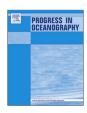
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How models can support ecosystem-based management of coral reefs



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ABSTRACT

Article history: Available online 21 January 2015 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 for dynamically modeling coral reef ecosystems and categorize them as minimal, intermediate and complex models. The categorization was based on the leading principle for model development and their level of realism and process detail. 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(s) to be answered. We contend that minimal and intermediate models are generally valuable tools to assess the response of key states to main stressors and, hence, contribute to understanding ecological surprises. As has been shown in freshwater resources management, insight into these conceptual relations profoundly influences how natural resource managers perceive their systems and how they manage ecosystem recovery. We argue that adaptive resource management requires integrated thinking and decision support, which demands a diversity of modeling approaches. Integration can be achieved through complimentary use of models or through integrated models that systemically combine all relevant aspects in one model. Such whole-of-system models can be useful tools for quantitatively evaluating scenarios. These models allow an assessment of the interactive effects of multiple stressors on various, potentially conflicting, management objectives. All models simplify reality and, as such, have their weaknesses. While minimal models lack multidimensionality, system models are likely difficult to interpret as they require many efforts to decipher the numerous interactions and feedback loops. Given the breadth of questions to be tackled when dealing with coral reefs, the best practice approach uses multiple model types and thus benefits from the strength of different models types.

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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

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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 US\$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

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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). 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).

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-equilibria, nonlinearity and threshold effects (e.g., Nyström et al., 2000; Mumby et al., 2007a). 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 (a phenomenon also known as hysteresis [Scheffer et al., 20011).

The complexity of coral reef ecosystems with their myriad 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 juggles 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) Interpolations to 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) Forecasting or hindcasting approaches, i.e., to make predictions for operational management when a system is varying within historical bounds.
- (3) Enhancement of systems understanding by quantification of a conceptual model (e.g., to calculate materials budgets) or to quantitatively test the plausibility of that conceptual model.
- (4) Developing ecological theory and generalizable ecological hypotheses.

- (5) 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.
- (6) Scenario evaluations for operational or strategic management.

With regards to these principles, we believe that each circumstance is best suited by a different model approach (Table 1). Other authors, who have discussed the selection of appropriate modeling approaches, 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.

Models, suited for coral reef managers who need to define management strategies for the entire coral reef ecosystem, need to consider interactions among system components and management sectors as well as cumulative impacts of disturbances to the system (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; Liu, 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 (Gribble, 2003; McClanahan, 1995; Tsehaye and Nagelkerke, 2008; Shafer, 2007). Few models dynamically couple ecological dynamics to socio-economic drivers and these models also focus on fisheries management (Kramer, 2007) with Melbourne-Thomas et al. (2011b) including a combination of fisheries, land-use and tourism.

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 (Kelly 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 site-specific management scenarios need to be simulated, 'end-to-end' or 'whole-of-system' models can be developed for the MSE. In more data-poor or time-limited situations or when less-specific scenarios with processes that are easily traced back are required, '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).

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