

Rebuilding Ecosystem Resilience: Assessment of management options to minimise formation of ‘barrens’ habitat by the long-spined sea urchin (*Centrostephanus rodgersii*) in Tasmania

Craig R. Johnson, Scott D. Ling, J. Craig Sanderson, J. Gabriel S. Dominguez, Emma Flukes, Stewart Frusher, Caleb Gardner, Klaas Hartmann, Simon Jarman, Rich Little, Martin P. Marzloff, Jean-Christophe Soulié, Jessica Melbourne-Thomas, and Kevin Redd

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Cover image: Extensive *Centrostephanus rodgersii* barrens at Elephant Rock (St. Helens) as imaged by Autonomous Underwater Vehicle, 15th June 2009. Seascape is ~27 m wide by 18 m high at a depth of ~25-30 m. Image credit to Stefan Williams and the Australian Centre for Field Robotics, The University of Sydney.

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1 NON-TECHNICAL SUMMARY

2007/045 Rebuilding ecosystem resilience: Assessment of management options to minimise formation of 'barrens' habitat by the long-spined sea urchin (*Centrostephanus rodgersii*) in Tasmania

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Objectives:

1. To assess the effectiveness of culling sea urchins by abalone divers during the conduct of their normal fishing activity, as a means of preventing expansion of incipient barrens and rehabilitating barrens patches.
2. To assess the effectiveness of translocating large rock lobsters (≥ 140 mm CL) *en masse* as means of preventing formation of incipient barrens and rehabilitating incipient and extensive barrens.
3. To assess the effectiveness of a range of management options (e.g. imposing upper size limits and spatial management) in building the biomass of large (≥ 140 mm CL) rock lobsters to levels sufficient to limit *C. rodgersii* populations.

Outcomes

1. The original proposal posited that if cost effective options could be identified to minimise the impact of *C. rodgersii*, either in preventing further barrens formation or in rehabilitating existing areas of *C. rodgersii* barrens, then the State management agency would attempt to develop and implement these options.

Largely (but not wholly) as a result of the findings of this study, the Minister for Primary Industries and Water announced in August 2013 support for a 10 year strategy to rebuild rock lobster stocks in eastern Tasmania by introducing spatial management of the rock lobster fishery in eastern Tasmania, and limiting the total allowable catch of the commercial sector in eastern Tasmania. Recovery of lobster biomass is likely to both improve the economic efficiency of the fishery as well as reduce the likelihood of significant ongoing *C. rodgersii* barrens formation.

2. Loss of productive reef from overgrazing by *C. rodgersii* has direct implications for Tasmanian fisheries, including the two most valuable, abalone and rock lobster. DPIPWE recognises that implementation of effective measures to control *C. rodgersii* populations strategically (on a large scale) and tactically (on a small scale) will have direct benefits in ensuring the integrity and biodiversity value of rocky reef systems on the east coast of Tasmania and the sustainability of the abalone, rock lobster and scale-fish fisheries that they support. As a result of this study, it is acknowledged by managers and other stakeholders that a multifaceted approach to managing the threat of establishment of *C. rodgersii* in Tasmania is warranted, including rebuilding biomass of legal-sized rock lobsters, facilitating the *C. rodgersii* harvesting industry, permitting and encouraging abalone divers to cull urchins while fishing (particularly in high-yield areas), and examining other means to reduce *C. rodgersii* densities.

Non Technical Summary:

By overgrazing seaweeds and sessile invertebrates, essentially back to bare rock, the advent of the long-spined sea urchin *Centrostephanus rodgersii* in eastern Tasmanian waters poses a significant threat to the integrity, productivity and biodiversity of shallow (<40 m) rocky reef systems and the valuable fisheries (principally abalone and rock lobster) that they support. The present research examined means of managing this threat at small, medium and large spatial scales.

Small scales – direct culling by divers

Divers have the opportunity to limit *C. rodgersii* densities at local scales by culling or harvesting to prevent formation or expansion of urchins 'barrens' habitat at incipient stages when barrens occur as small patches in seaweed beds. To ensure sufficient time for seaweed recovery in cleared patches, local control in this way requires that sea urchins show a high fidelity to their particular incipient barrens patch so that once a patch is cleared of sea urchins there is little likelihood of it being quickly recolonised by other individuals from nearby patches. We found that on all types of barrens habitat *C. rodgersii* is highly nocturnal in behaviour, and has a strong tendency to return to its home crevice at the end of each night. Individuals in incipient barrens patches show strong fidelity to their patch over periods of several months, with little tendency to cross the boundary between barrens and seaweed cover, such that mean net movement in small patches is less than 1 m in 3 months. Accordingly, there is little tendency to migrate among patches, which is explained in part by laboratory experiments indicating that *C. rodgersii* lacks a directional chemosensory response to either macroalgae or conspecifics. Thus, urchin behaviour suggests that localised culling is likely to be effective in rehabilitating existing incipient barrens patches and reducing risk of further patches forming.

However, this outcome is unlikely to be achieved by the activity of professional divers culling urchins while fishing for abalone. Our trials indicate that abalone divers are motivated primarily by catching abalone. Thus, while they can be effective at culling urchins from the individual incipient barrens patches they encounter so that seaweeds recover in these particular patches, the number of patches they are able to visit while fishing through an area is small so that the overall effect of their culling activity within the area that they fish is not detectable except at the scale of individual patches visited. Given typical revisitation times to fish in a given area, divers culling urchins while fishing abalone are unlikely to provide meaningful local control of urchin populations. In this context, systematic and targeted harvesting of urchins as an independent industry, or killing urchins with quicklime or by deploying divers whose sole task is to cull urchins, is likely to be much more effective (but at added cost).

Conclusion: Abalone divers culling *C. rodgersii* while fishing can be successful in helping to regenerate seaweed cover on particular targeted barrens patches, but this is unlikely to have any significant effect in controlling urchins at the level of dive sites or reefs. Abalone divers should be encouraged to cull *C. rodgersii* while fishing.

Medium scales – translocation of large rock lobsters

Within two scientific reserves closed to fishing, one established on extensive *C. rodgersii* barrens habitat and the other on incipient barrens where the seaweed bed was largely intact, the population of resident rock lobsters growing into the size class capable of preying on *C. rodgersii* (>140 mm CL) overtook the translocated population within the study period. Translocation of large predatory capable lobsters to the reserves demonstrated that large lobsters can establish home ranges on extensive barrens, and that barrens habitat will support large populations of large, but not small, lobsters. The large predatory lobsters reduced populations of *C. rodgersii* and the native sea urchin *Heliocidaris erythrogramma* at the reserve sites relative to control sites open to fishing and without added lobsters, and these effects were statistically significant in the incipient barrens but not in the extensive barrens. Large lobsters in the research reserves consumed an estimated 75,000 *C. rodgersii* and ~16,000 *H. erythrogramma* at Elephant Rock (extensive barrens), and ~18,000 *C. rodgersii* and ~125,000 *H. erythrogramma* at North Bay (incipient barrens). Flow on effects of the reduced urchin populations on algal cover at reserve sites were not detected on the extensive

barren, while in the incipient barrens the size of barrens patches declined significantly at the reserve site due to regrowth of seaweeds relative to nearby control sites in which the size of incipient barrens patches either increased or remained unchanged.

