Towards ecosystem-based management of Tasmanian temperate rocky reefs: Community dynamics models indicate alternative community states and management strategies

Martin Pierre Marzloff
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Declarations

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Abstract

Worldwide, ecosystems have demonstrated the potential for dramatic shifts to an alternative persistent state under gradual long-term environmental changes or following sudden short-term perturbations. Such shifts are documented for numerous marine examples from coral reef to pelagic communities and may become more common as ecological dynamics adjust to climate-driven changes. These shifts are often sudden, challenging to predict and can have disastrous and unpredictable consequences on both ecosystem functioning and the human activities that rely on the associated natural resources. They often result in irreversible dramatic changes in community structure and productivity and represent a growing concern for managers of natural systems.

In ecosystems where the presence of an alternative persistent state is well documented, the drivers of these shifts (e.g. anthropogenic stressors or changes in environmental conditions) can be analysed retrospectively so as to address key management questions, as has occurred in several applications on coral reefs. However, phase shifts are often swift and observed *a posteriori*, i.e. after the ecosystem has shifted to the alternative state. Thus, thresholds in ecosystem dynamics are difficult to identify empirically despite that this is crucial for sound management of marine resources. Additionally, controlled experimental assessment of the effects of alternative management scenarios on community state is hardly ever achievable in marine ecosystems. When they occur, phase shifts are unique to each ecosystem, hence case-specific simulation models present a valuable tool to explore ecological dynamics with alternative persistent community states, test the effects of management scenarios and inform decision-making.

On the east coast of Tasmania, shallow rocky reef communities on the exposed coast mainly occur in two alternative persistent states: (1) the seaweed bed state characterised by a dense productive canopy of macroalgae; or, (2) the sea urchin 'barren' state characterised by a poorly productive rocky habitat largely bare of seaweeds as a result of destructive grazing by the long-spined sea urchin (*Centrostephanus rodgersii*). The establishment of

these widespread sea urchin barrens result from a combination of both: (1) the climate-driven range extension of the long-spined sea urchin *C. rodgersii* from Australia's mainland to Tasmania; and (2) depletion of key reef predators by fishing. Large southern rock lobster (*Jasus edwardsii*) individuals constitute the main predator of the long-spined sea urchin in Tasmania. Relative to the seaweed bed state, *C. rodgersii* barrens represent dramatic losses of habitat, species diversity and productivity, including commercial species such as blacklip abalone (*Haliotis rubra*) and southern rock lobster, the two most valuable fisheries in Tasmania. Thus, the spread of sea urchin barrens presents a major and pressing threat for the lobster and abalone fishing industries.

This thesis presents a suite of models specifically developed to better understand the dynamics of Tasmanian rocky reef communities and inform management interventions to mitigate destructive grazing of seaweed beds by the invasive long-spined sea urchin.

Chapter 2 investigates the causal relationships between positive feedback and the occurrence of alternative states in community dynamics. Modelling of community feedback informed by available qualitative knowledge about ecosystem structure constitutes a valuable framework to detect the potential for alternative states in ecological dynamics as illustrated with some examples from Tasmanian rocky reef communities. Qualitative modelling assists to understand the essential features of temperate reef dynamics around Tasmania, and provides a useful first step towards quantitative modelling of rocky reef dynamics. The approach provides an ideal framework to (i) collate all available information about rocky reef ecology, (ii) test model structure uncertainty, and (iii) identify key drivers of alternative states in ecosystem dynamics.

The quantitative model presented in the subsequent chapters captures the dynamics of the three key groups or species (i.e. the rock lobster, sea urchin, and seaweed assemblage) directly involved in the positive feedback that drives the shift between alternative states on Tasmanian rocky reef. **Chapter 3** describes the development, parameterisation and calibration of a mean field model of the local dynamics (reef area of 100 m^2 - 10 ha) of a reef community. The model's ability to capture the potential for phase shifts, from dense seaweed bed to sea urchin barrens habitat and back, is validated against large-scale patterns observed on rocky reefs where *C. rodgersii* occurs. In the simulations, the time for extensive sea urchin barrens to form is of the order of two decades, while restoration of seaweed cover from the sea urchin barrens habitat takes about three decades if relying on management interventions that cannot effectively reduce urchin density to zero. Thus, restoration of seaweed beds seems unrealistic to implement within the current timeframe of management plans. Comprehensive model-independent sensitivity analysis of model behaviour to parameter estimates also suggests that, in addition to lobster fishing mortality, recruitment rates of sea urchins and rock lobsters, which are strongly influenced by large scale oceanographic features and highly variable in eastern Tasmania, are key factors in determining the potential for sea urchin barren formation in the model.

In **Chapter 4**, sets of Monte-Carlo simulations with this model are used to address three sets of questions related to management for mitigation of sea urchin destructive grazing of Tasmanian seaweed beds. Model behaviour suggests that thresholds in shifting from seaweed bed to sea urchin barren and restoration of seaweed cover reveal the existence of a hysteresis in model dynamics. The hysteresis implies that the establishment of sea urchin barrens cannot be reversed easily. These thresholds provide valuable ecological reference points to prevent the establishment of sea urchin barrens. The model indicates that culling of sea urchins appears as the most effective management strategy to minimise the ecological impact of *C. rodgersii* on Tasmanian reef communities. Indirect interventions relying solely on the rebuilding of rock lobster population (through reduction in fishing or implementation of a maximum legal catch size) perform poorly but, when combined with direct control of the sea urchin population, they can provide optimal outcomes both in terms of minimising barren formation and fishery performance. Finally, the model shows that to allow lobsters to play their critical ecological 'service' role in preventing sea urchin barrens formation, a reduction in lobster fishing mortality from current levels is required. A maximum sustainable yield as estimated from the single species stock assessment model does not account for the ecosystem service delivered by larger lobsters, and the models emphasise the need for an ecosystem-based fishery management approach.

This suite of models contributes to the general understanding of mechanisms and drivers that can facilitate shift between alternative states in ecological dynamics. The quantitative simulation model provides specific information to managers about the drivers of shifts between the seaweed bed and the sea urchin barren state in the dynamics of Tasmanian rocky reefs. In particular, the presence of a hysteresis in reef community dynamics means that effort to prevent barrens formation constitutes a more viable and cost effective management strategy than the restoration of seaweed beds once extensive barrens habitat has developed. The commercially-fished rock lobster is an essential reef predator delivering key ecosystem services to Tasmanian rocky reefs and model simulations highlight the necessity for fisheries management to move away from a single species focus and account for the ecological role of targeted commercial species. The tools implemented here to inform an ecosystem-based management of Tasmanian rocky reefs are generic and 'transportable' to other ecosystems with alternative states. While *C. rodgersii* barrens currently constitute a pressing concern for managers of reef communities and fisheries in Tasmania, the long-spined sea urchin is only one example of a species that is dramatically restructuring Tasmanian reef communities. There are many other 'natural' invaders, whose ecosystem roles and impacts are unknown, currently extending their distribution from Australia's mainland to the warming Tasmanian waters. In the coming decades, climate-driven changes are likely to bring more surprises to Tasmanian rocky reefs, and just as many challenges for the associated fisheries and their managers.

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Statement of co-author contributions

Prof. Craig Johnson (UTas) provided comments on the general sections of this thesis (**Chapters 1 and 5**).

Chapters 2 - 4 of this thesis have been prepared as manuscripts for submission to peer-reviewed journals. In all cases the design and implementation of the research, data analysis, interpretation of results and manuscript preparation were the responsibility of the candidate but were carried out in consultation with supervisors and with input from specialist contributors. These contributions are outlined for each of these chapters below.

Chapter 2: Dr. Jeffrey Dambacher (CSIRO), Prof. Craig Johnson (UTas) and Dr. Rich Little (CSIRO) contributed to the development of the ideas. Dr. Jeffrey Dambacher provided technical advice on qualitative modelling of complex systems' feedback. Prof. Craig Johnson, Ass. Prof. Stewart Frusher (UTas), Dr. Scott Ling (UTas), Dr. Elizabeth Strain (UTas) provided background knowledge about Tasmanian reef ecology. Contributing authors, as well as Dr. Elizabeth Fulton (CSIRO), Dr. Geoffrey Hosack (CSIRO) and two anonymous reviewers, provided comments on the manuscript.

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Chapter 1
Introduction

"Variability is normality." Valdivia (1978) about the northern Humboldt ecosystem following the 1973 collapse of the world champion Peruvian anchoveta fishery.

Variability across a range of scales in space and time is a key characteristic of ecological dynamics (Doak et al., 2008), underpinned by a suite of disparate causal mechanisms. Beyond short-term variability of natural dynamics (e.g. seasonal or interannual), environmental or anthropogenic perturbations can facilitate sudden shifts between alternative persistent community states (May, 1977; Scheffer et al., 2001; Beisner et al., 2003; Scheffer and Carpenter, 2003). In these cases, ecological communities can manifest 'phase shifts' in which large changes in species abundances are observed without any tendency to return to the previous configuration (Scheffer et al., 2001). Alternative states have been reported both in terrestrial and aquatic systems (Schroder et al., 2005), and shifts from one state to another can be continuous or discontinuous (Scheffer et al., 2001; Beisner et al., 2003). Discontinuous transitions represent ecological hysteresis, i.e. dynamics where a small change in parameters or species abundance can lead to a dramatic shift to a new community state that persists when the change is reversed (Donahue et al., 2011). However, detailed observations of this kind of transition in nature are scarce, in particular for communities with hysteresis. Indeed, such ecosystems (e.g. coral reefs or eutrophic lakes) are commonly described as in one community state or the other with some limited understanding of the actual transition dynamics (Scheffer et al., 1993; Scheffer and Carpenter, 2003). These shifts in community dynamics can dramatically alter ecosystem functioning and have disastrous consequences on the human activities that rely on use of natural resources (Scheffer et al., 2001). Phase shifts are challenging to anticipate and their consequences difficult to predict (Scheffer and Carpenter, 2003; Doak et al., 2008). While natural variability implies constant changes in environmental conditions (seasonal and interannual variability in environmental conditions), which make ecological dynamics difficult to predict (Doak et al., 2008) and the management of natural resources uncertain (e.g. years of low recruitment in fishery management), it can lead with no warning to dramatic changes in ecosystem functions and structure in dynamics with alternative states (Hastings and Wysham, 2010). Thus, detecting the potential for alternative states in ecosystems and better understanding these dynamics and their drivers are essential to maintain ecosystem well functioning and avoid the unpredictable consequences of discontinuous ecosystem shifts (van de Koppel et al., 1997; de Young et al., 2008; McClanahan et al., 2011).

Two main types of perturbations can alter the state of an ecosystem: 1) a sudden stochastic event that modifies state variables on short time scales (e.g. an extreme weather event that causes a dramatic mortality event for a population) and 2) a sustained external constraint (e.g. fishing pressure) that affects population growth rates (birth, mortality or migration) over long time scales (Scheffer et al., 2001; Beisner et al., 2003). There has been a resurgence of interest in phase shift theory over the last few decades (Petraitis and Dudgeon, 2004) as the effects of human activities on ecosystems become better understood (Scheffer et al., 2005; de Young et al., 2008; Ling et al., 2009*a*). Human-induced stresses on ecosystems can be categorised arbitrarily into two groups: 1) large scale atmospheric and oceanographic changes (e.g. as a result of anthropogenic carbon emissions) can affect most components of ecosystems, from the physical environment (e.g. temperature) to animal physiology (Cury et al., 2008; Running, 2008; Overland et al., 2010; Johnson et al., 2011); and 2) local human activity through direct exploitation of natural resources (e.g. fishing) or indirect human inputs (e.g. pollution) that can significantly affect the local natural environment (Scheffer et al., 2005; Edgar et al., 2009). The effects of both global climate-driven changes and local human activities can potentially have dramatic consequences on the dynamics of ecosystem with alternative persistent state as they can facilitate sudden shift to a less desirable ecosystem state (Scheffer and Carpenter, 2003; Genkai-Kato, 2007). Thus, better understanding anthropogenic as well as environmental drivers of phase shifts have become a major concern for the sound management of ecological systems (Folke et al., 2004; Genkai-Kato, 2007; de Young et al., 2008).

Because phase shifts are often swift, evidence for alternative states in nature are typically collated *a posteriori*, i.e. once a community has shifted to an alternative state and the dramatic consequences of a shift are observed (Scheffer et al., 2005; Ling et al., 2009*a*). While there exists a body of theoretical literature about alternative states and phase shifts, demonstrating their existence in natural systems (de Young et al., 2004; Petraitis and Dudgeon, 2004), characterising the nature of the anthropogenic and/or environmental drivers of these shifts (Scheffer and Carpenter, 2003), identifying key thresholds in ecological dynamics that manifest hysteresis (McClanahan et al., 2011), and predicting their effects on ecosystem function, each constitute major challenges for ecologists and for the robust management of human activities in systems with the capacity for rapid phase shift (de Young et al., 2008; Overland et al., 2008). Moreover, these features are also difficult to assess experimentally (Petraitis and Dudgeon, 2004). In particular, controlled experimental testing of the long-term effects of alternative management scenarios is effectively hard to achieve in 'real world' ecosystems (Scheffer and Carpenter, 2003). Therefore, mathematical models, albeit difficult to parameterise and validate, have a central role in helping to predict and understand alternative states in ecosystems where anthropogenic effects can lead to dramatic irreversible changes (Scheffer et al., 2001; Mumby et al., 2007; Firn et al., 2010; Melbourne-Thomas et al., 2010; Estes et al., 2011; Fung et al., 2011; McClanahan et al., 2011). Phase shifts are unique to each ecosystem, and so case-specific simulation models present a valuable tool to (i) explore ecological dynamics in which there are possible alternative community states, (ii) test the effects of management scenarios, and (iii) inform decision making (Scheffer and Carpenter, 2003; de Young et al., 2008). Several ecological models of marine ecosystems with potential alternative community states have been developed in recent years and applied usefully to management support of real ecosystems (see Mumby et al., 2007; Melbourne-Thomas et al., 2010 for some coral reef examples).

On the east coast of Tasmania in southeastern Australia (cf. map given in Fig. 1.1), shallow (< 35 m depth) exposed rocky reef communities mainly occur in two alternative persistent states: (1) the seaweed bed state characterised by a dense productive canopy of macroalgae; or, (2) as sea urchin 'barrens' habitat characterised by a poorly productive and bare rocky habitat following destructive grazing by the long-spined sea urchin (*Centrostephanus rodgersii*). The establishment of these widespread sea urchin barrens in eastern Tasmania results from a combination of (1) climate-driven range extension of the long-spined sea urchin *C. rodgersii* from Australia's mainland to Tasmania via strengthening eddy activity associated with southern incursions of the tropical East Australian Current (Ling et al., 2009*b*); and (2) the depletion of key predators of the sea urchin by fishing. Large southern rock lobster (*Jasus edwardsii*) individuals constitute the only effective predator of the long-spined sea urchin in Tasmania (Ling et al., 2009*a*). Sea urchin barrens are observed in many temperate regions around the globe (Lawrence, 1975; Mann, 1982; Chapman and Johnson, 1990; Steneck et al., 2004) and constitute an impoverished state compared to productive macroalgal beds in terms of productivity, complexity of habitat and species diversity (Ling, 2008). Since the 1980s, sea urchin barrens up to 10-50 ha in extent have become established in exposed shallow-water regions on the northeast coast of Tasmania as a consequence of destructive grazing by *Centrostephanus rodgersii* (Johnson et al., 2005; Ling et al., 2009*a*). Amongst other Tasmanian reef species, high-value blacklip abalone (*Haliotis rubra*) and southern rock lobster (*Jasus edwardsii*) fisheries, with a combined value of about AUD$150M pa, severely decline on urchin barrens (Johnson et al., 2005).

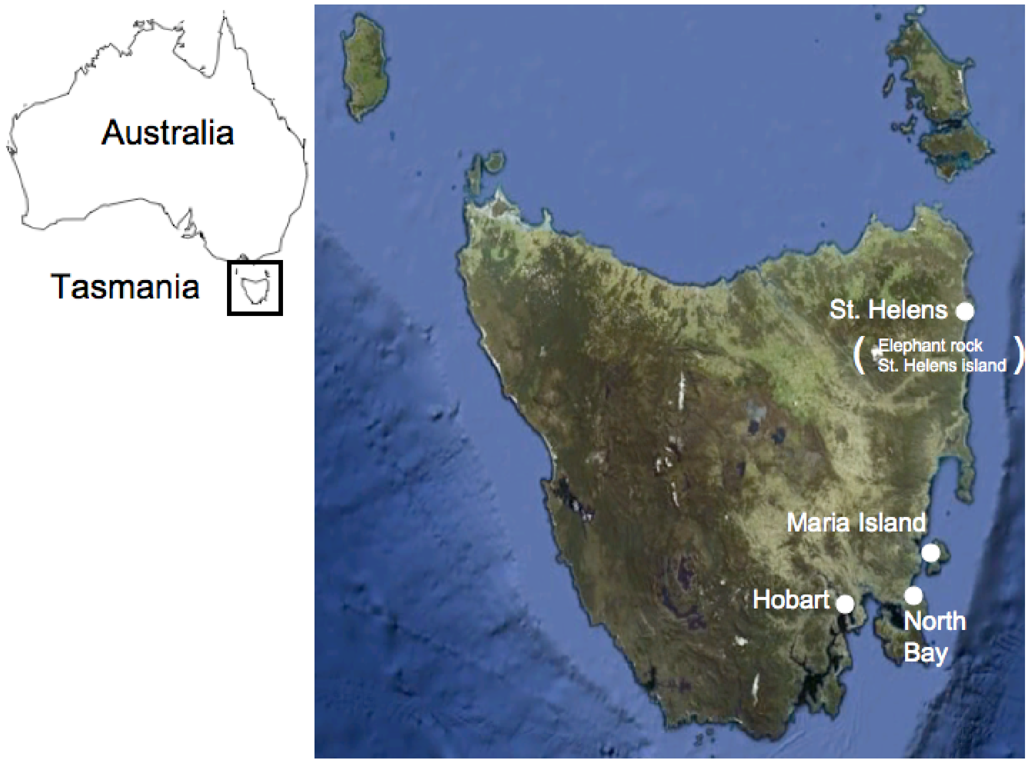

Figure 1.1: Map of Tasmania with the key sites mentioned in the thesis. The top left corner shows the position of Tasmania in the southeastern corner of Australia. Map credits: Google Earth.

