

Exploring ecological shifts using qualitative modelling: Alternative states on Tasmanian rocky-reefs

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Abstract: Alternative stable states characterise many natural ecosystems. Subtidal rocky-reefs on the east coast of Tasmania persist in a range of different configurations, including so-called sea urchin ‘barrens’ and dense seaweed beds with a closed canopy. In creating and maintaining barrens habitat on temperate reefs, sea urchins induce major losses of production, biodiversity and physical structure. The invasive long-spined sea urchin (*Centrostephanus rodgersii*) is able to form barrens across its newly extended range in Tasmania. Formation of urchin barrens on the east coast has been a rising concern in recent decades, in particular because the two most valuable fisheries in the state, for blacklip abalone (*Haliotis rubra*) and southern rock lobster (*Jasus edwardsii*), are not viable on barrens. Thus, identifying triggers of barrens formation is critical in the management of these reefs. Here we explore the dynamics of Tasmanian rocky-reef communities, including testing the effects of fishing, using qualitative modelling informed by a deep empirical knowledge of interactions among species. Loop analysis offers a holistic approach to address the structure and dynamics of the system. It sacrifices precision of particular dynamics to maximize reality and generality in providing a causal understanding of complex systems. The network topology forms emergent feedback patterns that cause meta-stable properties in this rocky-reef system, and the models capture formation of urchin barrens and the mechanisms of the phase shifts. Fishing is identified as a perturbation that can reduce resilience of the system in its original highly productive seaweed-dominated state. We show that qualitative loop models can be highly valuable in identifying the kinds of system dynamics that managers need to consider in ecosystem based management, but emphasise that they are not designed to act as definitive management models for specific instantiations.

Keywords: *Subtidal rocky-reef; Tasmania; community structure; phase shifts; alternative stable states; qualitative modelling.*

1. INTRODUCTION

Alternative stable states (ASS) are characteristic of many ecosystems worldwide, and among the best-documented examples are those in marine communities (Knowlton, 2004; Overland *et al.*, 2008). ASS have crucial implications for the management of natural resources (Folke *et al.*, 2004; Scheffer *et al.*, 2001) because the delivery of ecosystem services to human societies usually relies on functioning of a 'healthy' configuration of a given system, and so phase shifts to states representing dramatic reorganization of natural communities (Overland *et al.*, 2008) can be problematic (Collie *et al.*, 2004; Scheffer *et al.*, 2001).

As a complement to ecological theory, mathematical models are useful tools to refine current understanding of ASS and phase shifts (Jiao, 2009; Mantua, 2004). The broad goal of our study is to identify key features of ecological systems that give rise to discontinuous phase shifts. We use qualitative modelling as a holistic approach to explore the general dynamics of specific marine communities and their responses to perturbations. Although it sacrifices precision, qualitative modelling maximizes generality and realism in providing a causal understanding of complex systems (Dambacher *et al.*, 2007; Levins, 1966). It provides an appropriate framework to organise the available empirical and experimental knowledge of an ecosystem and assess the two major criteria necessary for ASS (Petraitis and Dudgeon, 2004), *viz.* 1) the test of origin to identify the perturbations or changes in environmental conditions that switch a system from one state to the other, and 2) the test of maintenance to ensure that each stable state is self-maintaining through time.

Subtidal temperate rocky reefs persist within a range of ASS (Knowlton, 2004). So-called sea urchin 'barrens' represent an impoverished alternative state to highly productive seaweed beds (Johnson and Mann, 1993; Ling, 2008). Overgrazing by sea urchins is known to create and maintain 'barrens' habitat worldwide (Lawrence, 1975), inducing major loss of productivity (Chapman, 1981), biodiversity (Ling, 2008) and physical structure on temperate reefs. On the east coast of Tasmania, the invasive long-spined sea urchin (*Centrostephanus rodgersii*) demonstrates the capacity to overgraze seaweed beds (Johnson, 2005; Ling, 2008). This has significant consequences for high-value reef-associated fisheries dependent on reef habitat, since densities of lobsters (*Jasus edwardsii*) and abalone (*Haliotis rubra*) on urchin barrens are too low for commercial harvesting (Johnson, 2005).