Modelling of lobster-urchin-seaweed interactions to assess management options at large spatial scales required knowledge of absolute predation rates of large lobsters on sea urchins, which was estimated at the translocation sites. We compared estimates based on changes in urchin numbers in the reserves (relative to control sites without added lobsters), with estimates based on detection of urchin DNA in lobster faeces. While the two methods give similar results at a broad level, results based on DNA in urchin faeces cannot be interpreted unambiguously because lobsters may ingest sea urchin DNA from sources other than by direct predation, and subjective decisions are required to interpret the molecular analysis. Given this, and significant declines in sea urchin densities at the sites with translocated lobsters, but inconsistent and non-significant changes at control sites, we take the change in urchin density at experimental sites over the ~2.5 years of the study, related to average abundances of large (>140 mm CL) lobsters, as a robust estimate of absolute predation. Decline in urchin numbers at translocation sites was exponential, suggesting a constant instantaneous predation rate and that the absolute numbers of urchins eaten by lobsters varies depending on urchin density.

Conclusion: Rebuilding populations of large lobsters (>140 mm CL) on incipient barrens can lead to predation rates sufficient to limit *C. rodgersii* populations and facilitate recovery of algal cover in barrens patches within a relatively short time, while over the same time frame recovery of any algal cover is unlikely on extensive urchin barrens with similar levels of large lobsters despite large numbers of urchins consumed.

Large scales – managing the rock lobster fishery to control urchins

Evaluation of management strategies to apply to the entire east coast of Tasmania was undertaken using three models, *viz.* an ecosystem model (TRITON) describing interactions between seaweed, *C. rodgersii* and rock lobsters; a model of *C. rodgersii* population dynamics; and the model of rock lobster population dynamics that is at the core of the current rock lobster assessment model for Tasmania. The first two models were developed as part of the present project. The TRITON ecosystem model captures shifts in state (in both directions) between intact seaweed beds and extensive barrens habitat, and is able to reproduce observations of urchin barrens in eastern Tasmania at a whole-of-site scale (10^2 - 10^3 m). Sensitivity analyses identified fishing mortality of predatory lobsters, sea urchin recruitment rate, and seaweed growth rate as the key parameters of influence on overall model behaviour.

TRITON indicated clearly that management intervention to prevent extensive urchin barrens from forming is much easier (and thus less costly) than rehabilitating extensive barrens by promoting regrowth of dense seaweed cover. The model indicates that reduced fishing of rock lobsters and direct culling or harvesting of sea urchins, particularly when undertaken in combination, is much more effective at reducing the risk of barrens formation than other measures such as implementing an upper size limit in the lobster fishery. The model was consistent with observations at the translocation sites in suggesting that, on time scales of >2 years, single translocations of large lobsters will have relatively little impact relative to reducing fishing pressure. At high fishing pressure, prediction of future rock lobster catches as a function of fishing mortality using TRITON are notably lower than catches estimated using a single species rock lobster population dynamics model (based on the population dynamics component of the current rock lobster stock assessment model) because TRITON accommodates the potential for and consequences of destructive grazing of seaweed beds by *C. rodgersii*. This work highlights the need for lobster fishery management to account for the pivotal ecological role of lobsters in this system, and provides guidance to revise key target points accordingly.

Models based on *C. rodgersii* population dynamics predict urchin densities and 'time to barrens formation' as observed on the east coast of Tasmania. In keeping with TRITON and the empirical observations at the translocation sites, the model also shows clearly that controlling urchins by rebuilding populations of large predatory capable rock lobsters is far more readily achieved in intact kelp beds or on incipient barrens than

on extensive *C. rodgersii* barrens. The model provides target densities of urchins, and therefore of predatory capable (>140 mm CL) rock lobsters, to achieve specified levels of risk of barrens cover into the future. Using the rock lobster stock assessment model, assessment of alternative management scenarios to achieve an optimum increase in large lobsters (>140 mm CL) on the east coast of Tasmania for least cost to the fishery also identified reduced catches as more effective than imposing an upper size limit. An upper size limit together with reduced catch achieves greatest biomass increase of large lobsters, but at greater cost to the fishery than alternatives. Consideration of reduced but realistic total allowable catches from the east coast indicates that mitigation of extensive urchin barrens formation on reefs currently supporting intact seaweed cover or incipient barrens is possible within a 20 year time frame. The best outcome in terms of minimizing barrens formation, and thus long term outcome for the fishery, will be to reduce catch quotas immediately as much as can be tolerated, with a view to increasing them once stocks rebuild.

Conclusion: Imposing a limit on the total catch to facilitate increased biomass and densities of rock lobsters in eastern Tasmania can greatly reduce risk of extensive barrens developing from incipient barrens or from healthy seaweed beds with no barrens cover. This measure will at the same time permit a viable – but initially reduced – rock lobster fishery. Maintaining the current management settings for the rock lobster fishery is likely to realize ~50% barrens cover on reefs at ~10-30 m depth in eastern Tasmania, with concomitant loss of habitat to support this and other (e.g. abalone) fisheries. Modelling confirmed the pronounced ecological hysteresis in this system which, in a management context, shows that management strategies to rebuild lobster stocks so that risk of extensive barrens formation in healthy kelp beds is greatly reduced will have little or no effect in rehabilitating seaweed cover on extensive barrens in a time frame of 2-3 decades.

Keywords: Sea urchin, *Centrostephanus rodgersii*, rock lobster, *Jasus edwardsii*, abalone, *Haliotis rubra*, sea urchin barrens habitat, ecosystem based management, modelling, stock rebuilding, maximum economic yield.

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3 BACKGROUND

This section is taken from the original project application, with minor updating as appropriate.

There is now widespread appreciation of the need for holistic management of ecological systems to maintain ecosystem function, biodiversity and biological productivity, particularly when systems are subject to harvest. An important component of this approach is management to maintain ecosystem resilience in the face of pressures that can cause ecosystems to shift to an alternative stable, but degraded, state (Scheffer et al. 2001; Hughes et al. 2003, 2005). In this context, ecosystem based fishery management is explicitly the goal of managing fisheries (Anon. 2005), and seeks to maintain the integrity of marine ecosystems that support important fisheries.

The threat of the long-spined sea urchin (*Centrostephanus rodgersii*) in Tasmania

Tasmania's two most valuable fisheries, black-lipped abalone (*Haliotis rubra*) and southern rock lobster (*Jasus edwardsii*), with a combined value of ~\$150-170M pa before processing, depend fundamentally on rocky reefs which support highly productive seaweed beds and a high diversity of associated other invertebrates. The single largest threat to the integrity of the shallow rocky reef system on the east coast of Tasmania is the long spined sea urchin (*Centrostephanus rodgersii*), which has only relatively recently established in Tasmanian waters (Johnson et al. 2005, 2011; Ling & Johnson 2008; Ling et al. 2008, 2009b). This large diadematid sea urchin is problematic because it has the capacity to overgraze seaweeds and invertebrates on rocky reefs, effecting a transition from highly productive and diverse seaweed-based systems to poorly productive 'barrens' habitat largely devoid of seaweeds, with greatly reduced invertebrate biomass and diversity, unable to support commercial fisheries for abalone or rock lobster (Johnson et al. 2005, 2011). Importantly, sea urchin populations are able to persist on and maintain barrens habitat indefinitely, and are themselves not threatened by the lower productivity of barrens (Johnson & Mann 1981). Removal of *C. rodgersii* from barrens inevitably results in recovery of seaweeds (e.g. Hill et al. 2003; Andrew & Underwood 1993), and experiments in Tasmania show that seaweed cover and community structure in plots from which sea urchins are removed converges with that of ungrazed control sites within 18 months of removal (Ling 2008).