The spread of extensive *C. rodgersii* barren is regarded as a principal threat to rocky reef fisheries in eastern Tasmania (Johnson et al., 2005; Pecl et al., 2009; Johnson et al., 2011). However fisheries management is single-species-oriented and does not account for the ecological impacts of *C. rodgersii*. On Tasmanian rocky reefs, manipulative experiments to examine effects of fishing have been carried out at small scales (e.g. 0.25x0.25m to 4x4m plots in Strain, 2009; Strain and Johnson, 2012). While these studies help to refine understanding of the ecology of individual species (e.g. Ling et al., 2009*b*) and a limited number of pairwise interactions (e.g. Strain, 2009), we lack the practical ability to carry out controlled experiments at a complexity and scale sufficiently large to understand how these species and interactions affect the dynamics of the larger system (Schroder et al., 2005). In particular, there is currently no framework to inform management interventions so as to mitigate the ecological effects of *Centrostephanus rodgersii* invasion along the east coast of Tasmania.

This thesis presents a suite of 'minimum realistic' ecological models (Fulton et al., 2003*a*) developed within the boundaries of current knowledge of Tasmanian reef ecology (empirical observations, results of manipulative experiments or existing models; e.g. Punt and Kennedy, 1997; Johnson et al., 2005; Guest et al., 2009; Ling et al., 2009*a*; Strain, 2009). These models are specifically designed to capture the potential for alternative community states characterised as either dense, diverse and productive stands of macroalgae, or poorly productive sea urchin barrens following destructive grazing of macroalgal beds by *C. rodgersii*. The art of building robust, reliable and hence useful ecosystem models lies in making a series of fine choices, which can be difficult to objectively assess (Klepper, 1997). The three primary chapters of this thesis (Chapters 2-4) describe a set of approaches to step-by-step (i) collate and synthesise available information about rocky reef ecology, (ii) develop, parameterise, test and validate a parsimonious simulation model of Tasmanian reef dynamics with alternative community states, and (iii) identify thresholds in ecosystem dynamics and inform effective management interventions.

Through qualitative modelling of community responses to long-term perturbations, Chapter 2 explores and defines generic mechanistic links between positive feedback and the occurrence of alternative states. Positive feedback diminishes a system's overall resistance to change, and can create and maintain correlations in the relative abundance of variables that coincide with alternative states. With specific models of the dynamics of Tasmanian rocky reef communities, which capture effects of climate change, fishing and persistent alternative states, we demonstrate the ability of qualitative modelling to predict the potential for alternative states in ecosystems and thus identify this possibility to managers and inform management intervention. We show that qualitative knowledge of community structure permits a thorough analysis of system feedback and an assessment of the potential for an ecosystem to exhibit alternative states.

While they may be deemed as essential to support decision-making, robust simulation models of ecosystems with alternative states are nonetheless challenging to build, test and validate. Chapter 3 develops TRITON (Temperate Reefs In Tasmania with lObsters and urchiNs), a model of the local dynamics of seaweed-based reefs with alternative community states, and presents simulation-based calibration and analyses of model sensitivity to input parameters. Pattern-Oriented-Modelling, i.e. comparing patterns emerging from model dynamics across Monte-Carlo simulations with large-scale observations of Tasmanian reef communities, provides a valuable approach to validate the dynamics of TRITON. Using the computationally efficient, model-independent extended Fourier amplitude sensitivity test (Saltelli et al., 1999), we rank the influence of key parameters on different aspects of model behaviour. The model validation exercise contributed to both (i) a better understanding of the key drivers of Tasmanian rocky reef dynamics (e.g. fishing of rock lobster), and (ii) identification of priority areas for further work through assessment of model limitations stemming from incomplete knowledge of seaweed-sea urchin-lobster dynamics.

In Chapter 4 we address a range of questions for the management of Tasmanian reef communities using Monte-Carlo simulations with TRITON. First, we use the simulations to help characterise thresholds in community dynamics. These tipping points constitute essential reference points for management to minimise the risk of barrens formation or facilitate the recovery of seaweed beds from the barren state, but it is difficult to directly observe them empirically (see Mumby et al., 2007 for a model-based derivation of thresholds in coral reef dynamics). Distinct differences in community thresholds for the "forward' shift' (i.e. barrens formation from high seaweed cover) and "backward' shift' (i.e. recovery of seaweed cover from the barrens condition) reflect a hysteresis in reef dynamics; once sea urchin barrens have formed extensively, restoration of dense seaweed beds is much more difficult to achieve than prevention of barren formation in the first place. Alternative management scenarios (i.e. a combination of reducing lobster fishing, implementing a maximum legal catch size to protect large lobster individuals as key reef predators, culling of sea urchins and translocating large lobsters from deep to shallow reefs exposed to destructive sea urchin grazing) are assessed both in terms of mitigating the ecological effects of sea urchin grazing and lobster fishery performance. Model simulations highlight the need for the Tasmanian rock lobster fishery management objectives to move away from a single-species-oriented maximum sustainable yield towards a more conservative ecologically sustainable yield that accounts for the ecosystem services delivered by rock lobster to rocky reef communities.

The General Discussion (Chapter 5) summarises all key findings, illustrates the complementarity of the different approaches applied in this thesis to comprehend the dynamics of Tasmanian rocky reefs, including the risks of moving between alternative community states, and attempts to inform an ecologically sound management of the Tasmanian southern rock lobster fishery. Over the last two decades, fisheries scientists have emphasised the necessity to better account for the ecosystem effects of fishing and to shift management practises away from the traditional single species focus towards an ecosystem-based approach (Cury et al., 2005; Smith et al., 2007, 2011). With this simple example from Tasmanian rocky reefs, on which rock lobsters exert essential predation control on sea urchins, we illustrate some of the misleading assumptions of single-species management in circumstances in which the target species delivers key services to the ecosystem. We highlight the need for fishery management targets, such as maximum sustainable yield (MSY), to account for the ecological services delivered by commercial species, and we show that a more holistic and conservative approach to maintain ecosystem functioning, where ecological dynamics can manifest alternative community states and where phase shifts are difficult to reverse, is essential for the long term sustainability of the fishery.

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Chapter 2 Exploring alternative states in ecological systems with a qualitative analysis of community feedback

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Chapter 3 Pattern-oriented validation and sensitivity analysis of a model with alternative community states: A simulation model of ecological dynamics of temperate rocky reefs in Tasmania

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Chapter 4 Alternative states on Tasmanian rocky reefs: Identifying thresholds in community dynamics and assessing management interventions to limit destructive grazing of sea urchins

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Chapter 5 Synthesis: Models to assist ecosystem-based management of rocky reef communities and the rock lobster fishery in eastern Tasmania

This thesis presents a suite of 'minimum-realistic' models (sensu Fulton et al., 2003*a*) developed to inform an ecosystem-based approach to management of rocky reef communities and the associated rock lobster fishery in eastern Tasmania. The modelling approaches build on available information about Tasmanian reef ecology (e.g. empirical observations, field experiments or existing models) to provide improved understanding and prediction of the dynamics of rocky reef communities in eastern Tasmania. From qualitative modelling of community feedback (Marzloff et al., 2011*a*; Chapter 2) to simulations with a parsimonious mean field model of the local dynamics of Tasmanian rocky reefs, key results highlight the need for the Tasmanian rock lobster fishery to move towards an ecosystem-based management that accounts for the important ecological service provided by lobsters in mitigating the effects of sea urchin destructive grazing of seaweed beds. Here the findings of this work are discussed in four sections.

(i) The first considers the value of each modelling approach in improving understanding and prediction of shifts between alternative community states in ecological dynamics.

(ii) In the second section we argue that, when considered together, the spectrum of different models we used, from qualitative to quantitative simulation models, demonstrate valuable complementarity to test model assumptions (structure, formulation, parameterisation) and provides a predictive framework that accounts for both model uncertainty and the variability of ecological dynamics.

(iii) In the third section we highlight the important results that can contribute to sound ecosystem-based management of Tasmanian reefs and the associated rock lobster fishery,

(iv) and in the final section we discuss the ecological impacts of the climate-driven incursion of *Centrostephanus rodgersii* into Tasmanian waters in the broader context of future climate-related changes that might be anticipated in the rapidly-changing marine environment around Tasmania.

5.1 A suite of tools to understand and predict shifts between alternative community states in ecological dynamics

The common focus across the different chapters of the thesis is the development and use of models to better comprehend the dynamics of alternative community states in ecosystems in general, and in eastern Tasmanian rocky reef communities in particular. Identifying and predicting phase shifts in ecological dynamics is a major challenge for ecologists, and the models applied here inform some important aspects of the presence of alternative states in ecosystems. The complementary approaches successively (i) inform the potential for alternative states and their persistence in Tasmanian rocky reef dynamics, (ii) identify the key drivers of community dynamics and decompose the different factors facilitating both the 'forward' shift (from dense and productive seaweed beds to sea urchin barrens habitat) and the 'backward' shift, (iii) characterise important threshold points and the presence of hysteresis in community dynamics, and finally (iv) enable assessment of the effects of alternative management approaches on the long-term state of reef communities and performance of the lobster fishery.

5.1.1 Qualitative modelling, positive feedback and alternative community states

Based only on qualitative knowledge of key variables and interactions, qualitative modelling provides a mechanistic understanding of how each variable's response will be influenced by the feedback properties of a perturbed system. While positive feedback is commonly associated with the concept of alternative community states in the ecological literature, other than simple conceptual diagrams, a causal explanatory framework to formally track the effects of positive feedback on the dynamics of ecological dynamics is often lacking (Scheffer and Carpenter, 2003; Suding et al., 2004). In systems with strong positive feedback, predictions from qualitative modelling can reveal correlations in community responses to sustained perturbations that are consistent with alternative states. In our qualitative models of Tasmanian rocky reefs, patterns in sign responses driven by the presence of positive feedback emerge in the adjoint matrices that are consistent with the alternative community states observed empirically. In considering the broad scale dynamics of Tasmanian shallow reef systems the qualitative approach identified alternative community states as dense seaweed beds supporting high abundance of lobsters or, a sea-urchin-dominated system with greatly reduced seaweed cover and lobster populations at low levels (Johnson et al., 2005; Ling et al., 2009*a*). In focussing on the dynamics of understorey communities beneath the macroalgal canopy, perturbations facilitate the establishment of either a brown- or a pink-benthos state, where abalone are typically lacking from the brown-state, and abundant in the pink-state (Strain and Johnson, 2010).

As exemplified by abalone in the broadscale models of canopy dynamics, model groups that are indirectly influenced by the positive feedback can manifest ambiguous responses, not necessarily in phase with the alternative states. Nonetheless, a thorough analysis of the qualitative adjoint matrix of a system can help detect regular correlations in variable responses, either across a subset of long-term perturbations or a subset of modelled variables. The sets of variables or species that react in phase with alternative community states are of particular interest for ecosystem monitoring and intervention. Thus, qualitative modelling helped to identify the most appropriate variables to reliably track the state of rocky reef communities with regards to sea urchin destructive grazing and on which to focus further quantitative modelling, i.e. they were the three key groups (seaweed assemblage, rock lobster and the sea urchins) involved in the positive feedback driving either the shift from high seaweed cover to sea urchin barrens habitat, or the reverse shift. While demonstration of dominant positive feedback in system dynamics does not constitute absolute proof of alternative persistent states (Scheffer et al., 2001) it nonetheless identifies a strong potential for it. Given the particular difficulties of managing a system in which there exists potential for alternative persistent states and hysteresis, and the heady consequences of phase shift, qualitative modelling is helpful in that it can quickly inform managers of the need for a precautionary approach without the need to develop more complex fully quantitative models which usually require many person-years of expensive empirical effort to parameterise. The qualitative modelling is also useful in identifying the need for dedicated manipulative experiments and/or quantitative modelling to more thoroughly investigate the presence of alternative community states. The approach can also inform about the relative balance between positive and negative feedback necessary for a system to display alternative states.

However, qualitative modelling is limited in what it can show about phase shifts between alternative states, and should be seen as complementary to field experiments or specific quantitative models (Scheffer et al., 2001; Scheffer and Carpenter, 2003). Field experiments or quantitative models are required to characterise the nature of the shift, confirm the existence of alternative states, and identify key thresholds in system dynamics (Scheffer et al., 2001). Nonetheless, the important points are that qualitative modelling (1) can be meaningfully undertaken with basic information about links in a system and before detailed and expensive parameterisation is pursued, and (2) can detect the potential for alternative states in ecosystem dynamics and thus flag the need for a precautionary approach in managing human activities in a system until community dynamics are more specifically and thoroughly investigated.

5.1.2 Calibration and sensitivity analysis of a model with alternative states

While they may be seen as useful, even essential, to support informed decision-making in management, robust simulation models of ecosystems with alternative states are challenging to build and validate. When there are alternative states in model dynamics, if follows that no trivial criteria can provide reliable metrics to assess the goodness-of-fit of such models. Chapter 3 presents a simulation-based validation and analysis of model sensitivity to input parameters of TRITON, the quantitative simulation model developed specifically to study phase shifts between alternative community states in lobster-sea urchin-seaweed dynamics. Pattern-oriented modelling, i.e. comparing patterns emerging from Monte-Carlo simulations of model dynamics with large-scale empirical observations provides a useful approach to calibration (Grimm et al., 2005) and, to a large extent can be accepted as validating the broad-scale dynamics of TRITON.

Using the computationally efficient, model-independent extended Fourier amplitude sensitivity test (Saltelli et al., 1999), we were able to rank the influence of key parameters on model behaviour. Through a set of independent sensitivity tests, the approach to first focus on the model's overall dynamics, and then decompose total model behaviour into the individual features that characterised the ‘forward’ and reverse shifts (van Nes and Scheffer, 2003) was powerful and informative. Rather than using one single global sensitivity test, the set of sensitivity tests provides a comprehensive analysis of the shift between alternative community states in the model. The simulations underlying the sensitivity tests also inform parameter influence on transition times in the model for shifts from one state to the other.

5.1.3 Simulation-based exploration of phase shift in modelled community dynamics, indicating thresholds and management interventions

Monte-Carlo simulation using TRITON helps tackle key questions for managing rocky reef communities in Tasmania by characterising key thresholds. These tipping points define important reference points (e.g. ∼6200 g of lobster. $200m^{-2}$ as the biomass density associated with a 5% chance of barren forming) to mitigate the risk of sea urchin destructive grazing. They also reflect a hysteresis in modelled community dynamics as evidenced by different thresholds associated with the ‘forward’ and the ‘backward’ shifts. Note, however, that because of spatial heterogeneity in ecological dynamics, captured in TRITON through Monte-Carlo simulations, no definite and precise threshold values can define the tipping points in the dynamics of a given ecosystem. If thresholds in ecological dynamics are challenging (Briske et al., 2010; Samhouri et al., 2010; McClanahan et al., 2011), but not impossible (Carpenter et al., 2011), to identify empirically, Chapter 4 suggests that tipping points are not that trivial to apprehend using simulation models. Generalised linear models can identify model groups that best relate to the likelihood of model shift and provide a robust framework to determine threshold points associated with a given level of risk that managers or industry are willing to take. However, community thresholds identified in terms of biomass densities on a local reef (∼100 m^2 to 10 ha) are not straightforward to transpose at the regional scale of fishery management in Tasmania (∼100 km). While estimates of community thresholds cannot directly informed definite target points for current lobster fishery management, Chapter 4 highlights the need for management objectives to minimise the risk of sea urchin grazing. The same Monte-Carlo simulation provides a valuable assessment of the tradeoffs between long-term ecological outcomes and fishery productivity under alternative management interventions. The discrepancies between simulations with TRITON and with the single-species stock assessment model for the rock lobster fishery reveal the need for fishery management to move towards an ecosystem-based approach to account for the key ecological role of rock lobster on Tasmanian rocky reefs.

This thesis illustrates the crucial role that modelling (i.e. qualitative, quantitative or simulation-based assessment of model sensitivity to parameter) can play in better appreciating and understanding alternative community states in ecological dynamics. The models are fundamentally useful to (i) detect the potential for alternative persistent states in reef dynamics from ecosystem feedback properties (providing critical information for managers), (ii) identify the existence of different ecologies and drivers of community dynamics in both the barrens and seaweed-dominated states, (iii) estimate of thresholds in reef dynamics, and (iv) assess the effects of management measures on ecosystem state. The results show clearly that qualitative modelling, the sensitivity analyses of TRITON to input parameters, and results from Monte-Carlo simulations, each contributes original and critical information about alternative states and hysteresis in community dynamics. The modelling is useful in complementing existing knowledge from field observations and empirical experiments. It is an important result that the modelling approaches show complementarity and help to both develop a more comprehensive picture of the potential for alternative states on Tasmanian rocky reef dynamics and to inform management about choices in management responses.