We explore the dynamics of Tasmanian rocky-reef communities and the effects of fishing using qualitative models informed by a deep empirical knowledge of interactions among species. The aims of the work are to use qualitative models to:

- (i) Develop a causal understanding of phase shifts between alternative states on the Tasmanian rocky-reefs and their impact on commercial and non-commercial species.
- (ii) Identify classes of mechanisms in natural systems that can lead to phase shifts, using Tasmanian rocky reefs as an example. We wanted to assess whether qualitative models and feedback analysis can be used to investigate the ability of natural systems to produce alternative stable states and predict the potential impacts of phase shifts.
- (iii) Explore whether alternative model structures (which arise through uncertainties in knowledge) and weak interactions alter model dynamics and predictions.

Using Tasmanian reefs as a case study, we show that the network topologies describing these systems form emergent feedback patterns that cause meta-stable properties in the system, and that the models capture formation of urchin barrens and the mechanisms of the phase shifts. We demonstrate the use of qualitative models as appropriate tools to investigate ecological phase shifts through both feedback loop analysis and qualitative prediction of ecosystem dynamics. Limits of the approach are also discussed.

2. MATERIAL AND METHODS

2.1. A qualitative modelling approach using loop analysis

Loop analysis provides a framework to organize available information to explore the structure and basic dynamics of complex systems. It can be particularly helpful as a first approach to analyse the complexity of a system without the need for detailed quantitative parameterisation (Puccia and Levins, 1985), especially in ecological models where the life history of species is often well known but rarely quantified (Dambacher *et al.*, 2003). We use qualitative analysis of the effects of sustained 'press perturbations' to explore the dynamics of the modelled communities. Loop models are also useful to identify feedback mechanisms responsible for producing alternative states in a given dynamics.

Signed digraphs and symbolism:

Qualitative modelling focuses on the analysis of the structure of ecological communities. The structure of interactions between different variables of an ecosystem is represented as a sign directed graph (or sign digraph) constructed from knowledge of the studied system. The variables or vertices of the digraphs are the objects - natural populations or environmental parameters - that constitute the modelled system. They are symbolised by nodes, and the nodes are connected by links that represent the sign of direct effects. An arrow (\rightarrow) signifies a positive interaction (e.g. a prey contributes to predators' diet); a line with a solid dot (\dashrightarrow) represents a negative effect (e.g. depletion of a prey population by a predator); and self-effects are represented as lines originating and terminating at the same variable (e.g. \cup).

A signed digraph can be mathematically expressed as a community matrix, either symbolically or as a qualitative matrix (Figure 1). The community matrix summarizes the signs of each direct effect a_{ij} of any variable j on any variable i (Dambacher *et al.*, 2002).