An important finding is that the urchin has a significant negative effect on abalone populations even when seaweed beds are fully intact and before there is any indication of destructive grazing. Experimental manipulations in intact seaweed beds show that while the presence of *H. rubra* had no detectable effect on *C. rodgersii* while, in marked contrast, the presence of *C. rodgersii* induced significantly lower total weight, reduced dry weight of stomach contents, and increased mortality in *H. rubra* individuals relative to control plots in the same area without urchins (Strain & Johnson, 2009). Moreover, in seaweed beds the abalone changes its behaviour in the presence of the urchin, spending significantly more time in cryptic habitat so that a greater proportion of the population is not available to the fishery (Strain 2010).

The southward incursion of *C. rodgersii* from NSW and its successful establishment in Tasmanian waters is most likely initially the result of transport of larvae, reflecting changes in the behaviour of the East Australian current driven by climate change (Johnson et al. 2005, 2011; Ling et al. 2009a). Evidence suggests that this species established in the Kent Group in Bass Strait in the 1960s and in northeast Tasmania in the 1970s. In the Kent Group ~50% of shallow reefs now exist as *C. rodgersii* barrens, reflecting the state of reefs on most of the NSW coast (Andrew & O'Neill 2000). Off Tasmania proper, *C. rodgersii* is now established along the entire east coast, and has latterly been discovered on the south and south west coasts at least as far west as Port Davey (Ling et al. 2009b; Johnson et al. 2011). Incipient barrens, occurring as bare overgrazed patches in seaweed beds, and fully developed barrens occur patchily on the east coast of Tasmania, usually associated with prominent headlands, as far south as the Tasman Peninsula (Ling et al. 2009b). There is clearly potential for *C. rodgersii* barrens to cover ~50% of nearshore reefs on the east coast of Tasmania, as is already the case in NSW and the Kent Group in Bass Strait (Johnson et al. 2005, 2011).

Recent research has shown that Tasmanian populations of *C. rodgersii* show a normal reproductive cycle with winter spawning, that fertilisation is effective during spawning and that winter water temperatures conducive to *C. rodgersii* larval development are likely to occur with increasing frequency (Ling et al. 2008). Given this situation, there is an imperative to explore options for management of *C. rodgersii* in Tasmania. In this context it needs to be emphasised that mechanisms underpinning the range extension of this species into Tasmanian waters, which is ostensibly the direct result of climate change (Johnson et al. 2011), are distinctly different from those leading to formation of barrens habitat (Ling et al. 2009a).

Barrens formation and the collapse of rocky reef ecosystems

All evidence to date indicates that barrens formation, which occurs when populations of adults increase to the point where overgrazing is initiated, may be the direct result of fishing reducing densities of large rock lobsters (*J. edwardsii*) on rocky reefs. This circumstance is not idiographic; it is already well established that *J. edwardsii* is the key predator of the smaller native sea urchin (*Heliocidaris eruthrogramma*) in eastern Tasmania (Pederson & Johnson 2006), and there is a wealth of evidence from elsewhere in the world that development of sea urchin barrens is linked to fishing of predators (e.g. Steneck 1997, 1998; Sala et al. 1998; Pinnegar et al. 2000; Jackson et al. 2001; Steneck et al. 2002; Tegner and Dayton 2000; Shears and Babcock 2003). On this basis, management intervention is justified.

A series of intensive field experiments in 'no take' marine reserves and adjacent areas open to fishing using tethered, caged, and tagged (but untethered) adult sea urchins, extensive use of remote underwater video, and other experiments in the laboratory have demonstrated unequivocally that large supra-legal rock lobsters (≥ 140 mm carapace length) are the principal predator of adult *C. rodgersii* in seaweed beds in Tasmanian waters (Ling et al. 2009a). Densities of lobsters of this size outside of marine reserves are extremely low on shallow reefs in eastern Tasmania, but there are a range of management options that might be implemented to develop larger populations of these important predators on fished reefs, thereby increasing the resilience of reefs to overgrazing by *C. rodgersii*.

Responding to the threat

Managing ongoing range expansion of *C. rodgersii* and managing barrens formation as a result of overgrazing by *C. rodgersii* are vastly different problems, reflecting vastly different underlying mechanisms. This proposal is concerned primarily with assessing management options to reduce the risk of further barrens formation and, to some extent, with rehabilitating existing barrens. It focuses on population control of *C. rodgersii* by divers and through manipulations of rock lobster population density and size structure as their key predator. The scope of the work does not extend to limiting the distribution of *C. rodgersii* in Tasmanian waters.

At a one-day workshop in December 2005, there was unanimous agreement among representatives of the rock lobster and abalone fisheries, State managers, peak industry and community groups, and scientists, that management responses to formation of *C. rodgersii* barrens in Tasmania should be evaluated. Deliberations during the workshop, and subsequently of the '*Centrostephanus* Working Group' (formed as a result of a recommendation from the workshop) identified two broad classes of options for management, namely strategic control of *C. rodgersii* populations at large scales by manipulation of their key predators, and tactical control at local scales by the targeted activities of abalone divers. It was widely acknowledged that there is unlikely to be a single management 'panacea', but that a multifaceted approach to the problem is likely to be most successful. Specific potential management options discussed included:

Large scale: Establishing upper size limits and/or instruments of spatially-specific management in the rock lobster fishery to build populations of large lobsters;

Meso scale: Translocating large rock lobsters to areas supporting established barrens, incipient barrens, and productive seaweed beds supporting *C. rodgersii*;

Small scale: Control of *C. rodgersii* populations at local scales through direct intervention by abalone divers.

Given the significant implications of implementing any change to existing management of the rock lobster fishery, or of amending regulations to enable abalone divers to cull or remove *C. rodgersii*, managers must have a high degree of certainty that any action taken is likely to yield the desired outcome in mediating effects of *C. rodgersii* grazing but not result in pernicious or other deleterious effects. Thus, the broad objective of the research outlined in this proposal is to evaluate the efficacy of several possible management strategies in responding to the threat of *C. rodgersii* in eastern Tasmanian waters. This research is designed to provide a knowledge base that will enable robust decisions about management actions to build ecosystem resilience to the threat of *C. rodgersii* on eastern Tasmanian reefs.

Structure of this report

The main body of the report is a condensed and simplified version of the research intended to be accessible to non-specialist readers. It provides a brief outline of methods, and focuses on key findings and their implications for managing the risk posed by *Centrostephanus rodgersii* to shallow reefs in eastern Tasmania.

A fully developed scientific context for each element of the work, detailed technical descriptions of methods and analyses used, technical presentation and interpretation of results, and implications of the findings are presented as a series of appendices at the back of the report.