5.2 Assessing model robustness and enveloping uncertainty in model predictions

To provide reliable information and support natural resource management, an ecological model requires both comprehensive testing of in-built assumptions and validation against available information on observed dynamics.

5.2.1 Qualitative Modelling to assess structural uncertainty

Testing for uncertainty in ecological models often focuses on sensitivity analysis of parameter values (Saltelli et al., 2000) while the question of uncertainty in model structure usually remains underestimated at best, or is unaddressed entirely (Laskey, 1996; Dambacher and Ramos-Jiliberto, 2007; Hosack et al., 2008). Chapter 2 emphasises the importance of assessing structural uncertainty in models of complex systems, especially in ecological models where the understanding of system interactions is typically incomplete. In the same sense that testing model sensitivity to parameter values is essential (Saltelli et al., 2000), questioning the qualitative information (e.g. about ecological interactions) used to build models is essential in testing assumptions about the model structure itself (Hosack et al., 2008). Qualitative modelling of feedback properties is well suited to assess structural uncertainty in models of complex systems (Hosack et al., 2008; Metcalf et al., 2008; Hosack et al., 2009). This approach enabled identifying the most parsimonious model structure to address the ecological effects of sea urchin destructive grazing (i.e. the need to include the minimum components of seaweeds, sea urchins and lobsters), and to assess options for management intervention.

5.2.2 Uncertainty in model formulation and parameterisation

Robust model parameterisation is key to any useful simulation framework and represents a major effort behind the development of the TRITON model (Appendix 3B). Even for the best-studied ecosystems, where observational or experimental data can support detailed model parameterisation, quantification of ecological processes is uncertain (Novak and Wootton, 2008), and so testing for model sensitivity to parameter values constitutes an essential ingredient of ecological modelling (Saltelli et al., 2000). Through a set of independent sensitivity tests (Saltelli et al., 1999), model dynamics can be analysed as a whole and decomposed to develop a comprehensive understanding of the key drivers, and assess. While sensitivity analyses based upon each model group can be informative, considering the overall community structure described by the first axis of the PCA on normalised outputs of the different model groups provide a reliable one-dimensional summary to assess sensitivity of model behaviour without having to screen each and every model group.

Pattern-oriented modelling (Grimm et al., 2005) offers a valuable approach to assess and calibrate the dynamics of a model with alternative states in circumstances where no objective quantitative validation criteria can easily be defined. Comparing patterns emerging from Monte-Carlo simulations with large-scale observations of Tasmanian reef communities helped to restrict values of sea urchin recruitment rates to a realistic range so that TRITON behaves as observed on rocky reefs in the ‘real-world’.

Comprehensively testing model assumptions, whether related to model structure, formulation or parameterisation, contributed to both:

(i) a better understanding of the key drivers of modelled community dynamics. Both lobster and sea urchin recruitment, and the level of lobster fishing and removal of sea urchins all emerged as important factors controlling the model's propensity to shift to sea urchin barrens. It is noteworthy that recruitment of both groups is highly dependent on large-scale oceanographic features in eastern Tasmania (Pecl et al., 2009; Johnson et al., 2011) and thus not able to be directly manipulated by human behaviour, while extraction of sea urchins and lobsters from the system is directly under human control;

(ii) and assessment of model limitations due to incomplete understanding of Tasmanian rocky-reef dynamics. Several ecological processes, which are unlikely to highly influence the broad dynamics of phase shifts, are coarsely or not explicitly captured in TRITON. In particular, the dynamics of other guilds and size groups within the seaweed bed community, the effects of storms and wave action on algal cover (Wernberg, 2005; Reed et al., 2011), and greater detail on the effect of sea urchin grazing on macroalgae (described after Hill et al. (2003) in TRITON) and of lobster predation rates on sea urchins across a range of densities of both predator and prey, would require further field observations and experiments to be finely captured in the model.

5.2.3 Accounting for space-time variability and assessing prediction uncertainty through Monte-Carlo simulations

Variability in space and time is a key feature of real ecological dynamics, and needs to be adequately captured in any realistic ecosystem model (Annan, 2001). However, seasonality and the frequency and magnitude of extreme events (i.e. storm surges) (Reed et al., 2011), which potentially play a role in sea urchin barrens formation, are not captured in TRITON because they are difficult to quantify and largely irrelevant to the long-term ecological dynamics of sea urchin destructive grazing. Due to the scarcity of information about temporal variability in most modelled process, the only source of stochasticity through simulations in TRITON comes from interannual variability in rock lobster and sea urchin recruitment rates.

In TRITON the distribution of each model parameter was estimated using data, mostly from Tasmanian-based empirical observations and experiments. Exploration of the 90% confidence interval of each parameter estimate through hierarchical Monte-Carlo simulations (Saltelli et al., 1999) account for uncertainty both, in individual processes captured in the model, and in the overall dynamics that emerge out of the complex interactions between these processes (Laskey, 1996; Melbourne-Thomas et al., 2011*a*; Polasky et al., 2011). Indeed, each set of Monte-Carlo simulations samples any combinations of input parameters, including the most extreme ones. Thus, while environmental variability through space (from reef to reef) is not easy to characterise, these simulations are likely to capture some of this heterogeneity in the environmental conditions found on Tasmanian rocky reef (e.g. in habitat, depth, exposure to urchin larvae, etc.). Assessing uncertainty in model predictions allows us to advise about the expected general consequences of alternative management options rather than prescribe definite recommendations for management (Francis and Shotton, 1997).

Both the qualitative and quantitative simulation modelling reveal the importance of non-trivial indirect effects (e.g. high level feedback or interactions between modelled processes) to the modelled community dynamics. Indeed, while qualitative modelling can track the influence of indirect effects and the contribution of high-level feedback to community dynamics (Marzloff et al., 2011*a*), simulation-based sensitivity analysis suggests that the quantitative model TRITON is mostly sensitive to interactions between modelled processes rather than to direct effects of changes in input parameters. Thus, both the qualitative and quantitative modelling approaches presented in this thesis provide valuable tools to capture and emphasise the importance of indirect responses of the reef community to perturbations, and also to test the non-trivial indirect effects of management interventions and environmental changes on ecosystem state. In keeping with previous work, the dominant influence of interactions between input parameters on model dynamics that we observed is common in models of complex dynamics (Saltelli et al., 1999, 2009). More generally, this thesis highlights the value of ecological modelling to adequately assess complex non-trivial responses of ecosystems to perturbations.

5.3 Towards an ecosystem-based management for Tasmanian rocky reef fisheries

The suite of models built and tested to realistically capture alternative states in seaweed-based reef community dynamics provides valuable information towards a more integrated ecosystem-based management of Tasmanian rocky reef communities and associated fisheries. Overall, these models help detect the potential for alternative community states and identify the key mechanisms driving these shifts. More specifically, they provide a framework to apprehend threshold points in reef community dynamics and test the effects of different management strategies on long-term ecosystem state and fishery productivity.

5.3.1 Qualitative modelling and general information for an Ecosystem-Based Fishery Management

Qualitative modelling can provide valuable insight into the indirect effects of human activities on ecosystem state, and qualitative predictions can help distinguish the most useful variables for both ecosystem monitoring and management intervention (Dambacher et al., 2009; Marzloff et al., 2011*a*; Metcalf et al., 2011). In the thesis, qualitative modelling helped understand the general dynamics of Tasmanian rocky reefs and in particular the potential for alternative community states both, in lobster-sea urchin-seaweed bed dynamics, and in the dynamics of epilithic algal assemblages under the macroalgal canopy: 1) under sustained changes in environmental conditions (e.g. climate-driven increase in sea urchin recruitment) or human impacts (e.g. harvesting of rock lobster), seaweed-based reef communities are predicted to respond towards either a dense seaweed bed supporting a high abundance of lobster or, alternatively, a sea-urchin-dominated barren with reduced seaweed cover and where lobster populations decline (Johnson et al., 2005; Ling et al., 2009*a*); 2) in the dynamics of understorey algal communities, the qualitative predictions suggest that removal of abalone by fishing will locally facilitate the establishment of the brown-benthos state where abalone density virtually collapses (Strain and Johnson, In press). The brown-benthos state, characterised by a matrix of filamentous and foliose algae, semi-consolidated sediment and sessile invertebrates, can overgrow the pink-benthos state dominated by crustose red algae where abalone are abundant (Strain and Johnson, 2010).

These examples show the capacity of qualitative modelling to indicate the general ecosystem effects of fishing rock lobster and blacklip abalone and the climate-driven increase in sea urchin recruitment on the state and well-functioning of Tasmanian rocky reef communities. While useful in generally describing the community effects of fishing (Dambacher et al., 2009), qualitative modelling does not provide any specific recommendations directly relevant to fishery management.

5.3.2 Development of a parsimonious simulation model and scenario testing

The quantitative modelling extends the consideration of broad dynamics illuminated by the qualitative approach to provide more specific recommendations for the lobster fishery. First, the set of global sensitivity analysis tests reveal high contributions to variance in simulation outcomes of parameters associated with lobster fishing, and culling of sea urchins. Along with lobster and sea urchin recruitment rates, harvesting of lobsters and sea urchins highly influences the model's ability to shift from dense seaweed cover to sea urchin barrens habitat, or the capacity for seaweeds to recover on sea urchin barrens, and so harvesting rates emerge as more effective management levers than implementation of a maximum legal size alone. The time for the model to shift from one state to the other is of the order of two to three decades, so it is therefore prudent that management focuses on the prevention of barrens formation rather than on restoration strategies that are unrealistic to implement over lengthy time frames (i.e. decades rather than a few years, which is the time scale of most management plans).

Finally, Chapter 4 provides information for current managers to better account for the important ecological role or 'service' that lobsters provide to Tasmanian rocky reef communities. Estimates of key thresholds in Tasmanian reef communities, which can constitute important reference points to mitigate the effects of sea urchin destructive grazing (e.g. ∼6200 g of lobster. $200m^{-2}$ as the biomass density associated with a 5% chance of barren forming), clearly identify a hysteresis in modelled community dynamics. This hysteresis highlights the need for management to focus on preventing the formation of sea urchin barren rather than on the far more challenging restoration of seaweed beds once extensive barren habitat has established.

When examining thresholds in modelled community dynamics, let us keep in mind that absolute model predictions always need to be considered with caution. It is well-accepted that due to model uncertainty, quantitative model predictions should advise about the expected general consequences of alternative management options rather than prescribe definite absolute recommendations for management (Francis and Shotton, 1997): the precision and the accuracy of absolute predictions from complex ecological models depend on the reliability of all input parameters, hence simulation outcomes are often interpreted in relative terms (e.g. comparisons among alternative scenarios; Smith et al., 2011) rather than as absolute predictions. However, absolute estimates of thresholds in community dynamics are essential to a sound management of Tasmanian rocky reef community, and if managers do not have access to the best absolute estimates that researchers can provide, even with all their caveats, they will make management decisions anyway. The simulations with TRITON, based upon the best available information about Tasmanian reef ecology, currently provide the most reliable and conservative estimates of thresholds in reef community dynamics: indeed, all model parameters were estimated using the latest and most comprehensive sources about Tasmanian rocky reef ecology, so estimates from simulations with TRITON summarise the best currently available knowledge to inform management. Note also that to tackle uncertainty in model prediction, parameter uncertainty has been addressed in both chapters 3 and 4: model sensitivity to input parameters was investigated comprehensively in Chapter 3, while the results presented in chapter 4 are from thousands of Monte-Carlo simulations to fully sample parameter space and account for parameter uncertainty in model predictions. Nonetheless there remains, of course, uncertainty in some assumptions and processes behind the TRITON model. However, decisions while developing the model were always made conservatively. As a consequence, absolute model predictions (and simulation-based estimates of threshold in community dynamics) are conservative in terms of estimating the risk of sea urchin destructive grazing of Tasmanian seaweed beds.

Direct culling of sea urchins together with a reduced harvest of lobsters is the most effective ecological intervention to minimise the impact of *C. rodgersii* grazing on Tasmanian reefs. The dual actions of reducing removal of lobsters and increasing removal of sea urchins is notably more effective than measures aimed solely at building lobster populations (e.g. reduction in lobster fishing or implementation of a maximum legal catch size). An important result of the modelling is that a maximum sustainable yield estimated from the single species stock assessment model does not account for the ecosystem service delivered by larger lobsters. Current management overlooks the potential for some form of depensation effect in lobster population dynamics, i.e. the decrease in recruitment due to the loss of seaweed habitat following sea urchin destructive grazing at low density of large rock lobsters. In this context, this thesis emphasises the need for an ecosystem-based management approach for the Tasmanian rock lobster fishery. While highlighting the need for fishery management to better account for the ecological role of lobster in Tasmanian rocky reef communities and revise key target points accordingly, the range of model simulations provide a valuable assessment of the tradeoffs in terms of both long-term ecological outcomes and fishery productivity associated with alternative management interventions.

5.3.3 Mismatch between the scale of rocky reef dynamics and fishery management

Simulation models constitute useful support tools to manage natural resources, especially as the consequences of alternative regulations or management scenarios are difficult if not impossible to assess experimentally at the spatial and temporal scales of ecological dynamics (e.g. Melbourne-Thomas et al., 2010, 2011*b*). However, in eastern Tasmania commercial fisheries are managed at the scale of regional 'blocks' (scale of 10^3 m), while sea urchins can deplete seaweed beds, create and maintain extensive 'barren' areas at the scale of individual reefs (scales of 10^2 - 10^3 m). While it is clear that *C. rodgersii* represents one of the major threats for Tasmania's subtidal rocky-communities and coastal fisheries (Johnson et al., 2005), a decision-support tool that adequately addresses both the spatial dynamics of sea urchin barrens formation and the effects of lobster fishing and fisheries regulations on the state of reef communities, is currently lacking. Such a tool, structured as a connected network of local models in which each represents the dynamics of individual reefs, is under development to support the management of rocky-reef communities at the scale of the entire east coast of Tasmania (Marzloff et al., 2011*b*). The regional dynamics in the model emerge from the combination of these local dynamics and dispersal of larvae between reef patches. Regional connectivity between reefs is derived from a particle-tracking model based upon patterns of surface circulation (Condie et al., 2005). This framework will to some extent bridge the current gap between the findings presented in this thesis about the dynamics of sea urchin destructive grazing at the scale of individual patches of reef (e.g. threshold points expressed a biomass density of rock lobster, defined in $g.200m^{-2}$), and actual regional management of the Tasmanian rock lobster fishery (under regional catch quotas, defined in Kt for management blocks covering large stretch of coastline). This mismatch between the scale of ecological dynamics and the scale of fishery management currently constitutes a major challenge for the implementation of sound ecologically sustainable management decisions for Tasmanian rocky reef communities.

5.4 Challenges to adapt to climate-driven changes in Tasmanian marine ecosystems around Tasmania

Under climate-driven large-scale changes in global ocean circulation, southeastern Australia, including eastern Tasmania, has been identified as a regional 'hotspot' with the ocean warming about three to four times faster than the global average (Holbrook and Bindoff, 1997; Ridgway, 2007*a*). In particular, the warm nutrient-poor tropical East Australian Current, which sweeps southwards along the East coast of Australia, is intensifying as part of large scale changes to the South Pacific Gyre (Ridgway, 2007*b*). The list of known and potential changes to the Tasmanian marine environment associated with these changes in larger-scale oceanographic features is long and expanding (Johnson et al., 2011). Notably, sea urchin and southern rock lobster recruitment processes in eastern Tasmania, both highly influential parameters underpinning the dynamics of TRITON, are largely determined by large-scale climate-driven oceanographic features (Banks et al., 2007; Bruce et al., 2007; Ling et al., 2009*b*; Johnson et al., 2011). Like many other species migrating poleward from Australia's mainland coast to Tasmanian waters (Redmap, 2010; Johnson et al., 2011), the long-spined sea urchin is now fully established, viable and, in some areas of northeast Tasmania, the dominant species on shallow reefs (Johnson et al., 2005, 2011). Populations of the sea urchin are constantly expanding, both in abundance and in space along the east coast of Tasmania (Ling, 2008; Ling et al., 2009*b*). Conversely, in eastern Tasmania there is some evidence that southern rock lobster larvae, ostensibly supplied from Victorian and possibly South Australian populations (Bruce et al., 2007), and lobster recruitment have declined over the last five to six years with the intensification of the East Australian Current (Johnson et al., 2011), although the trend is far from established. Accordingly, most long-term projections for southern rock lobster assumed more frequent failures in annual recruitment and predict a decline in populations in eastern Tasmania (Pecl et al., 2009; Johnson et al., 2011). While in the coming decades Tasmanian reef communities may see a partial substitution of southern rock lobster with their more northern counterpart, the eastern rock lobster (*Sagmariasus verreauxi*), precise predictions of shifts in species distribution and abundance are lacking and these climate-driven changes can only be described in broad qualitative terms.

