



# Sensitivity analysis and pattern-oriented validation of TRITON, a model with alternative community states: Insights on temperate rocky reefs dynamics



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## ABSTRACT

While they can be useful tools to support decision-making in ecosystem management, robust simulation models of ecosystems with alternative states are challenging to build and validate. Because of the possibility of alternative states in model dynamics, no trivial criteria can provide reliable and useful metrics to assess the goodness-of-fit of such models. This paper outlines the development of the model TRITON, and presents simulation-based validation and analysis of model sensitivity to input parameters. TRITON captures the local dynamics of seaweed-based rocky reef communities in eastern Tasmania, which now occur in two alternative persistent states: (1) either as dense and productive seaweed beds, (2) or as sea urchin 'barrens' habitat, i.e. bare rock largely denuded of macroalgae and benthic invertebrates due to destructive grazing by sea urchins. Pattern-oriented-modelling, i.e. comparing patterns in model dynamics across Monte-Carlo simulations with direct observations of Tasmanian reef communities over large scales, provides a valuable approach to calibrate the dynamics of TRITON.

Using the computationally efficient, model-independent extended Fourier amplitude sensitivity test, we identify fishing down of predatory lobsters, sea urchin recruitment rate, as well as seaweed growth rate as key parameters of influence on overall model behaviour. Through a set of independent sensitivity tests, we isolate different sets of drivers facilitating the 'forward' shift from the seaweed bed to the urchin-dominated state, and the reverse or 'backward' shift from denuded sea urchin barren to recovery of seaweed cover. The model suggests that rebuilding populations of large rock lobsters, which predate the urchins, will be effective in limiting ongoing formation of sea urchins barrens habitat, but that the chances of restoring seaweed beds from extensive barrens are relatively low if management relies solely on rebuilding stocks of large rock lobsters. Moreover, even when it does occur, seaweed bed restoration takes up to three decades in the simulations and so is arguably unrealistic to implement under short-term fishery management plans. The process of model validation provided both a better understanding of the key drivers of community dynamics (e.g. fishing of predatory lobsters), and an assessment of priority areas for future research.

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## 1. Introduction

Models of ecological dynamics can be helpful to inform decision-making and improve the management of human activities that rely on natural resources (Clark et al., 2001; Smith et al., 2011). More specifically, simulation models can be useful decision-support

tools to assess the effects of different management scenarios in ecosystems with alternative community states, where anthropogenic effects can lead to dramatic and possibly irreversible changes in structure and function across entire landscapes (Estes et al., 2011; Firn et al., 2010; Fung et al., 2011; Melbourne-Thomas et al., 2010; Mumby et al., 2007; Scheffer et al., 2001). However, building reliable simulation models requires a comprehensive understanding of key processes and drivers of system dynamics, and the accuracy of simulations will depend on the robustness of model parameterisation. Ecological processes, especially trophic interactions, are by essence variable and the dynamics of systems

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can be sensitive to this variation. However, ecological processes are usually difficult to measure precisely (Novak, 2010) and even in well-studied ecosystems, a complete and precise understanding and quantification of ecological processes is rarely possible. Thus, uncertainty arises as a major feature of ecological models, stemming from the variable nature of ecological processes, from imperfect understanding of the mechanisms underpinning ecosystem dynamics, and limited ability to quantify complex natural processes with precision (Saltelli et al., 2000).

In this context, useful ‘minimum realistic’ ecological models must adequately address questions of interest to management while accounting for the amount and reliability of the information available about the study system (Fulton et al., 2003). The art of ecosystem modelling lies in making a series of assumptions and, to a certain degree, an ecological model is only as reliable as the modeller’s understanding of system dynamics (Klepper, 1997). Therefore, simulation models require objective assessment prior to their application, and several approaches are available to validate and calibrate the dynamics of complex ecosystem models (Duboz et al., 2010; Klepper, 1997; Turley and Ford, 2009). Model calibration is often undertaken by optimising the fit of simulated community dynamics to available empirical observations. Snapshots or mean observations of the composition of the study system are often used as metrics for model validation (e.g. mean species biomasses; see Marzloff et al., 2009), although these criteria poorly characterise the variability of system dynamics, which may be of critical importance. In ecosystems that exhibit alternative states, ecologists can exhaustively study and describe communities in one state or the other, while discontinuous shifts in community dynamics are, by definition, swift and are thus rarely observed or monitored (Scheffer et al., 2001). Therefore, precise information of a system with hysteresis (i.e. where a small change in parameters or species abundance can lead to a dramatic shift to a new community state that persists even when the change is reversed; see Donahue et al., 2011) at its threshold points is nearly always lacking. Lack of observations of community dynamics for systems that manifest hysteresis, and lack of meaning in mean observations in these systems, make validation of ecosystem models with alternative states particularly challenging (Scheffer and Carpenter, 2003, but see Mumby et al., 2007; Lauzon-Guay et al., 2009; Fung et al., 2011 for examples of model validation).