4 NEED

There is clearly potential for *C. rodgersii* barrens to cover ~50% of nearshore reefs on the east coast of Tasmania, as is already the case in NSW and the Kent Group in Bass Strait. This would reduce both the Tasmanian abalone and rock lobster fisheries by ~15%, with a loss of value totalling ~\$25M (before processing). Recent widespread recruitment of *C. rodgersii* (the emergence of juveniles from cryptic habitat was recorded early in 2008) suggests that several areas of incipient barrens are soon likely to transition to extensive barrens, and further incipient barrens are expected to emerge within two years. The urgent need for a management response is self evident, and is being demanded by conservation interests and commercial and recreational fishers alike.

Large rock lobsters (≥ 140 mm CL) are the key predators of *C. rodgersii* in Tasmania, and experiments have shown clearly that established populations of large lobsters prey heavily on invading urchins, preventing their populations from building to the point where overgrazing occurs. There is urgent need to assess the viability of controlling *C. rodgersii* populations through changing current management of the rock lobster fishery, and through targeted culling of urchins by abalone divers as a tactical response on small scales.

However, before management measures are invoked to minimise the risk of further development of barrens habitat or rehabilitate existing barrens, it is imperative to carefully evaluate the effectiveness of potential management strategies. The research is intended to provide the necessary information and knowledge base to enable robust management decisions.

The work has strong support from managers, the fishing industry, recreational fishers and conservationists, and it is repeatedly identified as a high priority by the relevant Research Advisory Groups in Tasmania. The work addresses several high priorities on both the State and TAFI/IMAS strategic research plans.

5 OBJECTIVES

The objectives of the work, as outlined in the original project application, are:

1. To assess the effectiveness of culling sea urchins by abalone divers during the conduct of their normal fishing activity, as a means of preventing expansion of incipient barrens and rehabilitating barrens patches.
2. To assess the effectiveness of translocating large rock lobsters (≥ 140 mm CL) *en masse* as means of preventing formation of incipient barrens and rehabilitating incipient and extensive barrens.
3. To assess the effectiveness of a range of management options (e.g. imposing upper size limits and spatial management) in building the biomass of large (≥ 140 mm CL) rock lobsters to levels sufficient to limit *C. rodgersii* populations.

6 METHODS

Given the scale, complexity and interdisciplinary nature of the project, methods will be outlined separately to delineate the separate approaches to examining potential management responses at small, medium and large spatial scales.

Small spatial scales – Can abalone divers effectively control *Centrostephanus rodgersii* densities at local scales by culling them while fishing for abalone?

There were two steps required to address this question. First, *C. rodgersii* behaviour was examined to ascertain their movement patterns and extent of individuals' fidelity to particular sites or, in incipient barrens where barrens habitat occurs as patches in otherwise healthy seaweed beds, to particular patches. This was important to have confidence that an area largely cleared of *C. rodgersii* by divers would not quickly be recolonised from the surrounding population. The second step was to assess the effectiveness of divers at culling the urchins while they fished for abalone. Detailed technical accounts of the work to examine *C. rodgersii* behaviour and the effectiveness of abalone divers culling *C. rodgersii* while fishing for abalone are presented in Appendices 3 and 4 respectively.

Fine-scale behaviour of *Centrostephanus rodgersii*

Fine-scale movement of *Centrostephanus rodgersii* is an important element in understanding and quantifying the fidelity of individual sea urchins to their site or patch. This was assessed using time-lapse photography between November 2009 and February 2010 across a number of different sites with similar environmental and exposure regimes. These sites were chosen specifically for the type of barrens habitat they contained, with targeted monitoring carried out in three distinct habitat types: widespread barrens (grazed areas $> 10^4$ m²) composed of flat rock; widespread barrens composed of boulders; and incipient barrens (scale of grazed patches typically of maximum dimension $\sim 10^0$ - 10^1 m) representing the north-to-south gradient of decreasing grazing intensity across the sea urchin's range-extension region (Fig. 1).

Each monitored reef was characterised by moderate topographic relief reaching a maximum depth of 12-16 m, with a macroalgal canopy (where present) dominated by the laminarian *Ecklonia radiata* and furoid *Phyllospora comosa*. Movement was recorded over 15 different nights with time-lapse sequences using digital cameras equipped with red lighting to minimize disturbance of sea urchins throughout the nocturnal cycle (see Millot 1968; Gras & Weber 1983). Each sampling occasion was spatially independent, with a different area of reef and different sea urchins monitored in each of the photographic sequences. Image sequences spanned a minimum of 12 hours between 19:30 and 07:30, with a single photograph taken every five minutes. The time frame over which individual sea urchins could be reliably tracked was estimated from pilot trials examining urchin velocity. A frequency of photographing at ~ 5 minute intervals permitted unambiguous tracking of each urchin in the view field.

The path followed by an animal through time was reproduced and divided into a series of steps, stops and moves. A step was defined as the vector connecting two successive positions (five minutes apart), a stop as an interval where an individual remained stationary for at least two frames (10 minutes), and a move as the vector between two successive stops. An arbitrary minimum step length of 10 mm was used, below which movement was considered to be measurement error or indicating local spine movement of otherwise stationary individuals.