C. rodgersii barrens currently constitute a pressing concern for managers of reef communities and fisheries in Tasmania (Johnson et al., 2005; Pecl et al., 2009; Johnson et al., 2011). However, *C. rodgersii* is just one species among many others expanding their range to establish populations in Tasmania (Redmap, 2010), but whose ecosystem impacts are unknown. In the coming decades, climate-driven changes are likely to bring more surprises to Tasmanian rocky reefs, and challenging surprises for associated fisheries and their managers. The expected changes to come have the capacity to affect virtually every physical attribute of marine ecosystems in the Tasman Sea from nutrient load, temperature, salinity and pH, to biological components including plankton, seaweeds, other components of benthic communities, and ecosystems supporting pelagic fishes (Johnson et al., 2011).

Appendix A Derivation of parameter estimates for the local TRITON (Temperate Rocky reef communities In Tasmania with lObsters and urchiNs) model

A.1 Introduction

A.1.1 Context of the model: units, temporal and spatial scales

The variables in this local model of Temperate Rocky reef communities In Tasmania with lObsters and urchiNs (TRITON) are expressed in biomass density (g.200 m^{-2}). The default parameterisation corresponds to a 200 m^2 reef area, as both a coherent spatial scale on which to capture reef community dynamics and the most common scale used for underwater surveys and experiments available to inform model dynamics. Biomass is given as wet weight, which is often directly available from experiments or technical reports and represents an ecologically sound unit for trophic interactions (e.g. Christensen and Walters (2004)). Rates of change, defining population dynamics and trophic interactions, are given as annual.

For each parameter, we define a mean estimate as well as a probability distribution (e.g. uniform with a minimum and maximum bounds or normal with mean and standard error) to account for parameter uncertainty through Monte-Carlo simulations (e.g. Saltelli et al. (1999)).

A.1.2 Functional groups

The number of groups and/or species in the model is kept to a minimum (seaweed assemblage, sea urchin, rock lobster; see chapter 3) so as to focus on the impact of grazing by the invasive long-spined sea urchin *Centrostephanus rodgersii* on Tasmanian subtidal reef communities (Marzloff et al., 2011*a*). The model explicitly includes southern rock lobster, the main predator of the sea urchin in Tasmanian waters, to assess the community effects of alternative management strategies for this key Tasmanian fishery.

A.1.3 Appendix structure

This appendix details the parameterisation of all the processes explicitly modelled in TRITON and is organised in four main sections: (A.2) population dynamics of each of the three groups; (A.3) trophic interactions; (A.4) model closure and factors implicitly accounted for in TRITON; (A.5) Limitations and guidance for future research.

A.2 Population dynamics

A.2.1 Logistic population dynamics

Population dynamics following a logistic growth function can be expressed as:

$$\frac{dB}{dt} = \alpha B \left[\frac{K - B}{K}\right], \tag{A.1}$$

with B, biomass density (g. 200 m^{-2}); K, carrying capacity (g. 200 m^{-2}); α, intrinsic growth rate (year^{-1}); t, time expressed in year.

Defining logistic population dynamics

The following equation defines an analytical solution to Eq. A.1 (Kot, 2001):

$$B(t) = \frac{K}{1 + \beta \exp(-\alpha\, t)}, \tag{A.2}$$

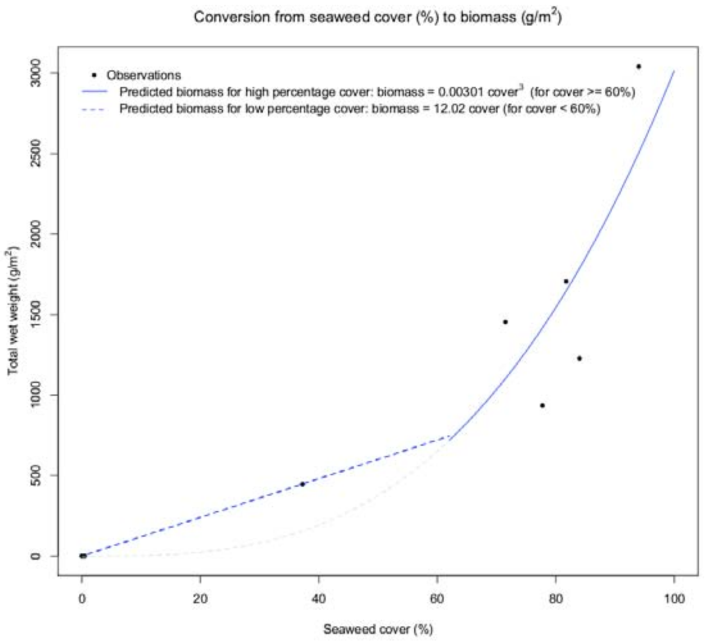
with $\beta = \frac{K - B_0}{B_0}$, where B_0 is the initial biomass density at time t=0.

Using observations of population biomass density through time (e.g. Fig.A.2 for the seaweed bed) standardised to a 200 m^2 area, the intrinsic growth rate α, the carrying capacity K and the constant β from Eq. A.2 were estimated using the non-linear least square function *nls* of the R language for statistical computing, version 2.12 (R Development Core Team, 2010).

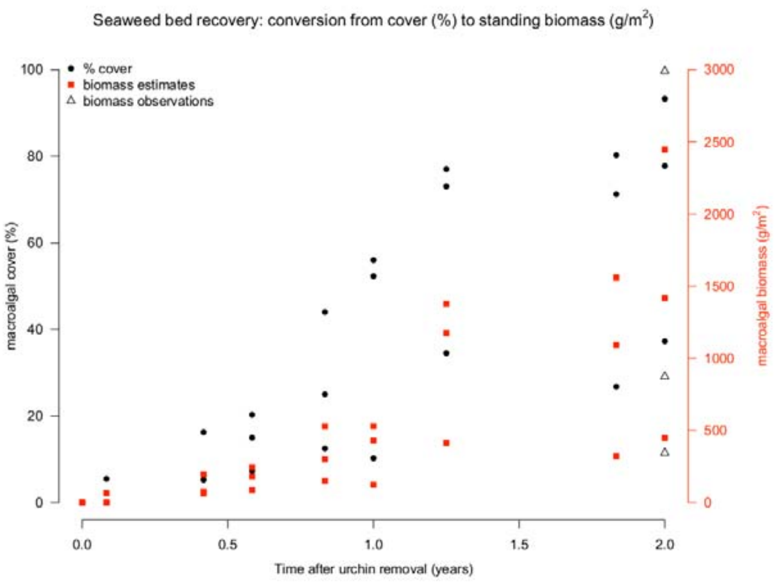
Seaweed bed logistic growth

Data Seaweed bed dynamics was defined based on data of seaweed bed recovery following the removal of grazers (Ling, 2008). The first step involved translating these data reported in percentage cover into wet biomass density of the seaweed bed (see Fig.A.1).

Parameter estimates Note that in one of the 3 experimental sites the seaweed bed did not significantly recover for various reasons (shade and unsuitable reef properties; S.D. Ling, personal communication). This site was ignored when fitting the logistic growth function (Fig.A.2). Parameter estimates for seaweed bed logistic dynamics (Eq.A.2) are given in Table A.1.



a)



b)

Figure A.1: a) Conversion from percentage cover (%) to biomass density (g.m^{-2}) for Tasmanian seaweed beds (*Ecklonia radiata, Phyllospora comosa*; Ling, unpublished data). b) Seaweed bed recovery data from Ling et al (2008), aggregated across quadrats for 3 experimental sites. The data originally in percentage cover (in %; black dots) were converted to biomass density (in g.m^{-2}; red squares).

Table A.1: Parameter estimates for the seaweed bed logistic growth function (Eq.A.2).

	Estimate	Standard error	t value	$Pr(>\|t\|)$
α_{SW}	4.43	1.65	2.690	0.0168
β_{SW}	1.35e+02	2.18e+02	0.621	0.5439
K_{SW}	3.4e+05	3.6e+04	9.488	9.94e-08

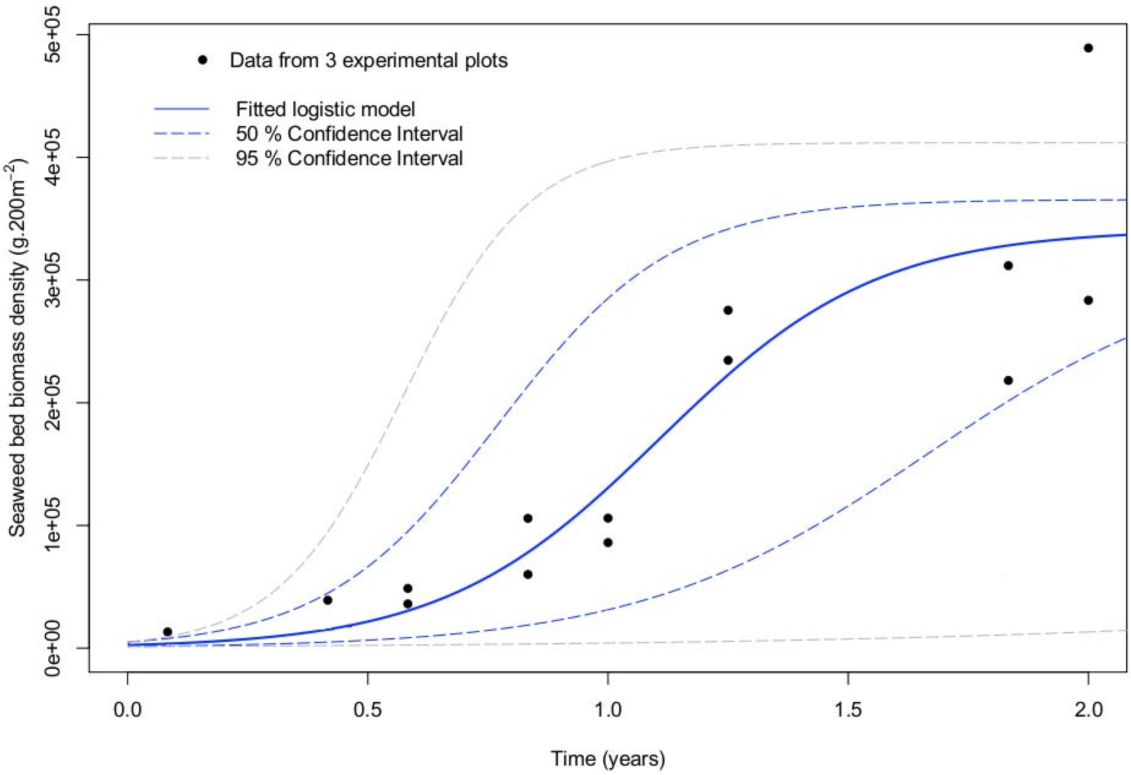


Figure A.2: Logistic growth model (with 50 and 95% confidence intervals) fitted to data of seaweed bed recovery following urchin removal (Ling, 2008). Light conditions and marginal habitat features did not allow the seaweed bed to recover at one of the three sites, which was excluded from this analysis. Depth: 9-15 m.

Limitations and other references Intrinsic growth rate for various temperate seaweed species are reported to vary from c. 4 to 7 year^{-1} under optimal conditions (Mohn and Miller, 1987; Lobban and Harrison, 1996).

Carrying capacity of temperate seaweed beds, i.e. maximum biomass density, can vary significantly depending on light (depth), exposure to swell, temperature and algal composition. Our estimate of maximum biomass density (wet weight) falls within the low range of reported values for carrying capacity of temperate seaweed beds: 4 kg kelp.m^{-2} in

Nova Scotia (Lauzon-Guay et al., 2009); 6-18 kg.m^{-2} for *Ecklonia radiata* beds in Western Australia (Kirkman, 1984).

In Tasmanian waters, *E. radiata* beds are the most at risk of destructive grazing by *C. rodgersii*. Several studies have measured individual *E. radiata* plant growth and productivity (Kirkman, 1984, 1989; Sanderson, 1990). *E. radiata* plant growth is often compared to a conveyor belt of tissue moving from the meristematic region near the stipe of the plant towards the extremity of the blades where it erodes (Sanderson, 1990). If both tissue production and erosion can be measured for *E. radiata* seaweed beds, the effects of urchin grazing on individual macroalgae is poorly known so this information available about the dynamics of individual macroalgae was not directly usable in TRITON. Additionally, other processes (e.g. wave action especially during storms) are not accounted for explicitly in the model. These processes can potentially erode macroalgal plants as much as sea urchin grazing (Reed et al., 2011). Seaweed bed dynamics and sea urchin grazing on macroalgae in particular would require some dedicated field experiments in the future to better represent sea urchin destructive grazing in the model.

Urchin logistic growth

Data The long-spined sea urchin has progressively extended its natural range southwards along the east coast of Tasmania over the last decades. *C. rodgersii* has progressively settled through time in Tasmania along a north-south gradient. From large-scale surveys of *C. rodgersii* population size-structure along the East coast of Tasmania (Johnson et al., 2005; Ling and Johnson, 2009), information about sea urchin population age and biomass density could be derived at different sample sites to describe population growth (Fig.A.3). Substituting space for time, this data provides information about urchin population dynamics (biomass building following first settlement). The 90% quantile of population age distribution is used as an estimate of the elapsed time since first settlement of *C. rodgersii* at a given site.

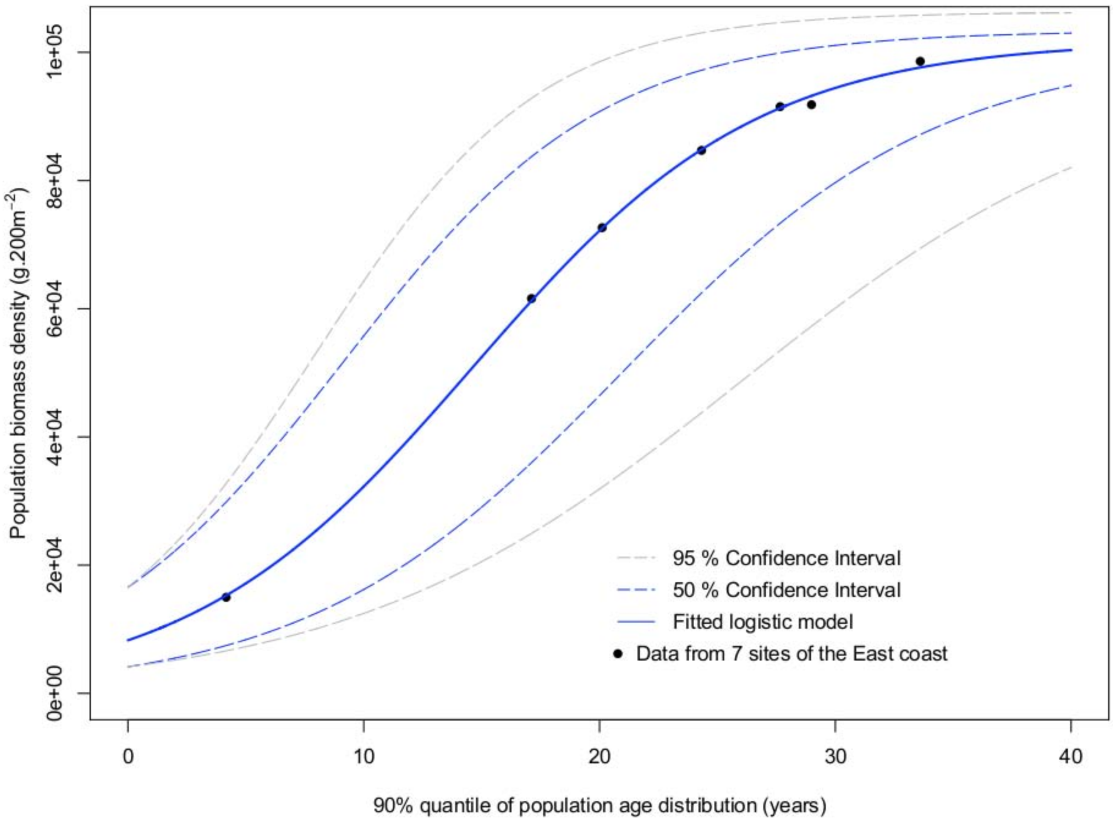


Figure A.3: Logistic growth model (with 50% and 95% confidence intervals) fitted to data from large-scale survey of *C. rodgersii* population on the east coast of Tasmania (Johnson et al., 2005; Ling and Johnson, 2009). The 90% quantile of population age distribution is used as a proxy for the time elapsed since first settlement of the urchin.

Rock lobster logistic growth

Data The Maria Island and Tinderbox marine reserves were implemented in 1991 and reef communities within the reserve have been monitored regularly following protection from fishing (Barrett et al., 2007; Edgar et al., 2009). Biomass density of lobster through time in these two reserves (Fig.A.4) is derived from size-structured survey of invertebrate abundance using the following length-weight relationship for southern rock lobster (*Jasus edwardsii*): $B = 0.000271\, L^{3.135}$ (Punt and Kennedy, 1997) relating individual lobster biomass (B) in grams to carapace length (L) in mm.

