categories (minimal, intermediate or complex) based on the leading principal for model development and on their overall complexity score related to the model conceptualism and process detail (Table 3). The mean complexity score reflect this continuous scale as model approaches overlap between the three categories. As we go from simple to complex models, a tendency in the leading principle is visible—from understanding towards prediction. The desired balance between these two objectives in a given study could therefore give some indication of the appropriate level of model complexity.

3. Multiple Model Strategies in Relation to Coral Reef Management

Combining models of different complexity

Modeling is an art that balances simplicity, realism, and accuracy of various dimensions (Levins 1966): time, space, trophic components, process details, human activities, boundary conditions, and forcings. Considering coral reef management, all model formats have their pros and cons, and need to be applied when they are fit for purpose. However, insights gained by one model can be useful for the application of another (Mooij et al. 2009). Moreover, multiple model types can be applied so that the combined outcomes exceed possible outcomes from using a single model alone. Approaches combining models of different complexities include:

- The ‘three-stage rocket approach’, in which first mini-models and then intermediate models can be used to identify the relevant variables or processes to steer on. The resulting intermediate model can then provide a basis for the complex model, with the aim of reaching a prediction that is based on understanding. A variant of this approach is to couple models of different forms and origin to piece together a more complete representation of the system. Such approaches are becoming increasingly popular in the research community, but care must be taken to understand how to propagate error and deal with scale differences between the model types.
- The ‘build then refine approach’, in which a complex model is used to identify key drivers of system responses, which can then be used to develop simpler, faster models (or statistic emulators) whose behavior can be more thoroughly characterized, providing more accurate predictions for a more limited range of scenarios (Robson, in press-a).

But, as discussed in the following paragraphs, there are more ways in which we can benefit from combining modeling approaches, including the ‘peeling off complexity approach’, which is the opposite from the ‘three-stage rocket approach’.

From understanding to projecting

Minimal models are important for the development of concepts and theory; they examine how certain phenomena can be reproduced and so reveal general explanations. They are also helpful in identifying and getting insight into processes that cause nonlinear system behavior. As such, minimal models can provide a conceptual framework wherein management scenarios can be explored. They can help managers to address the right questions, i.e., which process details and variables to focus on. Intermediate models include enough detail to couple different concepts and test these concepts relative to each other and relative to other factors, such as external forcings (e.g. nutrient input, hurricane damage) and simplistic management scenarios. Improved understanding is still the main aim of this model type, although the increased complexity requires more effort to trace underlying mechanisms. When the understanding of key ecological or socioeconomic processes is sufficiently enhanced one can continue with making projections. However, some of the questions raised by ecosystem managers are beyond intermediate models, as they miss the necessary details in the model conceptualism or the full suite of key ecosystem processes.

Model complexity can arise either by increasing the detail at which particular compartments or processes are represented or by broadening the scope of the model, for instance moving from a model of coral biology to a model of coral reef ecosystems to a model that also includes the human behaviors that affect those ecosystems. Many very complex biogeochemical models, for example, are narrowly focused, while broadly focused, integrated economic-ecological-biophysical models often represent their individual components with much less detail.

Well-formulated and comprehensive complex models are suitable for evaluating social, economic and ecological tradeoffs of alternative management scenarios but typically lack the straightforward validation needed to fully understand the model's projection capabilities. Very complex models, on the downside, may be too cumbersome to embed in end-user focused decision-support tools, and may be too computationally intensive to allow large numbers of scenarios or optimization runs to be conducted. They may also lack transparency, which (when these models are used without also employing simpler models) can make it difficult for policy makers to develop confidence in the models and insight into the tradeoffs and processes represented in the models.

Including socio-economics

Intermediate and complex models are difficult to parameterize, analyze, and validate and have a long development time. Because they often contain input from many experts, the model code may be less transparent and harder to maintain and debug, and the performance of these models is rarely thoroughly assessed. However, if these challenges can be overcome, they can include the whole ecosystem and socioeconomic components, and so can be instrumental for management options and strategy evaluations (Plagányi 2007). For coral reef ecosystems such models are rare. From the 26 reviewed model studies, only three model approaches explicitly included human socioeconomic drivers (Table 3, EwE model [#14], coupled biological and Bayesian human behavior model [#18], and an integrated agent-based model [#25]) although in some models, fishing activity is implicit in the model parameterization (e.g., EwE models [#11–14]). The significance of a change in ecosystem state to fisherman or the feedback between fishing pressure and ecosystem state (Cinner et al. 2011, Cinner et al. 2009), are important components for successful management (Hughes et al. 2010, Plagányi et al. 2013).