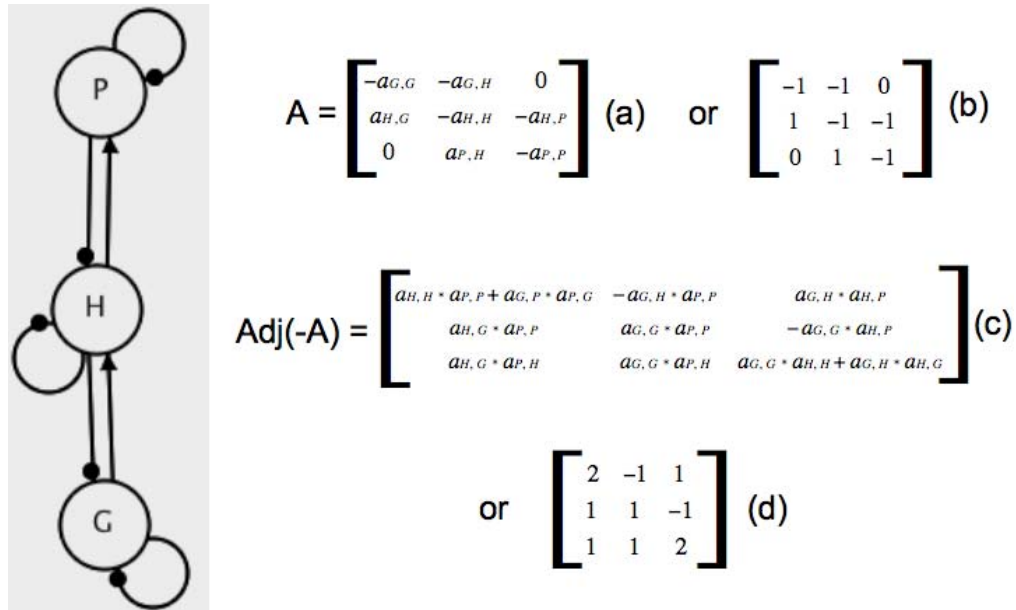


Figure 1. Example of a sign digraph, involving 1) a primary producer (G for Grass), 2) an herbivore (H) and 3) a predator (P). The graph is translated into both (a) symbolically specified and (b) quantitative community matrices, from which we can compute the adjoint matrices of (c) symbolic or (d) qualitative predictions.

Model outputs

Using loop analysis, the community matrix of a given system can be used to explore the qualitative effect of ‘press perturbations’ (Dambacher *et al.*, 2003). Now, the adjoint of the negative of the community matrix, $\text{Adj}(-A)$ (see Figure 1 c and d) sums up all the complementary feedbacks running from one variable to the other (see Dambacher *et al.*, 2002): we can thus use the adjoint of the community matrix to make qualitative predictions of the effects of external ‘press perturbations’ on the biological system. As complementary feedbacks add up, responses of each modelled variable to a perturbation can either be positive, negative, neutral, or even ambiguous if the same number of positive and negative links cancels each other out. For instance in Figure 1, the first column of the adjoint returns qualitative predictions for the response in abundance of each of the 3 variables (grass = 1st row; herbivores = 2nd row; predator = 3rd row) to a positive input in abundance of the first variable (grass). In our study, we investigated the qualitative effects on the overall dynamics of anthropogenic activity (e.g. fishing) or non-trophic perturbations (e.g. physical effects of storms on seaweed abundance).

In addition, each element of the adjoint matrix can be weighted by the total number of contributing feedbacks, both positive and negative (Dambacher *et al.*, 2002). We use this “weighted-predictions” matrix to assess the probability of qualitatively predicting the correct sign (see Hosack *et al.*, 2008).

2.2. Model specification

We collated empirical data on the different components of the subtidal rocky-reefs in Tasmania (Table 1). Each variable represents a species or functional group; only abalone (AB), southern rock lobster (RL) and

sea urchin (CR for *Centrostephanus rodgersii*) are considered as individual species. The total community that is the seaweed bed is given as SW, and includes canopy-forming algae such as *Ecklonia radiata*, *Macrocystis pyrifera*, and *Phyllospora comosa*, while basal level benthic communities are described as ‘pink’ benthos (PU: non-calcareous encrusting and non-geniculate coralline algae) and ‘brown’ benthos (BU: sessile invertebrates and a matrix of filamentous red algae and sediment). Table 1 provides a summary of the interactions between variables. We assume each variable is self-regulated, i.e. manifests density-dependent growth.

Table 1. Summary of interactions between different components of Tasmanian rocky-reefs. Interaction strength is explicitly described to identify the links to be tested in the models. SW: seaweed bed including canopy-forming macroalgae; CR: long-spined sea urchin, *Centrostephanus rodgersii*; RL: southern rock lobster, *Jasus edwardsii*; AB: blacklip abalone, *Haliotis rubra*; BU: ‘brown’ epilithic understorey of sessile invertebrates and a matrix of filamentous algae and sediments; PU: ‘pink’ epilithic understorey of non-calcareous encrusting algae and non-geniculate coralline algae; DA: drift algae.

Model interaction	Description	Strength
SW → RL	Provision of habitat and food	Strong
SW → AB	Provision of habitat and food (drift materials)	Strong
SW → CR	Source of food	Strong
SW → PU	Provision of optimal light conditions through shading	Strong
SW → BU	Sweeping of young plant recruits	Variable (Shallow)
RL → CR	Predation	Strong
RL → AB	Predation; reduced growth.	Weak (Uncertain)
CR → SW	Grazing	Strong
CR → AB	Competition for space and resource	Weak
CR → BU	Grazing	Strong
AB → BU	Grazing and trampling (bulldozing)	Variable
PU → AB	Provision of habitat for adult and juvenile stages	Strong
PU → BU	Anti-fouling by sloughing of epithelial cells, allelochemicals	Weak
BU → PU	Competition. Overgrowing of the pink algae.	Strong
BU → CR	Source of food	Strong
BU → SW	Sediment accumulation can block algae recruitment	Variable (Weak)
BU → AB	Once established, hostile habitat for adult and recruits.	Variable