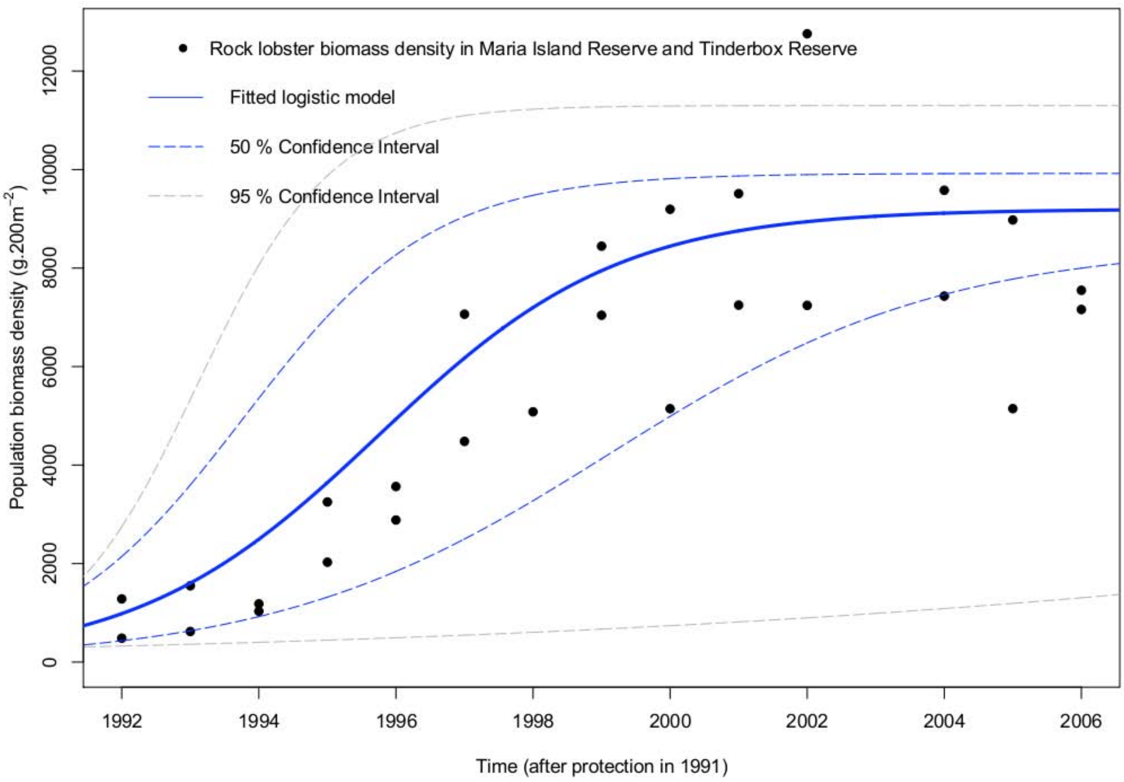


Figure A.4: Logistic growth model (with 95% confidence intervals) fitted to data from surveys of rock lobster mean biomass density in Maria Island and Tinderbox marine reserves following protection in 1991 (Barrett et al., 2007; Edgar et al., 2009)

A.2.2 Size-structured population dynamics

Both sea urchin and rock lobster dynamics are size-structured in TRITON. Thus, while figures A.3 and A.4 present the data used to fit sea urchin and rock lobster population dynamics, the following section provides the estimates of the parameters defining sea urchin and rock lobster population dynamics in the model. Size-structured population dynamics are defined for rock lobster and sea urchin populations based upon information about individual growth function (size-dependent mean and standard deviation of growth increment) and natural mortality rates (e.g. Punt and Kennedy, 1997). Length-weight relationships were required to convert from abundance to biomass to accomodate our biomass-based modelling approach.

Defining size-structured population dynamics

A size-structured population model with n size classes can be written for any class s as:

$$B_{s,t+1} = B_{s,t} \times \exp(-\beta) + \sum_{j=0}^{s} \left[\delta'_{s,j} B_{j,t}\right] - \sum_{i=s+1}^{n} \left[\delta_{i,s}\right] B_{s,t} \ (+r_t,\ \mathit{if{:}}\ s\ =\ \mathit{1}) \tag{A.3}$$

with $B_{s,t}$, biomass density of size class s at time t (g.200 m^{-2}); $\delta'_{i,j}$, biomass-based transition probability from size class j to i, (element of the i-th row, j-th column of the transition probability matrix; in $year^{-1}$); $\delta_{i,j}$, abundance-based transition probability from size class j to i (year-1); β, natural mortality ($year^{-1}$); r_t, recruitment rate into the first size class at time t (g.200 $m^{-2}.year^{-1}$). The size-structured population model relies on a transition probability matrix representing biomass fluxes between size classes. Size-structured population dynamics is defined following a stepwise process: 1) definition of recruitment variability (parameterisation of a stochastic function); 2) definition of the growth transition probability matrix; and 3) estimating mean recruitment rate and natural mortality by fitting simulated size-structured dynamics to available data.

Recruitment stochastic function Recruitment to the first size class is expressed as an additive stochastic term. Interannual variability in the magnitude of recruitment can be adequately represented using a lognormal stochastic function (M. Haddon, pers. comm.; see Eq.A.4). Lognormal stochastic recruitment rate at time t can be written as:

$$r_t = \mu \exp(\gamma + \sigma \times \epsilon) \tag{A.4}$$

with μ, mean recruitment rate (g.200 $m^{-2}.year^{-1}$); γ and σ, mean and standard deviation of the lognormal stochastic function defining the magnitude of interannual recruitment variability; ϵ, a random term following a normal distribution of mean 0 and standard deviation of 1; γ and σ can be derived from the mean m and the variance v of the observed lognormally-distributed variable as: $\gamma = log(m^2)/\sqrt{v + m^2}$ and $\sigma = \sqrt{\log(v/(m^2 + 1))}$. First, the standard deviation $\sqrt{v}$ of the observed lognormal distribution describing recruitment variability is informed using available time series, literature or expert opinion so as to derive γ and σ. We assume a mean m of 1 to centre the stochastic function on the statistically-estimated value of μ. Then, the mean annual recruitment rate μ and the natural mortality rate β are statistically estimated to optimise the fit of size-structured dynamics model against observations (Fig. A.3 and A.4).

Growth transition probability matrix Transition probability matrices are derived from individual growth functions describing size-specific growth increments (Punt and Kennedy, 1997). By definition, the matrices are abundance-based, i.e. apply to number of individuals present in each size class. Individual elements of the transition probability matrix ($\delta_{i,j}$ from Eq.A.3) are defined as:

$$\delta_{i,j} = \begin{cases} 0 & \text{if: } i < j \\ Pr\Big(L_j + \Delta_j \in \Big]L_i - \frac{c}{2}; L_i + \frac{c}{2}\Big]\Big) & \text{if: } i¿= j \end{cases} \tag{A.5}$$

with $\delta_{\mathrm{i,j}}$, abundance-based transition probability from size class j to i (year^{-1}); L_i, mean individual length in size class i (mm); ΔL_i, annual growth increment in size class i follows a normal distribution with mean and standard deviation derived from the individual growth function (mm.year^{-1}); c, width of each model size class (mm). To account for individual body growth in biomass, we represent incoming biomass from size class j to size class i using a biomass-based transition probability defined as $\delta'_{i,j} = \delta_{i,j} \times \frac{b_i}{b_j}$ with $\delta'_{\mathrm{i,j}}$, biomass-based transition probability from size class j to i (year$_{-1}$); $\delta_{\mathrm{i,j}}$, abundance-based transition probability from size class j to i (year^{-1}); b_i and b_j, mean individual biomasses in size classes i and j, respectively.

Mean recruitment and natural mortality rates The size-structured population dynamics model (Eq.A.3) is finally fitted to time series of species biomass density in order to estimate the most likely set of recruitment and natural mortality rates. The range of values explored is derived from literature for the natural mortality rate and from parameter estimates of fitted logistic model for the mean recruitment rate. The natural mortality rate β essentially influences the transfer efficiency of biomass from small into large size classes, while the mean recruitment rate μ regulates biomass influx into the first size class, hence restricting the maximum biomass density of the population (i.e. carrying capacity). Model residuals can be computed against each observation of biomass density at a given time t. A sum of squares of these residuals is estimated for each Monte-Carlo simulation and used as a measure of model likelihood.

Urchin size-structured dynamics

Variability in *C. rodgersii* annual recruitment on the East coast of Tasmania The early stages of *C. rodgersii* larvae can only develop if water temperature is above

12°C (Ling et al., 2008). Therefore, mean sea surface temperature in late winter (when sea urchin larvae disperse and settle) provides a good proxy for the likelihood of good recruitment. Time series (1970-2007) of sea surface temperature in Maria Island were used to characterise the frequency of annual recruitment events on the east coast of Tasmania for the recent decades (Fig.A.5). A binomial function brings stochasticity to sea urchin annual recruitment with a 0.4 probability of successful recruitment any given year (proportion of winters with sea surface temperature above 12°C; see Fig.A.5).

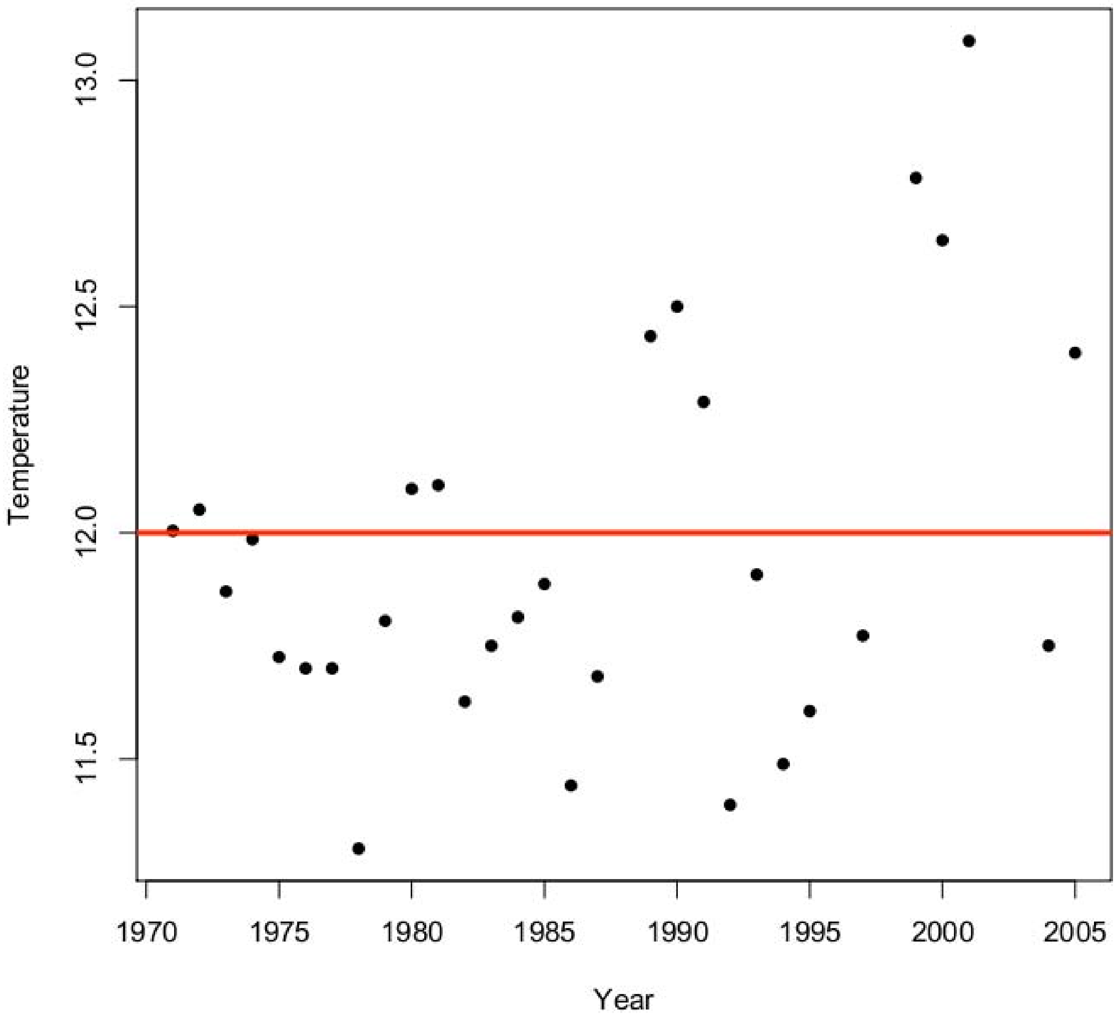


Figure A.5: Time line of mean sea surface temperature at Maria Island during winter months (August-September, i.e. time of spawning for *C. rodgersii*). The red line represents the 12°C threshold for urchin larvae to develop.

A lognormal stochastic function ($\gamma_{CR} = -0.15$; σ_{CR}= 0.5) is applied to scale the magnitude of annual recruitment rate in successful years. It captures the remaining interannual variability in recruitment to the first size class in the model (which depends on both larval settlement and juvenile survival). No specific records of variability in sea urchin annual recruitment exists in Tasmania, so the lognormal stochastic recruitment function was defined to mimic the frequency of good recruitment years indicated from field observations (about 1 or 2 good recruitment events per decade; Andrew and Underwood, 1989; CR Johnson and SD Ling, pers. comm.) and information for other urchin species (Hernandez et al., 2010).

Growth transition probability matrix The transition probability matrix is derived from a generalised inverse logistic growth model for *C. rodgersii* in fringe macroalgal habitat (Ling and Johnson, 2009). Ling and Johnson (2009) fitted a generalised growth function to describe *C. rodgersii* growth increment in jaw lengthΔ L as a function of jaw length L_t at time t, as follows:

$$\Delta L_t = \frac{\Delta L_{max} \times \Delta t}{1 + \exp\left[\log(19)\frac{L_t - L_{50}^m}{L_{95}^m - L_{50}^m}\right]} + \epsilon_{L_t} \tag{A.6}$$

withΔL $_{\text{max}}$ = 2.599, maximum annual growth increment; $\mathrm{L_t}$, initial length at time t; Δt, elapsed time; $L_{50}^m = 17.994$, $L_{95}^m = 27.290$, parameters defining the shape of the inverse logistic model; $\epsilon_{\mathrm{L_t}}$, additive and normal error term of mean 0 and standard deviation $\sigma_{\mathrm{L_t}}$ defined as:

$$\sigma_{L_t} = \frac{\sigma_{max} \times \Delta t}{1 + \exp\left[\log(19)\frac{L_t - L_{50}^m}{L_{95}^m - L_{50}^m}\right]} \tag{A.7}$$

with σ_{max}= 0.244.

Estimating mean recruitment and natural mortality Monte-Carlo simulations with the population dynamics model were completed with sets of mortality and mean recruitment rates covering the range of possible values (natural mortality rate β_{CR} in 0.05-0.22 year^{-1}, after Lauzon-Guay et al. (2009); mean recruitment rate μ_{CR} in 1000-20000 g.200m^{-2}.year^{-1}). The goodness of fit of the size-structured population dynamics model was assessed against available data of population biomass density since time of first settlement of the urchin (see Fig.A.3; data from Ling et al., 2009*b*). Table A.2 provides the 10% most likely sets of mean recruitment and natural mortality parameters for sea urchin size-structured dynamics model. Fig.A.6 compares the distribution of sea urchin biomass density across all size classes in simulation with observations in northeastern Tasmania on long-established barrens grounds (Ling et al., 2009*b*). Table A.2 gives the mean estimates of natural mortality and recruitment rates on which the simulated distribution is based.

Table A.2: Parameter estimates for sea urchin (*C. rodgersii*) size-structured population dynamics model (cf. Eq.A.3 and Eq.A.4).

	Unit	Mean	Range
Natural mortality β_{CR}	year^{-1}	**0.11**	0.1-0.15
Mean recruitment rate μ_{CR}	g.200m^{-2}.year^{-1}	**4100**	2500-10000

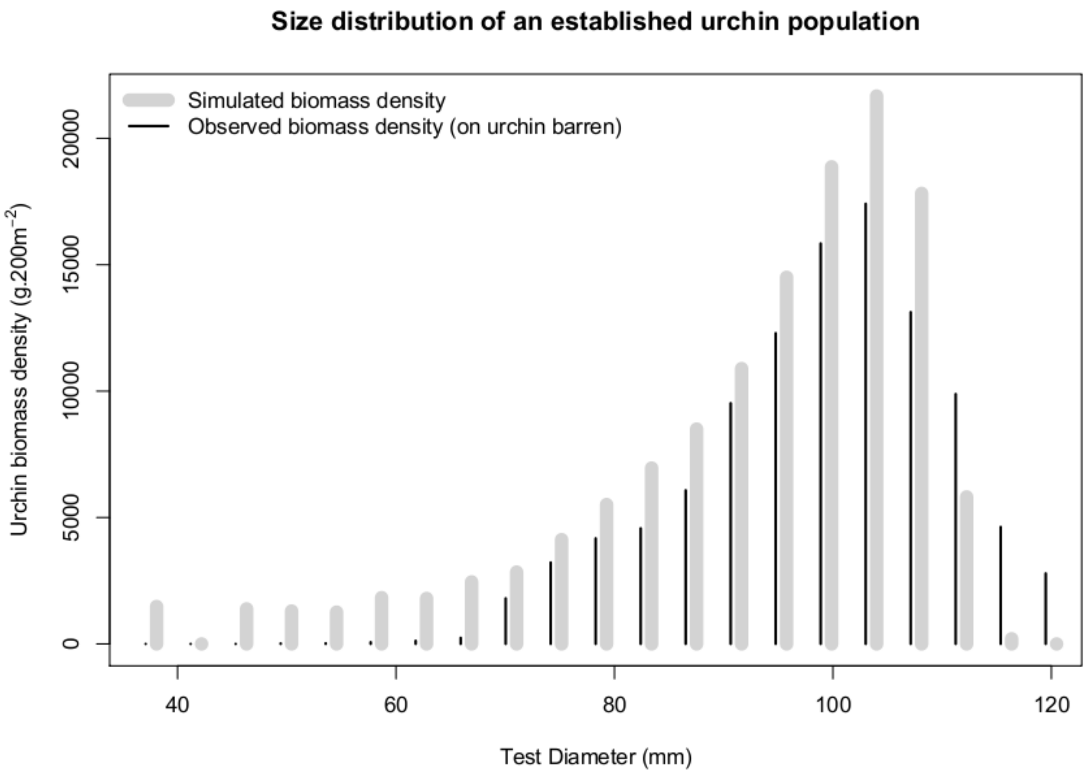


Figure A.6: Distribution of sea urchin biomass density across all modelled size classes for a fully-established urchin population (barrens state). Biomass densities (in g.200 m^{-2}) are from simulations using mean parameter estimates from Table A.2 (in grey), and from surveys at St Helens, northeastern Tasmania (in black; after Ling et al., 2009*b*).