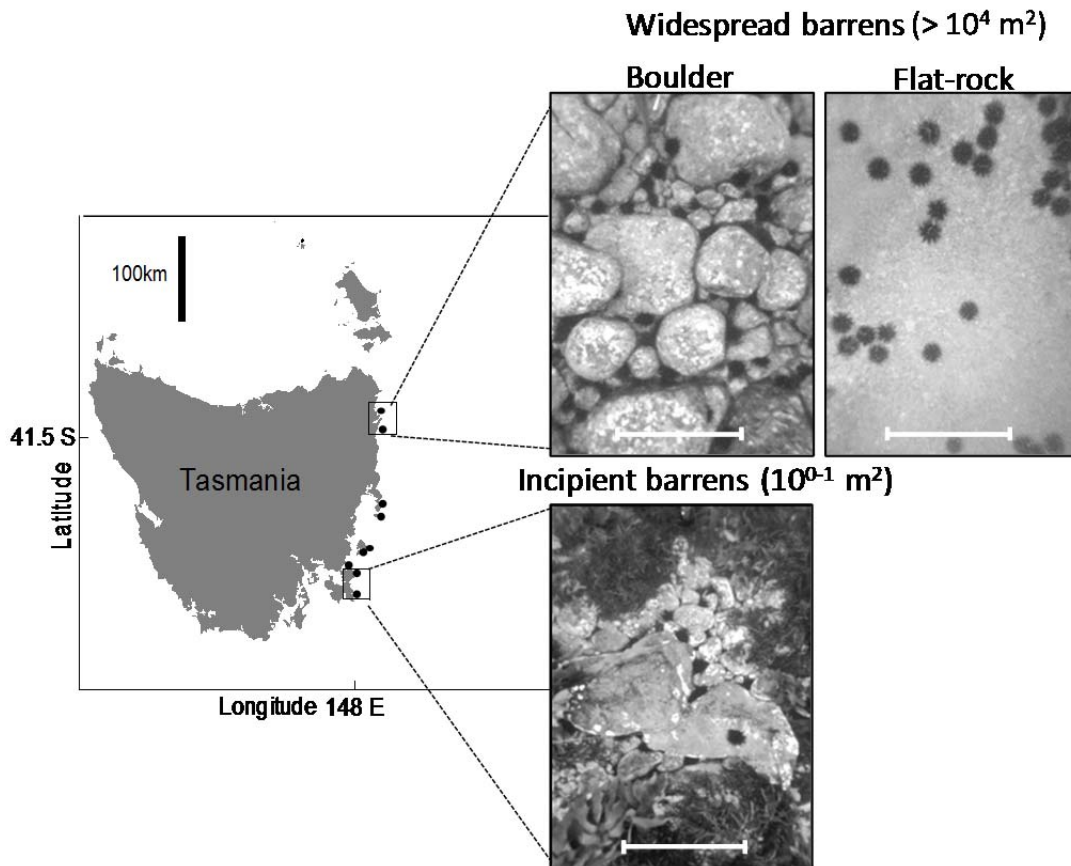


Figure 1. Map of south eastern Australia showing sites where movement of *Centrostephanus rodgersii* was assessed across different habitat types. Abundance of *C. rodgersii* and prevalence of barrens declines with latitude southward along the eastern Tasmanian coast (Johnson et al. 2005, 2011; Ling et al. 2009a) with widespread barrens (10^4 m^2) occurring in the north east region; while only smaller scale (10^{0-1} m^2) barrens patches are currently present in southeastern Tasmania. Expanded boxes indicate the two regions where movement was examined: NE widespread flat-rock (minimal cracks and crevices) and widespread boulder barrens; SE incipient barrens patches only. White bars indicate spatial scale of 1 m. Overgrazing progresses from incipient barrens centered on boulder habitat to widespread boulder barrens and finally, where grazing is most intense, flat-rock habitats are stripped bare of kelp. Sites where barrens patch-size dynamics were recorded by geo-referenced timed-swims (Nov 2008 to June 2009) are shown as filled circles. Ordered north to south, the sites were: Sloop Rock, St. Helens Is, Wineglass Bay, Trumpeter Bay, Mistaken Cape, Bunker Bay, Cape Paul Lemanon, North Bay, Fortescue Bay.

Movement of *C. rodgersii* was initially observed over the entire diel cycle (24 h) to properly quantify periods in which sea urchins were active. Preliminary analyses of these images indicated highly nocturnal foraging consistent with observations on mainland Australia, so all subsequent photography was from 19:30 to 07:30 (overnight, daylight-to-daylight). Images from the different habitat types were examined separately for temporal patterns in speed of movement. The frequency of sea urchins moving faster than the nightly average within each hourly period was calculated to identify times throughout the night corresponding with peaks in activity. Quantitative comparisons between distributions from each habitat type were made. Net displacement and total distance moved over the night were calculated for the subset of sea urchins within each habitat that remained in the field of view for the entire duration of nocturnal footage. Sea urchin density was estimated for each night of footage as the mean of five density measures taken at three hour intervals between 19:30 and 07:30.

To characterise movement in *Centrostephanus rodgersii*, observed movement paths were compared with paths simulated by a simple random walk model (for details see Appendix 3, Flukes et al. 2012).

Assessing fidelity to incipient barren patches

The fidelity of *Centrostephanus rodgersii* to individual patches over time scales of several months was evaluated by measuring movement and dispersal of tagged sea urchins at Fortescue Bay, Tasman Peninsula. Three incipient barren patches in close proximity (~20 m from nearest adjacent barren) were selected haphazardly from within the kelp bed at depths of 6-8 m. The patches varied in area (1.2 - 3.9 m²), perimeter (15 – 30 m), and the number of urchins they contained (6 – 22), and were broadly representative of the typical scale of patches in incipient barrens habitat. All *C. rodgersii* found within these patches ($n = 14, 22, 6$ individuals for patches I-III, respectively) were tagged to enable unique identification at the commencement of the experiment. All tagging was conducted *in situ* by SCUBA divers, and animals were returned to within 10 cm of their initial position immediately following application of the tag. *In situ* tagging in this way avoided any risk of behavioural changes that might result from removal to the surface and subsequent release.

Patches were searched for tagged sea urchins one week after tagging, and again every three weeks over a period of 90 days (total of six encounter occasions). The area of kelp immediately surrounding the patch was also searched on each occasion using a 5 m circular sweep around a central fixed point within the patch. Each time a tagged sea urchin was sighted, its identity was recorded, test diameter measured, and its location within the patch or surrounding kelp bed was triangulated with respect to two fixed pickets hammered into the reef. The position of each sea urchin was also recorded as “shallow” or “deep” depending on its location relative to the shore and pickets. These three measurements provided a unique set of co-ordinates, allowing calculation of the net distance moved since an animal’s previous sighting and displacement from its initial tagging position for each individual. The relationship between cumulative total distance moved (the sum of net movements between consecutive sightings) and overall displacement from the original position was examined for every resighting occasion and used to assess patch fidelity. Given evidence for a strong positive relationship between movement and body size in stronglycentrotid sea urchins (Dumont et al. 2004), size-specific movement was also examined. To verify that fidelity and movement estimates were not biased by some sea urchins moving beyond the boundaries of the experimental area, daily survival and resighting probabilities of individuals were assessed.

Role of chemosensory cues in determining patch dynamics

Fidelity to patches is, by definition, affected by behaviour at the boundary between the barrens patch in which attached seaweeds are absent, and the surrounding seaweed bed. We examined whether behaviour at this interface was influenced by chemosensory cues from food (seaweed) and conspecifics in a series of laboratory-based choice experiments. Sea urchins were collected and housed in flowing sea water tanks without food for a minimum of four weeks before trials commenced. Given an average gut passage time of 24-60 hours under normal feeding regimes across a number of sea urchin taxa, and a maximum food retention time of 1-2 weeks in starved sea urchins (see De Ridder & Lawrence (1982) and references within), a four week starvation period was assumed to be sufficient to ensure significant motivation to feed. Experiments were conducted in a 250 mm diameter Y-shaped maze constructed from PVC piping with section lengths of 0.5 m (arms) and 0.7 m (trunk). Each arm was connected to a header tank containing either a ‘stimulus’ or ‘blank’ seawater. A flow rate of 21 L min⁻¹ (velocity 0.24 m min⁻¹ in the main stem) was maintained throughout all trials, with dye experiments conducted regularly to verify minimal mixing of water upstream of the junction point. Only sea urchins with spine canopies less than 250 mm were used to ensure that they moved freely in the maze and were not impeded by the dimensions of the apparatus. The first two sets of trials tested the potential role of food cues in stimulating sea urchins to cross the barren-macroalgal boundary by using fresh *Ecklonia radiata* (simulating attached plants) and damaged / decomposing *E. radiata* (representing detached drift algae), both of which are known to be consumed by *C. rodgersii* (Andrew 1993, 1994; Hill et al. 2003). The third set of trials addressed the idea that patch fidelity of *C. rodgersii* may be maintained by attraction to conspecifics, and in these trials 15-20 sea urchins (depending on size, 0.3-0.4 urchins L⁻¹) were held in one of the header tanks. All trials were conducted at night between 21:00 and 05:00 in complete darkness during the peak of *C. rodgersii* feeding activity.