Since the main focus of this study was on alternative states of the reefs and effects of dynamics on commercial fisheries, we considered the overall dynamics in two clearly delineated subsystems: 1) the gross dynamics of macroalgal- and barrens-dominated habitat characterised by the presence or absence respectively of a dense macroalgal overstorey; 2) the dynamics of the basal level of epilithic understorey most closely associated with the benthos in the macroalgal dominated state, which exists in either a ‘pink’ or ‘brown’ configuration (Figure 2). This framework provides a coarse definition of the alternative states, and does not attempt to resolve variability in community composition within each configuration. Nonetheless, the different states we consider summarize the broad meta-stable configurations of the Tasmanian reefs in terms of general functioning, i.e. productivity, habitat structure and commercial fisheries.

3. RESULTS AND DISCUSSIONS

3.1. Overstorey dynamics in open coast

In Tasmania, formation of urchin ‘barrens’ associated with the invasive *Centrostephanus rodgersii* is the most important issue threatening the productivity of subtidal shallow reefs and the fisheries they support (Johnson *et al.*, 2005). Therefore, the bulk of our discussions focuses on the gross overstorey dynamics in the open coast.

The qualitative predictions provide a general understanding of the system dynamics (Table 2). Fishing rock lobster (4th column of the adjoint of model A) can indirectly diminish the support of the reef to commercial species by facilitating grazing of the seaweed bed by sea urchin. Fishing abalone (3rd column) has only localised effects on the abalone population itself. In model A (see adjoint matrix in Table 2), an increase in seaweed bed productivity (1st column) has direct positive effects on both commercial species (3rd and 4th rows), and ambiguous effects on the urchin population (2nd row). The positive input in the seaweed bed affects the urchin population both positively (as urchin grazing on macroalgae is directly enhanced), and negatively (as predation pressure by rock lobster also increases). A positive increase in urchin abundance on the reefs – as has occurred in the east of the state in the last decades with the southward range extension of

C. rodgersii – affects the overall dynamics by increasing grazing pressure on seaweeds, and so reduces the productivity of the reef.