Length-weight and allometric relationships Jaw length (JL in mm) can be converted to test diameter (TD in mm) as follows: $TD = 4.12 \times JL$ (Ling et al., 2009*b*).

The following length-weight relationship relates urchin biomass (B) in g to test diameter (TD) in mm: $B = \alpha \times TD^{\beta}$ with $\alpha = 0.00267$ (± 0.00042 standard deviation) and $\beta = 2.534$ (± 0.034 standard deviation) (data from Ling et al., 2009*b*).

Rock lobster size-structured dynamics

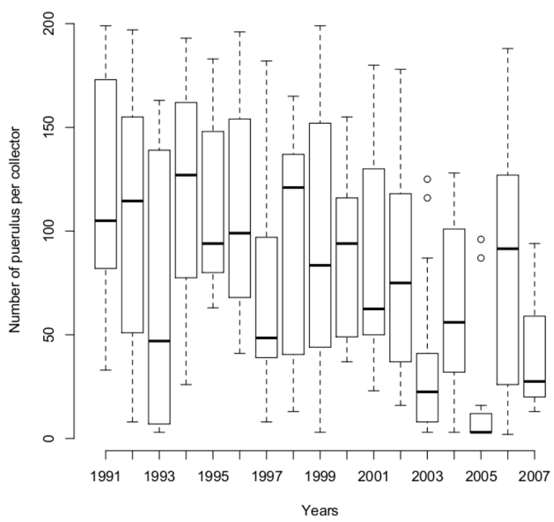
Variability of rock lobster annual recruitment on the East coast of Tasmania Lobster recruitment variability is assumed to follow a lognormal stochastic function (M. Haddon, pers. comm.; see Eq.A.4). Estimates of lobster recruitment are available from puerulus collectors on the east and southeast coast of Tasmania (Fig.A.7a and b) and from the southern rock lobster stock assessment model for the central east coast of Tasmania (Fig.A.7c). A lognormal stochastic function with standard deviation σ_{RL} of 0.6 (mean of the different estimates from Table A.3) defines inter-annual variability in lobster recruitment.

Table A.3: Estimates of the standard deviation of the lognormal distribution describing lobster recruitment inter-annual variability. Assuming a standard deviation of 0.593 coefficients for lobster stochastic recruitment function are $\gamma_{RL} = -0.15$ and $\sigma_{RL} = 0.55$ (Eq.A.4).

Site (recruitment data)	Standard Deviation
Bicheno puerulus collectors	0.52
Southeast puerulus collectors	0.53
Stock assessment for block 2	0.73

Growth transition probability matrix Lobster individual growth (mean growth increment and standard deviation) is described by third degree polynomials in the Tasmanian southern rock lobster stock assessment model (McGarvey and Feenstra, 2001). These growth functions are sex-specific and vary seasonally and spatially for each management block. Growth transition probability matrices $\mathrm{M_{s,z,t}}$ can thus be computed for each sex s, zone z and period t of the year following Eq.A.5. We averaged these matrices to produce annual transition probability matrices for each management zone across both sexes and all 4 periods of the year (because this level of details was unnecessary in our ecological model of Tasmanian reef dynamics) as follows:

$$M_z = \sum_{s=1}^{2} \Big[\prod_{t=4}^{t=1} M_{s,z,t} \Big] \times \frac{1}{2} \tag{A.8}$$



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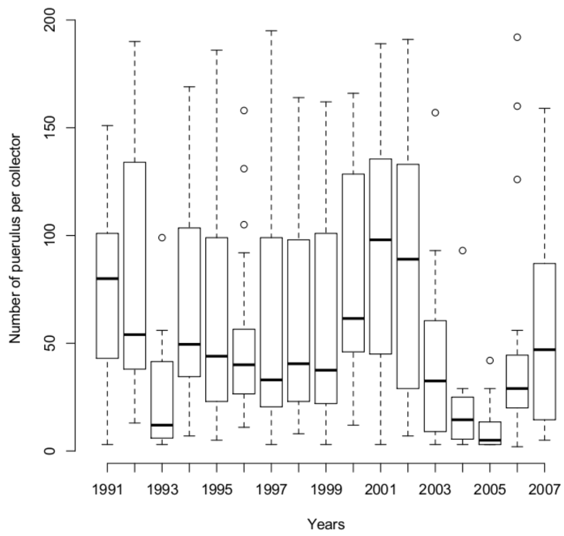

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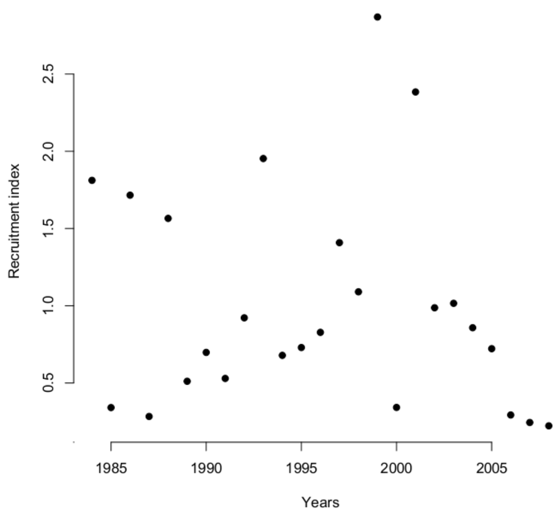


c)

Figure A.7: Estimates of mean annual lobster recruitment on the east coast of Tasmania from puerulus collectors (Frusher, unpublished data) in a) Bicheno and b) in southeastern Tasmania from 1991 to 2007 and b) from the lobster stock assessment for management block 2, central east coast of Tasmania (Gardner, unpublished data).

For all simulation results presented in this thesis, the rock lobster size-structured model is based on the polynomial growth function for management block 2 (central east coast) in the Tasmanian rock lobster assessment model (K. Hartmann, pers. comm.; McGarvey and Feenstra, 2001).

Estimating mean recruitment and natural mortality Monte-Carlo simulations with the size-structured population dynamics model were completed with sets of mortality and mean recruitment rates covering the anticipated range of values (natural mortality rate β_{RL} in 0.1-0.3 year^{-1}, after Frusher et al. (2008) and Frusher and Hoenig (2003); mean recruitment rate μ_{RL} in 50-2000 g.200m^{-2}.year^{-1}). The goodness of fit of the lobster size-structured population dynamics model was assessed against data of lobster population biomass recovery from underwater surveys following the establishment of the Maria Island marine reserve (see Fig. A.4; data from Barrett et al., 2009; Edgar et al., 2009). Table A.4 provides statistics of the 10% most likely sets of mean recruitment and natural mortality parameters for the lobster size-structured dynamics model. Fig. A.8 shows the distribution of rock lobster biomass density across all size classes i) in simulations based on mean estimates of natural mortality and recruitment rates and ii) as observed in Maria Island marine reserve 10-15 years after protection from fishing (2000-2007) (Barrett et al., 2009). Note that due to the low sample size in the surveys, aggregation of data in 5 mm bins of carapace length results in an uneven distribution of biomass density across all sizes (Fig. A.8). The distribution of the biomass density from simulations (in grey) is discontinuous across the small size classes because of the stochasticity of annual recruitment rate μ_{RL} to the first size class.

Table A.4: Parameter estimates for southern rock lobster size-structured population dynamics model (cf. Eq.A.3 and Eq.A.4).

	Unit	Mean	Range
Natural mortality β_{RL}	year^{-1}	**0.23**	0.20-0.26
Mean recruitment rate μ_{RL}	g.200m^{-2}.year^{-1}	**350**	200-800

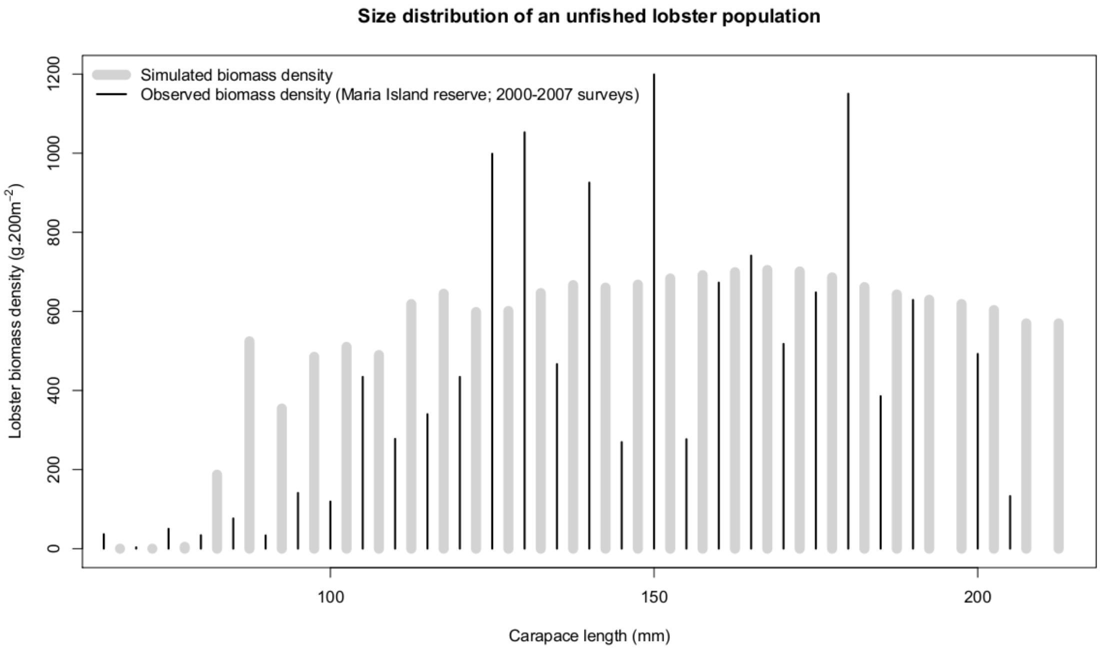


Figure A.8: Distribution of rock lobster biomass density across all modelled size classes. Biomass density (in g.200 m^{-2}) are from simulation based on mean parameter estimates from Table A.4 (in grey) and from visual surveys in Maria Island in 2000-2007 (in black; after Barrett et al., 2009).

A.2.3 Lobster dependency on the state of the seaweed bed

The rationale behind scaling lobster population dynamics by the local extent of barrens habitat relies on expert opinion and empirical evidence (e.g. Guest et al., 2009) suggesting that dense seaweed beds provide an essential habitat and source of food to rock lobster (directly and indirectly in hosting a range of small invertebrates species). Recruitment of juveniles is possibly facilitated by the presence of a seaweed canopy that provides a three-dimensional structure for the pelagic larvae to settle. Therefore, barrens formation is likely to induce a significant loss of productivity and/or recruitment for lobster population (Johnson et al., 2005; Ling, 2008).

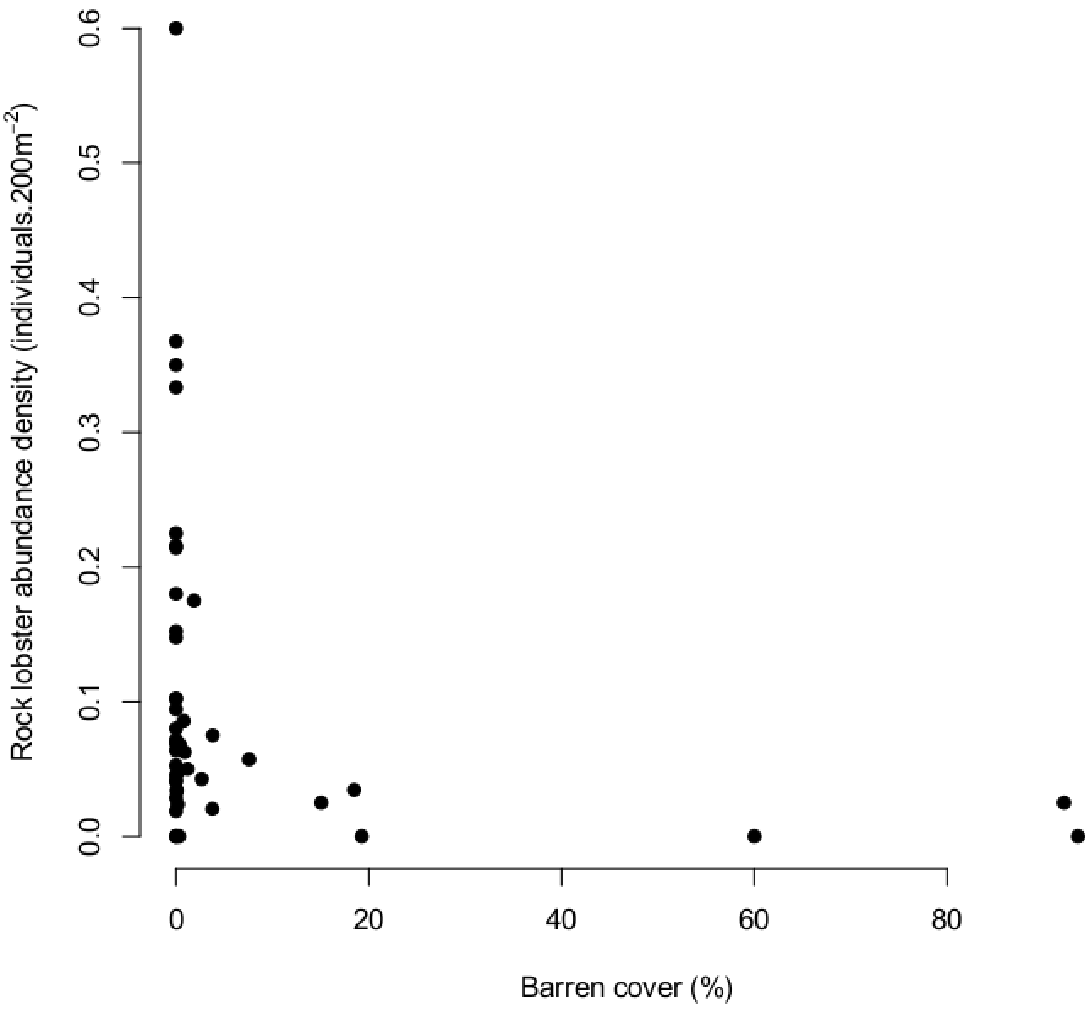


Figure A.9: Sea urchin barrens percentage cover against rock lobster density. These data from large-scale surveys of *C. rodgersii* barrens on the east coast of Tasmania are aggregated by subsite (Johnson et al., 2005).

Correlative data from large-scale survey A large-scale survey of sea urchin barrens was conducted in 2000 along the east coast of Tasmania from the Kent group (Bass Strait) to Recherche Bay (southeastern Tasmania) (Johnson et al., 2005). Sampling was hierarchically structured with 16 primary sites (13 on Tasmanian mainland; three in the Furneaux Islands group) approximately equidistant every 25-30 km along the linear coastline, which were each sub-sampled at 3 sub-sites ca. 0.3-0.5 km apart. For each sub-site, divers surveyed i) seaweed cover and composition, ii) barrens area, and densities of iii) sea urchins, iv) rock lobsters and v) abalone to 1 m on each side of four 100 m transect lines. Data were aggregated at the sub-site level (mean across all 4 transects) to quantify rock lobster population reliance on the state of the seaweed bed. The original survey data used to quantify lobster dynamics on the state of the seaweed bed is presented in Fig.A.9.

To match the scaling coefficient that defines lobster population dynamics dependency to seaweed bed in the model, barrens cover was translated into seaweed bed biomass density using the conversion factor presented in Fig.A.1a. Size was not reported for lobster individuals, so abundance density was assumed to be linearly related to biomass density (unit of model state variable). To obtain an estimate between 0 and 1, both lobster and seaweed bed densities were expressed as relative densities standardised by the maximum observed density.