Trials commenced with a single sea urchin placed in the centre of the main Y-stem. Its location was monitored every 10 minutes for a period of 40 minutes, and a choice was considered to have been made when an individual moved either side of the junction and its centroid crossed the entrance to one arm of the maze. Each sea urchin response was scored as positive (towards stimulus), negative (away from stimulus), or no response (no choice made between either arm). Water inflows were swapped after every second trial to eliminate any potential bias in the apparatus.

Scaling per capita grazing impact with barrens patch size

In the context of culling urchins in incipient barrens patches, it is useful to know whether the per capita impact of *Centrostephanus rodgersii* grazing scales linearly with the size of barrens patches. If it doesn't, then divers could be more effective overall by targeting either smaller or larger patches (depending on the nature of any non-linearity). The grazing impact of *C. rodgersii* individuals was assessed by broad-scale diver surveys in incipient barrens habitat across nine sites in eastern Tasmania (Fig. 1). Over a total of 20 geo-referenced timed swims (surface GPS towed by diver for 30-45 minutes, $n = 4$ swims per site for North Bay and $n = 2$ swims for all other sites) between 5 and 15 m depth, divers searched for incipient barrens patches and estimated patch sizes *in situ* using a 1 x 1 m quadrat for calibration. Abundance of *C. rodgersii* within each patch was estimated for patch sizes up to a maximum of 5 by 5 m (25 m²) in area (beyond this size patches became too large to efficiently estimate urchin abundance; see Fig. 1 caption for more detail). The relationship between planar grazed area of each barrens patch and *C. rodgersii* abundance was assessed. To assess overall impacts of urchin grazing on kelp beds (i.e. beyond the individual patches considered above), data from belt-transects assessed by divers (from Johnson et al. 2005) were re-analysed to determine the relationship between mean *C. rodgersii* density and mean percentage cover of barrens habitat for 13 sites across the sea urchins' range-extension region (means of $n = 3$ sub-sites per site, with sub-site estimates obtained from the mean of 4 belt transects; see Johnson et al. 2005 for the full method).

Culling sea urchins (*Centrostephanus rodgersii*) while fishing for abalone

Work to this point enables a comprehensive assessment of the detailed behaviour of *Centrostephanus rodgersii* in terms of the fidelity of individual sea urchins to particular sites or barrens patches, and thus the likelihood of local areas that are largely cleared of urchins being rapidly re-invaded by urchins from the surrounding population. What remains is to assess the effectiveness of professional divers culling the sea urchins at local scales while they fish for abalone. Here the overall approach was to liaise closely with the industry to delineate three locations suitable for fishing abalone in which culling would take place, with adjacent control areas where fishing for abalone would be also conducted but where no culling would occur. By monitoring the density of *C. rodgersii* and abalone at several spatial scales, and overall community composition of the benthos at 'cull' and control sites, before and on several occasions after culling commenced, it was possible to quantify the effectiveness of the culling effort.

Through liaison with the Tasmanian Abalone Divers Association, the locations were chosen randomly from a suite of potential areas identified as supporting suitable reef habitat from ~5-15 m depth where abalone divers normally fish for abalone, and which also supported incipient *C. rodgersii* barrens patches (10⁰-10¹ m²). At each location there was a single cull site and nearby control site, each extending for ~500 m of linear coastline (Fig. 2).

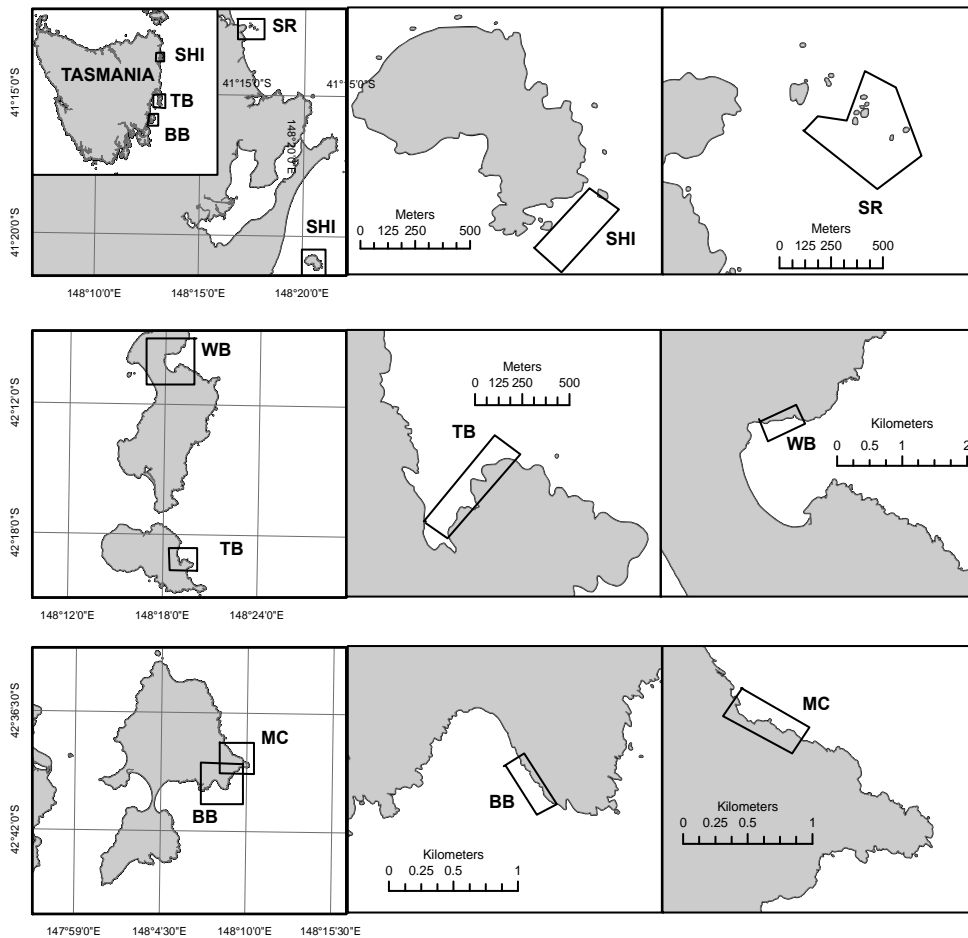


Figure 2. Location of cull sites and associated control (no-cull) sites at 3 regions in eastern Tasmania (see inset, top left: region 1 = St Helens, 2 = Freycinet Peninsula, 3 = Maria Is.). Left hand panels indicate proximity of cull and control sites in each region, middle panels identify cull sites, while right hand panels show the location of the control sites. Upper, middle and lower panels show regions 1-3 respectively. SHI = St Helens Island, SR = Sloop Rock, TB = Trumpeter Bay, WB = Wineglass Bay, BB = Bunker Bay, MC = Mistaken Cape.

Culling operated over the period May 2009 - July 2010, with a minimum of three dives completed within each of the culling areas. It was emphasized to divers that the project was about culling urchins while they fished for abalone and not a targeted 'culling-only' exercise. In culling urchins, divers were instructed to create a hole of at least 10 mm diameter in the test to cause a mortal wound. This was inflicted with an 'abalone iron' (the usual tool carried by divers for prising abalone from the rock substratum, resembling a large knife with a blunt end). In most cases, the test of targeted urchins was simply smashed by the iron.