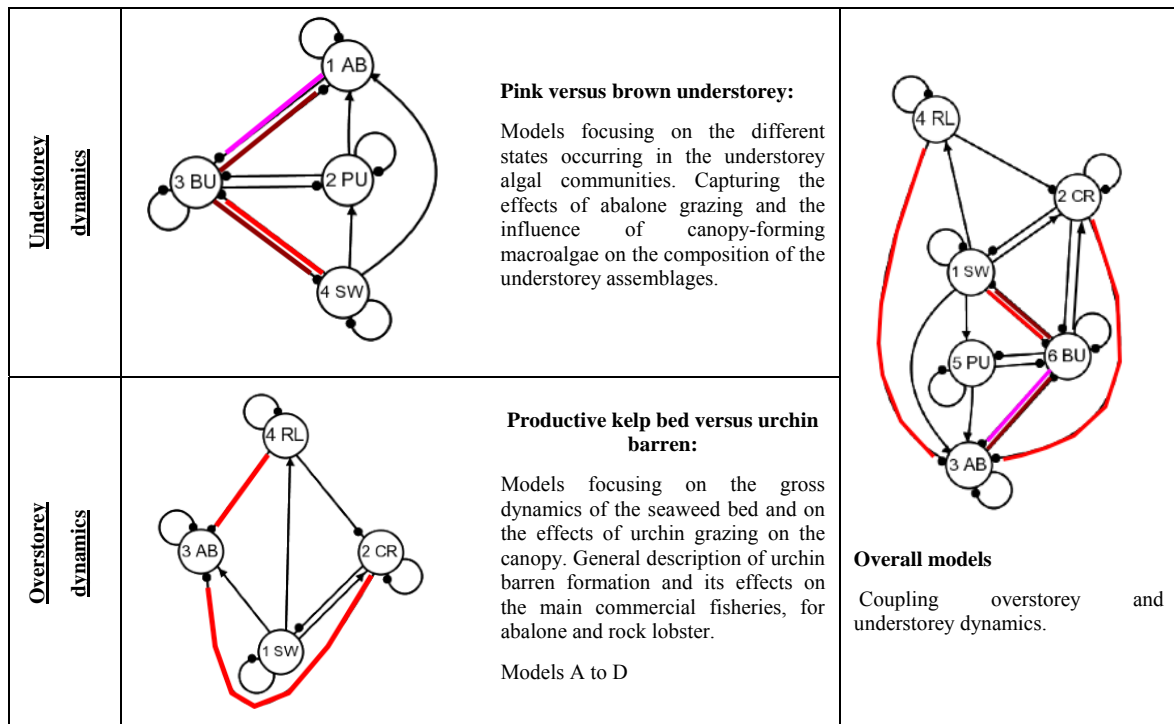


Figure 2. Models describing dynamics on Tasmanian rocky-reefs. The alternative states of the basal level of the benthos are defined as pink (encrusting non-calcareous red and non-geniculate coralline algae) and brown epilithic understorey (matrix of filamentous red algae and sediment; sessile invertebrates). Pink and brown coloured interactions are strengthened in presence of a pink or a brown benthos respectively. Red coloured interactions are weak or uncertain; the effect of their inclusion was tested (cf. interaction strength in Table 1) since qualitative modelling provides a framework to test the effects of neglecting or including uncertain interactions on the dynamics of the models. The digraphs presented here refer to the dynamics on the open coast where *Centrostephanus rodgersii* dominates and forms barrens.

Feedback patterns emerging from the network topology

As observed in the adjoint matrices of models A to D (Table 2), the urchin population (2nd row in the adjoint matrix) reacts to most perturbations in the opposite direction to that of lobsters (4th row), abalone (3rd row) and the seaweed bed (1st row). Thus, the responses of this simple system to perturbations will push the system towards one of two states. State I is a productive seaweed bed supporting high abundances of lobster and abalone with a low grazing pressure by the urchin, while State II is a poorly productive overgrazed reef dominated by sea urchins. Two main feedback mechanisms are responsible for these abundance patterns between the different species within the system.

A simple predator-prey relationship between the urchin population and the seaweed bed is the most parsimonious descriptor of the effects of urchin grazing and urchin barren formation. This simple Lotka-Volterra system continuously evolves between two extreme boundaries, from a productive and healthy seaweed bed under low grazing pressure to greatly depleted seaweeds under high grazing pressure.

The positive feedback loop between sea urchins, the seaweed bed and lobsters (CR→SW→RL→CR) establishes the correlations in species abundances evident in the adjoint matrices. This loop brings instability to the system dynamics, and so pushes or maintains the system towards either State I or State II.

Model structure uncertainty

Models B to D (Table 2) include weaker interactions (see Table 1) that might potentially affect the detailed dynamics of the reef community, but which are left out in model A. However, inclusion or otherwise of these interactions does not affect the broad dynamics and stability properties of the system, as they do not introduce new feedback loops. Including these weaker interactions modifies the dynamics of abalone (3rd row of the adjoint matrix) in that, in model A, abalone only receive feedback through the seaweed bed, while in models B-D, inclusion of one or both of the negative interactions adds ambiguity and / or changes

the sign of the qualitative response of abalone to perturbations in one of the other 3 variables. Indeed, if only interaction (1) (= predation by rock lobster on abalone RL→AB) is included, or if both interactions (1) and (2) (= competition between the sea urchin and abalone CR→AB) are included as shown in models B and D respectively, then the qualitative response of abalone abundance to any perturbations to the other three variables becomes more ambiguous. In both of these situations, a positive input to the productivity of the seaweed bed propagates as the same number of positive and negative effects on abalone, which cancel each other. Relative to model A, the inclusion of lobster predation on abalone (interaction 1) in model B reverses the sign of abalone response to a change in lobster abundance (3rd row – 4th column: positive in model A / negative in model B).

Table 2. Adjoint matrices for qualitative predictions and matrices of probabilities of correct predictions for the different possible models of the overstorey dynamics in open coast. The inclusion of the 2 uncertain interactions, for (1) predation by rock lobster on abalone RL→AB and (2) competition between the sea urchin and abalone CR→AB, is tested. 1: SW; 2: CR; 3: AB; 4: RL.