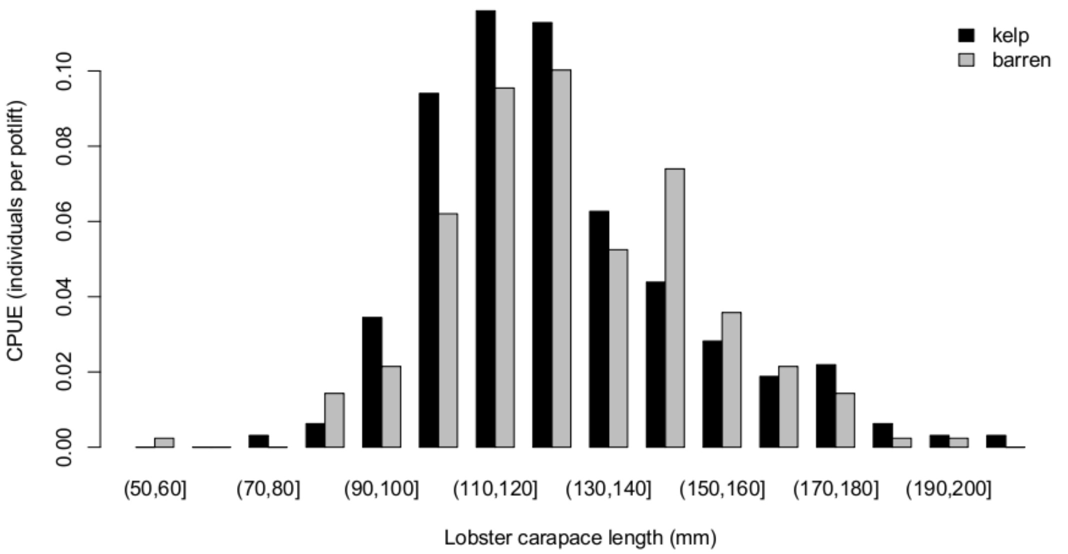
The relationship between extent of barrens (we used seaweed cover as biomass density for consistency with explicit model groups) and lobster abundance is characteristic of a factor-ceiling distribution. Therefore, analysis techniques for triangular distributions were applied to quantify the relationships between extent of barrens and lobster abundance (Thomson et al., 1996; Koenker and Park, 1996). We used the non linear quantile regression function *nlrq* (Koenker and Park, 1996) from R's *quantreg* package (R Development Core Team, 2010) to estimate the three parameters of a n-th power function defined as: $B_{RL} = \alpha + \beta(B_{SW})^{\gamma}$ with $\mathrm{B_{RL}}$ rock lobster relative density and $\mathrm{B_{SW}}$ seaweed bed relative biomass density.

Comparing catch data in barrens and kelp habitat An alternative and more conservative approach to scale lobster dynamics to the state of the seaweed bed relies on fisheries-independent estimates of lobster abundance (size-specific catch per unit of effort) in both kelp and barrens habitats. Large lobsters were translocated onto extensive sea urchin barrens areas off the coast of Tasmania. The experimental site at Elephant Rock was closed to fishing for the past three years to gauge the efficiency of translocating deep sea lobsters (carapace length (CL) superior to 140 mm) as a management option to restore seaweed habitat from fully-established urchin barren (Johnson, unpublished data). Both translocated and resident lobster populations were sampled bi-annually using fishing traps. Note, that the extensive sea urchin barrens at Elephant Rock has adjacent kelp habitat in the shallow (depth inferior to 12 m), which is typical of extensive *C. rodgersii* barrens on the east coast of Tasmania.

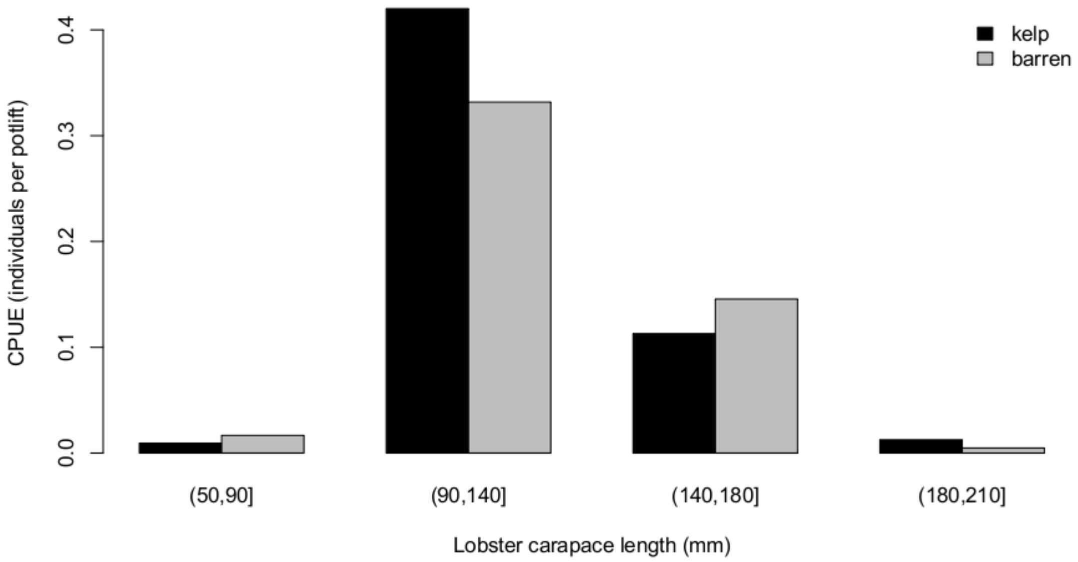
Catchability estimates vary between the two habitats (barrens versus seaweed beds) with lobster being more catchable on barrens grounds (more mobile and possibly foraging more actively). Capture-mark-recapture modelling of tagged animals in the Elephant Rock experimental site provides habitat-specific estimates of catchability coefficients (as percentage of the population sampled through potting) across all size classes of lobster. Depending on the assumptions of the fitted model (independent population on barrens and seaweed bed habitat; single population with individuals migrating between the two habitats), the estimated percentage of the population sampled by pot-fishing vary between 1.4 (+/- 1.7) - 9.9 (+/- 10.0) % in the kelp bed or 7.5 (+/- 2.3) - 11.6 (+/- 2.8) % (+/- standard error) on barrens habitat. Ratio in catchability between the two habitats (kelp bed versus barrens ground) estimates to be 0.18 to 0.85. Similar work on habitat (barrens versus kelp bed)-specific catchability for American rock lobster in Nova Scotia suggests a ratio of 0.766 of catchability in kelp bed relative to barrens habitat (Miller, 1989) .

Figure A.10 shows the size-structured distribution of catch per unit of effort in both habitats. To interpret these data in terms of effects of barrens habitat on lobster population abundance and dynamics, we excluded the lower (carapace length $<$ 90 mm) and upper (carapace length $>$ 180 mm) tails of the size distribution because of the low sample size (less than 0.02 individuals per potlift). Additionally, only the abundance of smaller size classes of lobster (carapace length inferior to 140mm) is lower on barrens ground than in adjacent kelp beds (see Fig. A.10). The abundance of large lobsters (carapace length $>$ 140 mm) looks similar in both habitats. This suggests that large lobsters do equally well in both habitats. Therefore, only lobster recruitment is scaled by the state of the seaweed bed in the model.

To account for the effects of clustering the catch data across individual sizes, we used different levels of aggregation (size classes of 10 or 20 mm, or 4 size classes defined as: 50 - 90 mm; 90 - 140 mm; 140 - 180 mm; 180 - 210 mm; cf. Table A.5) to compare the abundance of lobster on barrens ground compared to adjacent seaweed beds. The abundance of small size classes of lobster (carapace length between 90 - 140 mm) on barrens is 0.76 (+/- 0.13 standard deviation; $\beta_{RL,SW}$ parameter in TRITON) times the abundance of similar sizes in the adjacent seaweed beds.



a)



b)

Figure A.10: Size-structured catch per unit of effort (individuals per potlift) in the Elephant Rock experimental area following protection from fishing in both seaweed (black) and barrens (grey) habitats.

Table A.5: Size-Structured catch per unit of effort (CPUE; the unit is individuals per potlift) in the St Helens experimental site following protection from fishing for resident lobsters onlye (translocated animals are excluded). We use different levels of aggregation across size classes for both seaweed bed and sea urchin barrens habitat. The ratio of $CPUE_{barren}$ to $CPUE_{kelp}$ provides a proxy for the effects of extent of barrens on lobster abundance. The ratios of CPUE account for differences in catchability in the two habitats; indeed, catchability estimates from Elephant Rock suggest that 9.9 % of the resident population was sampled through potting in the kelp bed against 11.6% on barrens ground.

	Lobster CL (mm)			
	50-90	90-140	140-180	180-210
$CPUE_{kelp}$	0.01	0.42	0.113	0.01
$CPUE_{barren}$	0.02	0.33	0.146	0.004
$CPUE_{barren}/CPUE_{kelp}$ (corrected for catchability)	1.52	0.67	1.10	0.32

Lobster CL	Width of size classes	Mean of $CPUE_{barren}/CPUE_{kelp}$ (+/- Standard deviation)
Raw catch data		
90-130 mm	20 mm	0.753 (+/- 0.145)
130-190 mm	20 mm	0.999 (+/- 0.353)
90-140 mm	10 mm	0.766 (+/- 0.117)
40-180 mm	10 mm	1.187 (+/- 0.423)
Catch data corrected for habitat-specific catchability		
90-130 mm	20 mm	0.64 (+/- 0.12)
130-190 mm	20 mm	0.85 (+/- 0.30)
90-140 mm	10 mm	0.65 (+/- 0.10)
40-180 mm	10 mm	1.01 (+/- 0.36)

A.3 Trophic interactions

A.3.1 Sea urchin grazing on seaweed

Data The estimate of *Centrostephanus rodgersii* grazing rate on seaweed was derived from a feeding experiment completed *in situ* in New-South-Wales (Hill et al., 2003). For 4-5 days, individual sea urchins were fed a range of algal species similar to those encountered on Tasmanian rocky-reefs.

Parameter estimate Overall, daily consumption of seaweed per individual sea urchin (of test diameter between 80 and 90 mm) was 3.23 g (Hill et al., 2003). Using the length weight relationship for *C. rodgersii* in Tasmania ($B = 0.00267 \times TD^{2.53}$ with B individual biomass in g; TD test diameter ranging from 75 to 95 mm to conservatively envelop uncertainty), the biomass-based sea urchin grazing rate on seaweed, $\beta_{SW,CR}$, was 5.94 ($\pm$ 1.10 standard deviation) year^{-1} (i.e. g of seaweed. g of urchin^{-1} .year^{-1}).

Comparison with other estimates of grazing rates In a model of urchin feeding fronts in Nova Scotia, Canada (Lauzon-Guay et al., 2009), grazing rate is a constant and takes values of either zero, or a positive constant once sufficient individuals gather to form a feeding front. The assumption that sea urchins have to aggregate to a threshold density for efficient grazing does not apply to *C. rodgersii* grazing on Tasmania rocky-reefs, as *C. rodgersii* does not form feeding aggregations. Destructive grazing of seaweed beds appears to occur as the sum of independent grazing by individual urchins.

Our estimate of urchin grazing rate from Hill et al. (2003) is of the same order as other studies of temperate sea urchin species, even though the mean value is almost twice half that on feeding fronts in Nova Scotia (rate of 10.9 g of seaweed. g of urchin^{-1} .year^{-1}) (Lauzon-Guay et al., 2009). This reflects a difference in the per capita intensity of urchin grazing in Tasmania compared to destructive grazing in feeding fronts consuming northwestern Atlantic seaweed beds.

Functional response The effects of grazing rate formulation can have significant effects on the behaviour of marine ecosystem models (Fulton et al., 2003*b*). Experiments have identified consequences of grazing by temperate sea urchin to be density-dependent (Hill et al., 2003; Wright et al., 2005). In models of plant-grazer dynamics, a range of density-dependent functional responses have been used to represent the grazing terms, including both Holling type III (e.g. Scheffer et al., 2008) and Holling type II (e.g. Sommer, 1999) functional responses. However, quantitative observations or experimental evidence are lacking to guide the choice of the most appropriate functional response for grazing by *C. rodgersii* in Tasmania. In particular, knowledge of the effects of both seaweed and urchin biomass density on *C. rodgersii* grazing rate is lacking. However, our sensitivity analysis indicates that the influence of grazing rate and its formulation on model dynamics is minor relative to other parameters such as lobster predation rates on urchin, recruitment rates or fishing mortality.

For the purpose of simplicity and in the absence of supporting data, the intensity of urchin grazing in TRITON is simply assumed to be linearly proportional to sea urchin biomass density. The use of this simple representation of urchin grazing on seaweed is justified because our model focuses on the top-down effect of urchin grazing as a destructive process depleting Tasmanian seaweed beds. The actual intake of food through grazing does not affect sea urchin population dynamics in the model since sea urchin populations are able to feed on drift materials and sustain high biomass density on barrens in the absence of standing macroalgae (Ling and Johnson, 2009).

Limitations and future improvements The contribution of storm events to the depletion of kelp beds is not explicitly addressed in our model. It is possible however that storm events may significantly facilitate barrens formation with swell action physically removing large macroalgal individuals (Reed et al., 2011), which supply propagules to the environment as well as shelter for juvenile plants. However, this phenomenon is currently little documented and quantified around Tasmania.

Kelp blades can have a whip lashing effect on sea urchin in exposed reefs (Clemente and Hernandez, 2008). However, *C. rodgersii* has been observed to climb up individual plants, so that adult macroalgae do not attain a size refuge. *C. rodgersii* also graze on the holdfast binding the plant to the reef, which can cause loss of biomass. In term of long-term biomass loss, the effects of urchin grazing on adult plants may well be as important as on juvenile ones, although further observations are required to represent the effects of urchin grazing on individual macroalgae with finer details. In summary, we assume that the whole pool of seaweed is grazed upon by sea urchins, as size-specific availability of seaweed to urchins is not currently quantified.

A.3.2 Lobster predation on sea urchins

Lobster predation rates on sea urchins

Data from *in situ* predation experiments Survivability estimates of sea urchins were available from a tagging experiment within and outside two marine reserves on the East coast of Tasmania, where rock lobsters are the only effective predator of *C. rodgersii* (Ling et al., 2009*a*). Urchin biomass density was relatively even across all sites (48 tagged urchins were released in each site). Despite some contrasts in lobster density between sites (especially between fished and unfished areas), fitting predator-dependent functional responses (Skalski and Gilliam, 2001; Kratina et al., 2009) of sea urchin mortality due to lobster predation was not meaningful . Note that 1) the density of sea urchins is very low in this manipulative experiment (about 20 times sparser than observed density in barrens habitat), and that 2) sea urchin survival in fished areas, where predation-capable lobster abundance is very low, does not provide information about lobster predation but rather about other sources of mortality. Some estimates of lobster predation on urchin can be derived from this data (Table A.7) but it is essential to keep in mind that the density of urchin was very low in this experiment.

Data from DNA analysis of lobster faeces at two experimental sites Data from DNA analysis of prey items in lobster faecal pellets provided an alternative source of information about the frequency of lobster predation events on urchin (Redd et al., 2008). Samples of lobster faecal pellets were collected from two experimental sites (Redd, unpublished data) at Elephant Rock near St Helens (594 samples) and North Bay on the Forestier Peninsula (692 samples), where extensive and incipient sea urchin barrens occur respectively.

However, these data require cautious interpretation as rock lobster faeces can be positive to DNA of the sea urchin through scavenging of sea urchin remains, or ingestion of *C. rodgersii* faecal pellets from the sediment. Thus, presence of urchin DNA in the sediment constitutes a possible source of false positives.

Potential false positives in the DNA signal was accounted for in several ways.

(i) Weak positive signals are excluded as likely artefacts by using a threshold number of polymerase chain reaction (PCR) cycles (Kevin Redd, pers. comm.). A threshold of 40 cycles was chosen to exclude these weak positive signals. Comparison of predation estimates based upon DNA analysis against estimates calculated from the observed decline in urchin density at the North Bay experimental site supports the choice of this threshold.

(ii) To minimise the risk of false positives due to scavenging activity on urchin decaying carcasses, we exclusively considered DNA information for large lobster individuals capable of preying on any size of *C. rodgersii* individuals (Carapace length >= 140 mm). On average in recorded encounters of lobsters and sea urchins in the field, S.D. Ling observed 5 scavenging events for 4 predation events for small size classes of lobster, while larger size classes (carapace length >= 140 mm) did not demonstrate scavenging behaviour (data from video monitoring of predation events in Maria Island reserve; see Ling et al. (2009*a*)).

All these filters for false positive were applied to faecal pellets positive to *C. rodgersii* DNA for large lobster individuals. Thus, despite the potential for false positives, the DNA-based estimates of predation presented here (see Table A.7) are conservative.

DNA from *C. rodgersii* is detectable in rock lobster faecal samples within seven hours and up to 60 hours after ingestion (Redd et al., 2008). The proportion of lobsters feeding on the urchin (30.4 - 50.2 % of large lobster individuals eat a sea urchin every 60 hours) indicates that a large rock lobster eats 44 - 73 urchins per year. This corresponds to an overall biomass-based estimate of lobster predation rate on *C. rodgersii* of 7.5 (+/- 2.6; standard deviation) year^{-1} (i.e. g of urchin/ g of lobster/ year) across all DNA samples. Please refer to Table A.7 for site-specific estimates of predation from DNA assays of lobster faecal pellets.

Estimates of predation rates Overall, the different estimates of lobster predation from predation experiments, DNA analysis and declines in sea urchin abundance at experimental sites with known densities of predation-capable lobsters are in agreement (i.e. of the same order with values ranging from 0.3 to 9.4 g of urchin per g of lobster per year; cf. Table A.7). For the DNA-based estimates, data are only presented for large lobster (carapace length > 140mm).

Table A.7: Estimates of lobster predation rates (g of sea urchin / g of lobster / year) on sea urchins based from different data sources. Large lobsters correspond to individuals with a carapace length >=140mm.