Given the inability to formally and comprehensively validate the accuracy of ecosystem models against reality, predictions from ecosystem models are inherently uncertain. Uncertainty in simulation models can be broken down into three main components:

- (i) structural uncertainty, which refers to model structure and its resolution, e.g. the extent to which species are aggregated, or the nature of functional groups; the number and certainty of trophic and other ecological interactions considered; and the spatial and temporal scales of relevant physical and ecological processes (Hosack et al., 2008; Laskey, 1996; Marzloff et al., 2011);
- (ii) choice of model formulation, which includes programming choices (e.g. discrete versus continuous time (Deng, 2008), the timing of processes operating at different scales, and whether the model is spatially explicit) as well as the particular representation of ecological processes in the model (e.g. alternative ways to account for density-dependence in functional responses; Skalski and Gilliam, 2001);
- (iii) uncertainty in model parameterisation; uncertainty in individual parameter estimates, which can rapidly compound depending on interactions in the model, contributes directly

to uncertainty in model outputs (Cariboni et al., 2007; Saltelli et al., 2000).

Assessing these different sources of model uncertainty is an essential ingredient of ecological modelling (Marzloff et al., 2011; Saltelli et al., 2000). An added complication for models with alternative community states is that sensitivity analysis can be of limited value (van Nes et al., 2003). This is because simulation outcomes may only reflect whether the community reaches one state or the other and only partially depict hysteresis in model dynamics. Additionally, the modelled community is more prone to shift to an alternative state when parameter space is near bifurcation points, so linear and partial sensitivity tests are limited because they typically neglect the influence of interactions between multiple input parameters giving rise to complex non-linear dynamics (Saltelli et al., 1999; van Nes et al., 2003).

In this paper, we explore and validate the behaviour of a model of subtidal seaweed-based reef community dynamics in eastern Tasmania, south east Australia. These temperate rocky reefs occur in two alternative community states: productive and diverse stands of canopy macroalgae referred to as ‘seaweed bed’ habitat; or as bare rocky expanses known as sea urchin ‘barren’ habitat (Johnson et al., 2005; Ling et al., 2009a). On the east coast of Tasmania, the climate-driven range extension of the long-spined sea urchin *Centrostephanus rodgersii* represents a major threat to endemic seaweed bed communities (Ling, 2008) including high value commercial species such as rock lobster and abalone (Johnson et al., 2011). Within its new eastern Tasmanian range, *C. rodgersii* forms and maintains extensive barrens habitat, i.e. areas of bare rock up to tens of hectares, following the destruction of seaweed beds by its grazing activity. Large lobsters (carapace length > 140 mm) constitute the only efficient predators of *C. rodgersii* in south eastern Australian waters (Ling et al., 2009a), so that commercial and recreational fishing of lobsters directly facilitates the formation of *C. rodgersii* barrens. Compared to the seaweed beds, sea urchin barrens have dramatically lower productivity (Chapman, 1981), habitat complexity and species diversity (Ling, 2008). Note that key commercial species do not occur in commercially harvestable quantities on barrens habitat (Johnson et al., 2005, 2011). Thus, preventing the formation of further *C. rodgersii* barrens, and promoting the reverse shift back to seaweed beds where barrens now occur, is a priority for the management of reef communities and fisheries in eastern Tasmania (Ling et al., 2009a). It is therefore important that managers understand the fundamentally different ecologies operating within each alternative state, the ecological mechanisms that drive the shift from dense seaweed bed to urchin barrens and vice versa, and the circumstances in which these shifts are likely to occur. Here, we calibrate and validate model behaviour against observed patterns that describe community dynamics, including shifts between these alternative states. Structural uncertainty has been comprehensively tested in this model (Marzloff et al., 2011) and hence this paper focuses on sensitivity to uncertainty in model formulation and parameterisation. Using Monte–Carlo simulations, we explore the effects of parameter uncertainty on the behaviour of the model.

Our work comprises three steps: first, we quantify model sensitivity to alternative formulations and input parameters using the extended Fourier amplitude sensitivity test (FAST), a quantitative model-independent sensitivity analysis technique for complex simulation models (Saltelli et al., 1999). The extended FAST assesses the contribution to model output variance of each input parameter, including through interactions with other factors. We analyse model global behaviour as well as specific components of its dynamics; by decomposing overall model dynamics into ‘forward’ shift (from seaweed bed to barren) and ‘backward’ shift (from

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