Model	RL → AB	CR → AB	Adjoint	Probability of predicting the correct sign
A			$\begin{bmatrix} 1 & -1 & 0 & 1 \\ 0 & 1 & 0 & -1 \\ 1 & -1 & 1 & 1 \\ 1 & -1 & 0 & 2 \end{bmatrix}$	$\begin{bmatrix} 1.0 & 1.0 & 1.0 & 1.0 \\ 0.50 & 1.0 & 1.0 & 1.0 \\ 1.0 & 1.0 & 0.77 & 1.0 \\ 1.0 & 1.0 & 1.0 & 1.0 \end{bmatrix}$
B	√		$\begin{bmatrix} 1 & -1 & 0 & 1 \\ 0 & 1 & 0 & -1 \\ 0 & 0 & 1 & -1 \\ 1 & -1 & 0 & 2 \end{bmatrix}$	$\begin{bmatrix} 1.0 & 1.0 & 1.0 & 1.0 \\ 0.50 & 1.0 & 1.0 & 1.0 \\ 0.50 & 0.50 & 0.77 & 0.77 \\ 1.0 & 1.0 & 1.0 & 1.0 \end{bmatrix}$
C		√	$\begin{bmatrix} 1 & -1 & 0 & 1 \\ 0 & 1 & 0 & -1 \\ 1 & -2 & 1 & 2 \\ 1 & -1 & 0 & 2 \end{bmatrix}$	$\begin{bmatrix} 1.0 & 1.0 & 1.0 & 1.0 \\ 0.50 & 1.0 & 1.0 & 1.0 \\ 0.77 & 1.0 & 0.77 & 1.0 \\ 1.0 & 1.0 & 1.0 & 1.0 \end{bmatrix}$
D	√	√	$\begin{bmatrix} 1 & -1 & 0 & 1 \\ 0 & 1 & 0 & -1 \\ 0 & -1 & 1 & 0 \\ 1 & -1 & 0 & 2 \end{bmatrix}$	$\begin{bmatrix} 1.0 & 1.0 & 1.0 & 1.0 \\ 0.50 & 1.0 & 1.0 & 1.0 \\ 0.50 & 0.77 & 0.77 & 0.50 \\ 1.0 & 1.0 & 1.0 & 1.0 \end{bmatrix}$

With the comparison of these alternative models, we emphasise how qualitative modelling can be used as a baseline to develop quantitative ecosystem models, to both test the assumptions built-in a model structure, and identify the most appropriate network topology.

3.2. Other components of the rocky-reef dynamics

Similar to the set of models A-D discussed above in capturing the overstorey dynamics in the open coast, we elaborated different suites of models focusing on other components of the reef dynamics (cf. Figure 2). In the presentation, we also refer to the following sets of models to illustrate how loop analysis can inform the potential of specific dynamics to lead to alternative states:

(a) models of the understorey dynamics characterized by abalone mediating competition between the pink and brown states of the epilithic benthos. Dynamics of the sessile benthic community depend on community structure since different interaction patterns are enhanced or weakened depending on the dominant state of the epilithic understorey (pink and brown interaction in Figure 2). As a grazer, abalone plays a crucial role in maintaining the ‘pink’ state; and

(b) models coupling over- and understorey dynamics. These models combine the dynamics captured in the previous ones.

4. CONCLUSIONS

This suite of qualitative models provides a useful set of tools to assess the effects of fishing lobster and abalone on the overall functioning and state of rocky-reef communities in eastern Tasmania. Fishing

abalone mostly affects the nature of the basal benthos, which then has implications for abalone themselves, while harvesting lobsters alters the overall resilience of the reefs to urchin grazing because large lobsters (carapace length > 140 mm) are the most effective predators of the urchin. The comparison of alternative model structures allows testing the effect of uncertainty in model structure, and establishes the ground to develop fully quantitative models of reef communities. Loop analysis can be a valuable tool to identify both the potential (inherent to the structure of the modelled community) of ecological systems for ASS and the implications of phase shifts on community dynamics. However, we emphasize that qualitative modelling can only identify the necessary but not necessarily the sufficient conditions for ASS.

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