Data source	Mean	Std. Dev.
Tagging experiment		
All lobster	0.29	0.14
Large lobsters	0.64	0.3
DNA analysis of faecal pellets	(Large lobsters)	
Elephant Rock site	9.40	3.00
North Bay site	5.71	1.82

Functional response A range of alternative functional responses dependent on lobster and urchin biomass density (Holling type I, II or III) were fitted to urchin mortality estimates using the *nls* function of the R language for statistical computing, version 2.12 (R Development Core Team, 2010). Shape of the functional response was estimated using biomass density estimates of lobster and sea urchin across all sizes (as opposed to size-specific functional responses). The most likely functional responses were selected using both Akaike and Bayesian Information Criteria. Currently available data were not sufficient to objectively inform the most adequate functional response for lobster predation.

Therefore, the most common functional responses used to describe decapod predation were reviewed from published literature (cf. Table A.8). Dependency of predation rate on lobster density (i.e. allowing for interactions among lobsters in their access to prey as described by the Beddington-De Angelis functional response; van der Meer and Smallegange, 2009) was ignored due to low contrast in lobster density in the data. Only Holling Type I, II and III functional responses were fitted to available estimates of lobster predation rate on *C. rodgersii* (cf. Table A.7).

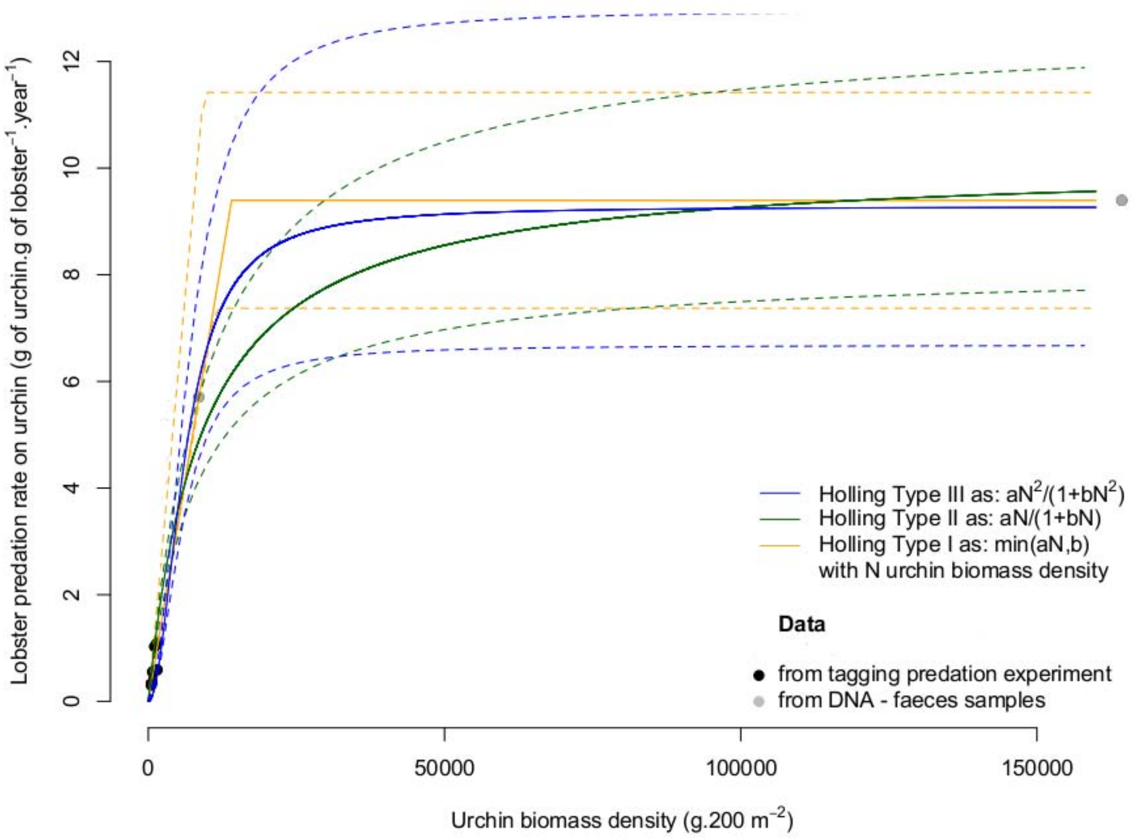


Figure A.11: Estimates of lobster predation rate on *C. rodgersii* and fitted Holling Type I (orange curve), II (green curve) and III (blue curve) functional responses to urchin density. Data from predation experiments (Ling et al., 2009*a*) in marine reserves are shown in black and data from DNA analysis of lobster faecal pellets in grey. The dotted lines represent the 50% confidence interval of the fitted functional responses.

Table A.8: Functional responses used to describe decapod predation rates. In general, a Type II functional response is well-suited if handling time is limiting at low prey density, whereas Type III responses are more appropriate if encounter probability is more likely to be limiting.

Predator	Prey	Functional response	Size-specific	Reference
American lobster *H. americanus*	Green sea urchin *S. droebachiensis*	Type III	All size	Breen, 1974; Evans and Mann, 1977 Hagen and Mann, 1992
American lobster *H. americanus*	Green sea urchin *S. droebachiensis*	Type II	Large prey only	Breen, 1974; Evans and Mann, 1977 Hagen and Mann, 1992
Shore crabs *C. maenas*	Mussel *M. edulis*	Beddington-DeAngelis (predator density-dependence)		van der Meer and Smallegange, 2009 Smallegange and van der Meer, 2010
Shore crabs *C. maenas*	Mussel *M. edulis*	Type III		Griffen and Delaney, 2007
Blue crab *C. sapidus*	Clams *M. arenaria, M. balthica*	Type III (field)		Seitz et al., 2001
Crab *C. irroratus*	Scallop *P. magellanicus*	Type II (lab.) Type III (field)	Evidence of size-structured interactions	Barbeau et al., 1998 Wong et al., 2010 Wong and Barbeau, 2006
Crabs *C. sapidus*	Clams *M. arenaria, M. balthica*	Type III (lab.) Type II (field)		Eggleston et al., 1992 Iribarne et al., 1995
Crab *C. sapidus*	Oysters *C. virginica*	Type III		Eggleston, 1990

Parameter estimates Table A.9 presents parameter estimates for the Holling type I, II and III functional responses of lobster predation on urchin.

Table A.9: Parameter estimates for the Holling Type I, II and III functional responses of lobster predation on sea urchins, $\beta_{CR,RL}$, (g of CR. g of RL^{-1}. year^{-1}) defined with N sea urchin biomass density (g.200m^{-2}) and where β and β' are scalars defining the shape of the functional response. Data from the in situ predation experiment (Ling et al., 2009*a*; Ling and Johnson, In press) and DNA analysis of lobster faecal pellets (Redd, unpublished data).

	Estimate	Standard error	t value	$Pr(>\|t\|)$
Holling Type I as $\beta_{CR,RL} = min(\beta\, N, \beta')$				
β	6.68×10^{-4}	2.27×10^{-5}	29.4	1.35×10^{-8}
β'	9.40	3.00		
Holling Type II as $\beta_{CR,RL} = \frac{\beta\, N}{1+\beta'\, N}$				
β	11.09×10^{-4}	1.68×10^{-4}	6.62	0.0003
β'	1.10×10^{-4}	0.20×10^{-4}	5.61	0.0008
Holling Type III as $\beta_{CR,RL} = \frac{\beta\, N^2}{1+\beta'\, N^2}$				
β	2.35×10^{-7}	0.55×10^{-7}	4.32	0.0035
β'	2.50×10^{-8}	0.60×10^{-8}	3.92	0.0058

Size-structured predation of lobster on sea urchin

Predation of rock lobsters on sea urchins is size-structured reflecting that the size of a lobsters' first pair of walking legs limits its ability to handle sea urchin (Ling et al., 2009*a*). To capture this physical threshold restricting predation, the minimum rock lobster carapace length (CL_{min}, in mm) required to predate upon sea urchin individuals of a given test diameter (TD, in mm) was defined after Ling et al. (2009*a*) as $CL_{min} = \alpha \log(TD) - \beta$ with $\alpha = 43.48$ and $\beta \in [48.91; 71.01]$ (mean of 59.96; standard deviation of 15.63).

Table A.10: Summary of all parameter estimates and confidence intervals for TRITON.

Parameter	Units	Estimate	Standard error	Confidence interval
Seaweed bed logistic growth				
α_{SW}	year^{-1}	4.43	1.65	$1.72 - 7.14$
K_{SW}	g SW.200 m^{-2}	3.4×10^5	3.6×10^4	$2.8\times10^5 - 4\times10^5$
μ_{SW}	g SW.200 m^{-2}.year^{-1}	**5000**		$2500 - 10000$

with α, intrinsic growth rate; K, carrying capacity; μ, mean annual recruitment rate.

Sea urchin size-structured population growth
Growth transition matrix derived from Ling and Johnson, 2009.
β is the annual natural mortality; μ, the mean annual recruitment rate.

β_{CR}	*year*$^{-1}$	**0.11**		$0.1 - 0.15$
μ_{CR}	g CR.200 m^{-2}.year^{-1}	**4100**		$2500 - 10000$

The annual stochastic recruitment function follows a binomial with a 0.4 probability of success, which is combined with a lognormal with a standard deviation σ_{CR} of 0.5.

Lobster size-structured population growth
Growth transition matrix derived from McGarvey and Feenstra, 2001.
β is the annual natural mortality; μ, the mean annual recruitment rate.

β_{RL}	*year*$^{-1}$	**0.23**		$0.20 - 0.26$
μ_{RL}	g RL.200 m^{-2}.year^{-1}	**350**		$200 - 800$

The annual stochastic recruitment function follows a lognormal with a standard deviation σ_{RL} of 0.6.

Lobster dependency on the state of the seaweed bed
Lobster recruitment is scaled by: $(1-\beta)\times(1-\frac{B_{SW}}{K_{SW}})$
with B_{SW}, seaweed bed biomass density; K_{SW}, seaweed bed carrying capacity.

$\beta_{SW,CR}$	constant	0.64	0.11	$0.46 - 0.83$

Parameter	Units	Estimate	Standard error	Confidence interval
Urchin grazing rate				
$\beta_{SW,CR}$	g SW.g CR^{-1}.$year^{-1}$	5.94	1.10	$4.13 - 7.75$
Functional responses of lobster predation on urchin				
With B_{CR}, urchin biomass density (g. $200m^{-2}$): Holling Type I as $\beta_{CR,RL} = min(\beta B_{CR}, \beta')$				
β	g RL^{-1}.$year^{-1}$	6.68×10^{-4}	2.27×10^{-5}	6.31×10^{-4} - 7.05×10^{-4}
β'	g CR.g RL^{-1}.$year^{-1}$	9.40	3.00	4.46 - 14.33
Holling Type II as $\beta_{CR,RL} = \frac{\beta B_{CR}}{1+\beta' B_{CR}}$				
β	g RL^{-1}.$year^{-1}$	11.09×10^{-4}	1.68×10^{-4}	8.34×10^{-4} - 13.85×10^{-4}
β'	g CR^{-1}	1.10×10^{-4}	0.20×10^{-4}	7.76×10^{-5} - 14.19×10^{-5}
Holling Type III as $\beta_{CR,RL} = \frac{\beta (B_{CR})^2}{1+\beta' (B_{CR})^2}$				
β	g CR^{-1}.g RL^{-1}.$year^{-1}$	2.35×10^{-7}	0.55×10^{-7}	1.46×10^{-7} - 3.25×10^{-7}
β'	g CR^{-1}.g CR^{-1}	2.50×10^{-8}	0.60×10^{-8}	1.47×10^{-8} - 3.60×10^{-8}

Allometric and other size-based relationships

Length-weight relationship for the long-spined sea urchin
$B = 0.00267 \times TD^{2.534}$,
with B, urchin individual weight (g); TD, urchin test diameter (mm).

Length-weight relationship for the southern rock lobster
$B = 0.000271 \times CL^{3.135}$,
with B, lobster individual weight (g); CL, lobster carapace length (mm).

Size-Structured predation of lobster on urchin
$CL_{min} = 43.5 \times \log(TD) - \beta$, with $\beta \in [48.91 : 71.01]$
with CL, lobster carapace length (mm); TD, urchin test diameter (mm).

A.4 Implicitly accounting for other factors in the model

A.4.1 Other biotic factors: model closure

The number of functional groups explicitly described is minimal to capture the gross dynamics and focus on the effects of overgrazing of seaweed beds by the invasive long-spined sea urchin. Natural mortality accounts for other sources of mortality affecting modelled groups or species, such as predation (e.g. octopus predation on lobster) or intraspecific competition.

A.4.2 Abiotic factors: temperature, seasonality, habitat and depth

Seasonality

Several model parameters are likely to change seasonally, *viz.* growth, recruitment (spawning and settlement of pelagic larvae) and trophic interactions (catchability of southern rock lobster varies throughout the year and directly relates to lobster foraging activity). Autoregressive functions (Annan, 2001) can be implemented to capture stochasticity due to temporal variability of parameter values: $r_{t+dt} = \mu + (r_t - \mu) \times AR_{coef} + \epsilon$, with r_t, parameter value at time t; μ, the mean parameter value; $\mathrm{AR}_{\mathrm{coef}}$ constant autoregressive parameter (lag 1 autocorrelation coefficient); ϵ a random variable taken from a Gaussian distribution with mean 0 and standard deviation s_o. The variance s_r of the resulting time series is given by the equation: ${s_r}^2 = {s_o}^2/(1 - AR_{coef})^2$ (Annan, 2001).

The current version of the model does not incorporate seasonality because implementing autoregressive stochastic functions considerably increases model complexity in terms of parameterisation, and specific information about the seasonality of the different model processes is lacking.

Temperature

Sea surface temperature essentially controls two processes in the model, urchin recruitment and lobster growth (see the section about size-structured population dynamics).

Sea urchin recruitment Sea urchin early larval stages can only develop successfully if the ambient temperature is above 12°C (Fig.A.5; Ling et al., 2008).

Discrepancies in lobster growth Lobster growth rates increases significantly with temperature on the east coast of Tasmania, and in eastern Bass Strait lobsters moult twice a year compared with a single annual moult in southern Tasmania (Punt and Kennedy, 1997). For simplicity, growth rate for the central east coast of Tasmania (i.e. region of main focus for management of sea urchin barrens in Tasmania) is used in TRITON.

Effects of habitat and depth: patchiness of reef communities

Abiotic factors that are not explicitly captured in TRITON can influence modelled processes. Model dynamics can mostly be affected by: i) depth, which correlates with declines in both swell action and light levels, which influences seaweed growth; ii) habitat structure, which can significantly influence sea urchin survival (Ling and Johnson, In press). These processes essentially affect seaweed mortality (abrasion by wave action) and growth rate (exposure to light), urchin natural mortality (exposure to predators) and the strength of lobster predation on urchin. Thus, changing the mean values of these rates through Monte-Carlo simulations with TRITON constitutes a rigorous representation of spatial patchiness in reef dynamics.

A.5 Limitations and guidance for future research

Building an ecological model provides a good opportunity to synthesise the current state of knowledge about the dynamics of a given ecosystem. Emphasising the limitations of the model due to lack of information about ecosystem processes is important to both i) recognise limitations and sources of uncertainty in model predictions, and ii) prioritise future research in addressing knowledge gaps. Limitations in current understanding of Tasmanian rocky-reef community dynamics are outlined following. Some of the data available could not be fully-exploited because the experimental context (e.g. spatial scales) was not always clearly reported, which highlights the value of sharing and reporting data from field experiments and observations in a transparent format for future re-uses.

A.5.1 Seaweed bed dynamics

Our definition of seaweed bed dynamics is based upon a single experiment, where recovery of seaweed communities from a barrens state was monitored off the coast of Bicheno, eastern Tasmania. Inclusion of additional experiments across different sites with different features in terms of depth, habitat, latitude and temperature would allow refinements of the current estimates. Additionally, it would be useful to represent guilds of seaweeds rather than represent them as a single variable.

Conversion from percentage cover to wet weight Most experiments and observations report seaweed cover in percentage cover, and only few measurements of both percentage cover and standing biomass were available to define a conversion factor from percentage cover to biomass.

Effects of depth Studies (e.g. Kirkman (1989) in Western Australia) have investigated the effect of depth on seaweed bed productivity, but this information was not readily included into TRITON, which does not account for depth explicitly.

A.5.2 Dependency of lobster dynamics to the state of the seaweed bed

Current data from large-scale surveys of the extent of sea urchin barrens and lobster density provides the best information to quantify the effect of barrens habitat on lobster population dynamics (recruitment rates in particular). However, the effect of barrens on the lobster life cycle (e.g. puerulus settlement or growth) may not be responsible for these large-scale patterns (Johnson et al., 2005). Other causal mechanisms such as local depletion of lobster abundance by fishing could drive correlations observed between lobster abundance and seaweed bed cover.

A.5.3 Urchin grazing rate on seaweed

In the model, all of the seaweed standing biomass is assumed to be available to sea urchins for consumption. A more realistic representation of these processes would require further studies on the effects of urchin grazing on seaweed holdfasts and the temporal dynamics of individual macroalgal abrasion of the substratum following sea urchin grazing. Additionally, no data are currently available to quantify density dependence of the grazing rate on either the seaweed bed cover or sea urchin density.

A.5.4 Predation rate

While predation estimates from DNA analysis may be skewed by false positive signals (under current investigation), *in situ* predation experiments were completed at very low urchin density (an order of magnitude sparser than on urchin barren). Thus, our current estimate of predation rate could be refined based on further analysis of DNA sample and further field experiments with higher densities of sea urchin. More sophisticated functional responses (e.g. Beddington-De Angelis accounting for dependency to lobster biomass density) would also require further manipulative experiments.

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