'Peeling off' approach

As said above, a major criticism of complex models is the difficulty in understanding the underlying mechanisms of their outcomes. To improve our understanding of the way in which these models generate their results we need to peel off the many layers of complex models to effectively reduce their output to explore the key feedback mechanisms and their response to changes in conditions (Van Minnen et al. 1995, Van Nes and Scheffer 2005). Tools to do this include sensitivity analysis, network analysis of model output, and construction of materials budgets to trace dominants pathways of carbon, energy or nutrients through the system. This approach helps to base complex models upon a proper understanding of the feedback mechanisms explored in minimal models and only those dynamic mechanism and responses that are key to the system's behavior should be incorporated (Fulton et al. 2005), keeping in mind that synergistic effects may occur. This resulting set of mechanisms and responses should then be augmented by incorporating spatial and environmental parameters that are thought to cause shifts in system states and for which these relationships between state variables were explored (Van Nes and Scheffer 2005). In this approach the results of complex model can be better validated using existing ecological theory and empirical data (Sebastián and McClanahan 2013).

Stability versus complexity

Another recurring criticism of complex models is that community models (e.g., based on Lotka–Volterra equations) become increasingly unstable as complexity increases (May 1972). However, field and experimental observations have shown that ecosystem complexity enhances resilience and stability (Burgess et al. 2013, Folke et al. 2004. Friedrichs et al 2007, Hughes et al. 2005, Pasari et al. 2013). Previous work has shown the critical role of space as a resource in marine systems, combating the complexity-stability conflict (Fulton et al. 2004). Findings from food web theory show that to improve a model's stability, the modelled food web should consist of multiple trophic levels and capture other food web features, such as, weak links and mechanisms that weaken the interactions, such as, asymmetric feeding and non-feeding interactions (Fulton et al. 2003, Neutel et al. 2007, Rooney et al. 2006, Travers et al. 2010). When models include sufficient interactions, simulated community stability increases rather than decreases with model complexity (Baird, 2010).

Most dynamic ecosystem models include non-linear functional response curves that greatly contribute to system stability, e.g., when predators are capped by a carrying capacity they can no longer drive prey to extinction. Also refugia, migration or dispersal terms and adaptive behavior or plasticity can be built into models to prevent species to die out completely. However, particularly in more complex models, it may be difficult to justify the use of all these stabilizing mechanisms as it is often challenging to obtain realistic parameter values and identify the actual shape of each response curve. The uncertainty of parameters and the complexity of the model makes it difficult to foresee the consequences of model behavior other than bringing stability, i.e., even if the model fit is good, it may be based on the wrong assumptions. Sensitivity analysis and peeling off complexity at the level of these stabilizing mechanisms could provide the required insights.

Ensemble modeling

A way to deal with limits on predictability is to run a complex model with different initial conditions and model formulations and explore the outcomes to assess the likelihood of certain events rather than give a single deterministic or tactical projection (Hannah et al. 2010). This approach is called ensemble modeling (another form of ensemble modeling is to compare the results of the application of different model frameworks to the same scenario, see below). Outcomes can then be compared with multiple minimal models for confirmation of results (Fulton et al. 2003), with long term field data (Sebastián and McClanahan 2013) or expert judgment (Mauser et al. 2013). Often, the most interesting and useful results are obtained when the model does not agree with expert judgment, as this indicates either a real, but unforeseen system behavior, which will have implications for management or a fault in the conceptualization of the system as represented by the model, which indicates that further thought or research is needed.

Another form of ensemble modeling is when different models are applied to a single system. The resulting bandwidth of outcomes can give insight in the ‘structural uncertainty’ of the inevitable artifacts in the model formulations. This type of uncertainty can only be studied by concurrently applying multiple models and as this approach is rarely taken this type of uncertainty is often ignored. However, structural uncertainty might be as important as or even more important than the uncertainty in model output arising from uncertainty in the numerical inputs to the model (e.g., parameters, initial conditions, forcing functions, boundary conditions). Handling and quantification of uncertainty typically focuses on the latter numerical uncertainties (e.g., Hoeke et al 2011, Pandolfi et al 2011, Yara et al 2014 for uncertainties related to climate change and coral reef trajectories).