Participating divers carried forms on which was recorded, for every dive, the date and position of the dive; dive time; depth range of the dive; number of sea urchins culled; estimated breakdown of time during the dive devoted to catching abalone *versus* culling sea urchins; abalone catch; and any additional comments that divers wished to note. A subset of divers carried GPS and depth loggers on each dive. Subsequent downloads confirmed good agreement with divers reporting.

The effectiveness of culling urchins was monitored by comparing characteristics of cull and control sites at each location using three methods, *viz.* belt transects, timed swims during which the features of incipient barrens patches were recorded, and photographic monitoring of individually marked incipient barrens patches.

Monitoring the effect of culling urchins – belt transects

The distribution and abundance of *C. rodgersii* and the associated benthic community was monitored at ‘cull’ and ‘control’ sites on three occasions (using $n = 6$ replicate belt transects at each site on each occasion; Table 1). Each transect was 50 m in length and deployed parallel to the coast at a depth of 8-12 m. Start and finish locations for transects were noted as GPS coordinates at the first survey prior to culling, and for subsequent surveys transects were laid over the original locations. Divers swam on each side of the line transect, each surveying a corridor 1 m in width and for every 5 m length of transect recorded the abundances of sea urchins (*C. rodgersii* and *Heliocidaris erythrogramma*), abalone (*Haliotis rubra*) and rock lobsters (*Jasus edwardsii*). In addition, in each 1x5 m section, the percentage cover of canopy-forming algae and conspicuous understorey seaweed species (or species complexes), the percentage of reef grazed by sea urchins (barrens), and cover of conspicuous sessile invertebrates (largely sponges and bryzoans) was estimated by eye. The first survey was conducted prior to sea urchin culling, and there were two subsequent surveys, the final being at least six months after culling activity had finished (Table 1). For each site the total area monitored (i.e. the smallest area within which each set of 6 transects lay) was determined from the GPS positions using the ARC mapping software and SeaMap Tasmania benthic habitat maps.

Table 1. Dates of culling and pre- and post-cull surveys using belt transects and timed swims at each of the sites. In addition to the dates shown, a third post-cull assessment was undertaken early in 2011 using timed swims only (St Helens Is, 11th March; Sloop Rock, 21st February; Trumpeter Bay, 2nd March; Wineglass Bay, 25th February; Bunker Bay, 9th March; Mistaken Cape, 9th March).

Site	Treatment	Initial Survey	Cull dates	Post Cull 1	Post Cull 2
REGION 1					
St Helens Island	Cull	7 - 9/12/2008	8/06/2010 21/07/2010 28/09/2010	16/03 - 14/04/2010	11/03/2011
Sloop Rock	Control	2 - 18/06/2009		19/05/2010	14 - 23/12/2010
REGION 2					
Trumpeter Bay	Cull	11/03/2009	20/05/2009 10/12/2009 23/12/2009 20/05/2010 23/06/2010	21/04/2010	2/03/2011
Wineglass Bay	Control	18/03/2009		21 - 22/04/2010	25/02/2011
REGION 3					
Bunker Bay	Cull	18/11/2008	27/01/2010 6/05/2010 25/06/2010	30/04/2010	9/03/2011
Mistaken Cape	Control	2 - 6/03/2009		25/03/2010	18/02/2011

Monitoring the effect of culling urchins – timed swims recording patch characteristics

On each survey occasion at each of the 6 sites, and on a fourth occasion in early 2011, two 30-minute swims using SCUBA were undertaken to assess the density and size of *C. rodgersii* incipient barrens at each of the sites, thus there was one 'pre cull' and three 'post cull' surveys (Table 1). Divers swam parallel to the coast within the depth range in which the incipient barrens were most prevalent. This was site specific but mostly between 8-12 m. Divers swam at constant velocity and noted every incipient barren patch they encountered, recording the time into the swim that each patch was encountered, and its depth, estimated area (calibrated by divers carrying a 1m² quadrat), substratum type, the number of large and small emergent *C. rodgersii*, and number of *H. erythrogramma*, in the patch. Divers towed a floating GPS which recorded the track of the diver, and the start and finish times of the swim were also recorded. Positional information from the tracks was used to calculate the length of track swum by the diver and enabled mapping incipient barrens patches at each of the six sites. On each survey occasion care was taken that swim tracks of dive teams did not overlap. At some sites there were patches whose longest dimension exceeded 10 m and for these large patches start and finish times of the diver swimming over the boundary of the patches was recorded and the length of the patch estimated from the GPS track. Urchin numbers were estimated (rather than counted directly) for these large patches by counting them in a proportion of the patch and scaling accordingly.

Monitoring the effect of culling urchins – photographic monitoring of patch size

Immediately after the culling exercise had been completed, six incipient barrens patches were marked at each site for observation and photographic monitoring (in October and November 2010). At the cull sites in two of the regions, patches in which culling had taken place were readily identified as containing no or low numbers of *C. rodgersii* and by the presence of abundant test fragments and spines on the reef substratum. Culled patches could not be unequivocally determined at the Bunker Bay cull site due to the high rugosity of the substratum and the wave exposed nature of the site, so monitoring was confined to St Helens Island and Trumpeter Bay and their associated 'control' sites.

Divers assessed and photographed the subset of individually marked patches at each assessment immediately post culling, and again ~6 months later (in February and March 2011). The diver took photographs using a Nikon D300s with wide angle lens at a distance above the substratum that would include the entire patch in the photograph frame (a square 1 m² quadrat was deployed for scale). Where it was not possible to get the desired distance above the substratum while maintaining good visibility, multiple photographs were taken and a photomosaic of the entire patch constructed. For each patch, the diver also recorded depth, estimated total area of the grazed patch, estimated planar area of the grazed area, and number of cryptic and exposed *C. rodgersii* and *H. erythrogramma*. Estimated planar area was a useful record to assist in determining that the correct boundaries were selected from the patch photographs as these were not always clear on the photographs. The total surface area was estimated because the planar area did not always reflect the total area available to urchins within the patches due to variations in surface topography (e.g. vertical rock surfaces). For *in situ* estimates of area, divers carried a 1 m² quadrat to use as a reference calibration.

The planar area of the patches was calculated from the photographs by digitising the boundary of the barrens-kelp interface. Photographs were manipulated using Microsoft® PowerPoint and measurements of the patches were done using the ImageJ software (<http://imagej.software.informer.com/>).

Details of the statistical analysis of data are given in Appendix 4.

Meso scale – Can translocating large lobsters to shallow reefs control *Centrostephanus rodgersii* numbers at meso scales?

The intent of this work was to (1) assess the dispersal and behaviour of large lobsters (capable of predating emergent *Centrostephanus rodgersii*) translocated to two experimental sites closed to lobster fishing (one an extensive *C. rodgersii* barrens, the other an incipient barren at an early stage of seaweed destruction), (2) monitor the direct effects of the lobsters on sea urchin (both *C. rodgersii* and *Heliocidaris erythrogramma*) abundances and their indirect effects on benthic community structure as a whole relative to control sites, and (3) use molecular and other techniques to estimate predation rates of lobsters on sea urchins at the translocation sites. A detailed technical account of the methodology is given in Appendices 5-7 covering, respectively, assessment of lobster dispersal, behaviour and population dynamics (Appendix 5); monitoring benthic community responses to the lobster translocations (Appendix 6); and estimating lobster predation rates on sea urchins (Appendix 7).