4. Concluding remarks

From this review of model types, one might conclude that there is something to gain from investing time in appreciating the identity and potential of each of the three model types in its own right and in concert. Each of the discussed model types can be helpful, but each also has limitations, when used in a management-oriented context. Minimal coral reef models are crucial in our understanding of ecosystem feedback loops and their response curves. Understanding the drivers of change in a system's state will improve effective management responses—to reverse, prevent or mitigate this change. Intermediate models can assist managers with projections of ecosystem responses and indirect outcomes through the inclusion of a broad (but potentially still incomplete) set of key system components. Intermediate coral reef models can be used to answer many questions as they not only include key biological components, but also various environmental or anthropogenic forcings. For some questions (e.g., when there are multiple interacting drivers) more complex models are the most informative decision-support tools, as they include the major dimensions (i.e., spatial, temporal, taxonomic, nutrient, human activities) and, therefore, incorporate the often synergistic effects of various dynamic mechanisms and responses that are beyond what can be represented in minimal or intermediate models that sacrifice on these dimensions in return for an easier way to understand the model outcomes. For example, system-level models are useful for evaluating the economic and ecologic tradeoffs of various management scenarios, as these more complex models contain the extra detail that is required to capture the feedbacks of interest. However, complex models are not suitable in all situations; in other cases managers value the speed and transparency of simple models.

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Appendix A. Overall scoring to categorize models into Minimal (MI), Intermediate (IN) and Complex (CO).

Criteria/Score	**1**	**2**	**3**	**4**	**#1**	**#2**	**#3**	**#4**	**#5**	**#6**	**#7**	**#8**	**#9**	**#10**	**#11**	**#12**	**#13**	**#14**	**#15**	**#16**	**#17**	**#18**	**#19**	**#20**	**#21**	**#22**	**#23**	#24	**#25**	**#26**	**#27**
Conceptualization of structure*																															
# plankton grps	0	1-2	3	> 3	1	1	1	1	1	1	1	1	1	1	2	4	2	4	1	1	1	1	1	2	1	1	1	1	1	2	4
# benthic grps	1	2	3-4	> 4	3	1	2	3	3	3	2	2	2	2	2	3	1	4	1	4	2	4	1	1	4	3	4	3	3	4	4
# invertebrate grps	0	1-2	3-4	> 4	1	2	1	1	1	1	2	2	1	2	3	3	2	4	1	2	1	1	1	1	1	1	2	0	1	3	1
# vertebrate grps	0	1-2	3-5	> 5	1	2	2	1	2	2	2	2	1	3	2	2	2	4	1	2	2	1	1	1	1	1	3	2	2	4	1
Mean # trophic groups					**2**	**2**	**2**	**2**	**2**	**2**	**2**	**2**	**1**	**2**	**2.3**	**3**	**1.8**	**4**	**1**	**2.3**	**2**	**1.8**	**1**	**1.3**	**1.8**	**2**	**2.5**	**1.5**	**1.8**	**3.3**	**2.5**
Conceptualization of space**	non-spatial	lump-ed	grid or cell based		**1**	**1**	**3**	**2**	**1**	**2**	**3**	**3**	**2**	**2**	**2**	**2**	**2**	**2**	**3**	**3**	**2**	**3**	**3**	**3**	**3**	**2**	**3**	**3**	**3**	**3**	**3**
Process Details																															
trophic interactions														x	x	x	x	x		x	x						x	x	x	x	x
inter/intra species competition					x	x	x	x	x	x				x	x	x	x	x		x	x	x	x		x	x	x	x	x	x	x
age structured																		x	x			x	x			x	x	x	x		
biogeochemistry						x			x		x	x	x	x									x	x						x	x
hydrodynamics							x				x	x												x			x				x
Sum dynamic processes					**1**	**2**	**2**	**1**	**2**	**1**	**2**	**2**	**1**	**3**	**2**	**2**	**2**	**3**	**1**	**2**	**2**	**2**	**3**	**2**	**1**	**2**	**4**	**3**	**3**	**3**	**4**
Overall average complexity score					**2.3**	**3.3**	**4.3**	**2.8**	**3.4**	**2.9**	**4.4**	**4.4**	**2.6**	**5.0**	**4.1**	**4.5**	**3.9**	**6.0**	**3.0**	**4.6**	**3.8**	**4.4**	**5.0**	**4.1**	**3.4**	**3.8**	**6.8**	**5.3**	**5.4**	**6.1**	**6.8**
Leading principle					**MI**	**MI**	**MI**	**MI**	**MI**	**MI**	**MI**	**MI**	**MI**	**IN**	**IN**	**IN**	**IN**	**CO**	**IN**	**IN**	**IN**	**IN**	**IN**	**IN**	**IN**	**IN**	**CO**	**CO**	**CO**	**CO**	**CO**

*groups can be individual species or aggregated species groups
**lumped has a single output of entire modelled area, grid or cell based represents uniform or non-uniform grid or vectors