Lobster translocations: Lobster dispersal, population dynamics and behaviour

The key objectives of this component of the project were to assess (i) whether translocated lobsters would establish at their release sites or disperse from them, (ii) whether large lobsters would inhabit extensive *C. rodgersii* barrens given existing data from fished areas (and thus based largely on small lobsters) showing that lobsters are rare on extensive barrens, and (iii) the effect of establishment of research reserves closed to fishing on lobster populations.

While conceptually straightforward, much of the work conducted in this part of the study and analysis of the results was of a technical nature, so here is provided only a broad overview while a complete technical account is given in Appendix A5. Based on previous work that identified large lobsters (*Jasus edwardsii*) as the principle predator of emergent *C. rodgersii* in Tasmania (Ling et al. 2009a), large predatory-capable lobsters (≥ 140 mm carapace length [CL]) were purchased from the commercial fishery at cost and translocated to two sites on the east coast established as scientific research reserves closed to fishing of rock lobsters (and abalone, *Haliotis rubra*) for the purposes of the project. A total of 933 large lobsters were released at the Elephant Rock Research Reserve (ERRR) in north east Tasmania, while 732 lobsters were released into the North Bay Research Reserve (NBRR) in south east Tasmania (Fig. 3). The ERRR site supported extensive tracts of *C. rodgersii* barrens habitat, and so it was possible to delineate separate areas of kelp cover and barrens habitat at this site, while NBRR in the south east was a largely intact kelp bed supporting scattered small patches of incipient *C. rodgersii* barrens, which were mapped. To the north and south of each of the research reserves, but not contiguous with the reserve areas, were established nearby 'control' sites that were in a similar state to the research reserves at the point of declaration of the reserves, but which were not protected from fishing and which did not receive added lobsters (Fig. 3). Thus, control sites in the south east were characterised as incipient barrens, while in the north east control sites supported extensive *C. rodgersii* barrens with adjacent kelp habitat (usually) in shallower water.

All lobsters were uniquely tagged prior to release, and their dispersal was followed in two ways. First, at both sites a small number of individuals were tagged with acoustic transponders and their detailed movement and behaviour followed over several weeks with a VRAP telemetry system. Acoustic telemetry was undertaken during summer at both ERRR and NBRR, and in winter at ERRR. Second, animals were recaptured (and immediately re-released at the site of capture) in a series of extensive 'trapping' surveys conducted over the ~2.5 year study. These surveys were undertaken by setting lobster traps on a regular spatial grid throughout the reserve areas and on reef open to fishing contiguous with the reserve boundaries. Details of all recaptured lobsters were recorded, and newly trapped resident lobsters were tagged before their release at the site of capture.

Extensive habitat mapping at the sites enabled detailed movement of lobsters carrying acoustic transponders to be interpreted in terms of their association with particular habitat types. The home ranges and activity areas of these animals were also determined. From the trapping exercise, estimates of the total

lobster population at the reserve sites and in adjacent fished areas, and estimates of population by size class, were determined based on mark-recapture modelling. This modelling was also used to estimate the lobster population by habitat. Patterns of habitat use by lobsters inside and outside the reserve were corroborated by *in situ* diver-based surveys conducted at the reserve sites and nearby control sites.

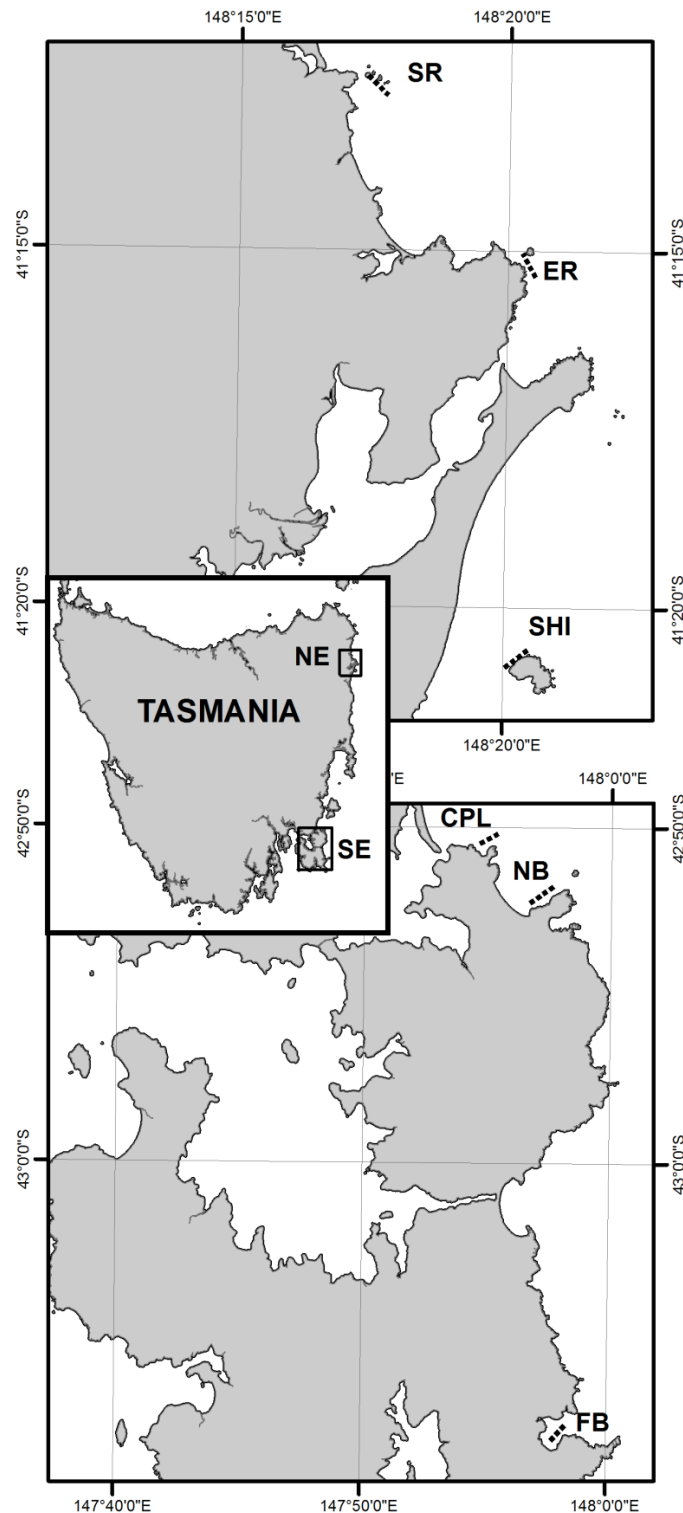


Figure 3. Map showing ‘experimental’ sites to which large lobsters were translocated and which were declared as research reserves and protected from fishing for the purposes of the project, and adjacent control sites without added lobsters and open to fishing. In the north east (NE in inset map of Tasmania), the lobster translocation site was at the Elephant Rock Research Reserve (ERRR, ER on this map), and the two control sites were Sloop Rock (SR) and St. Helens Island (SHI). In the south east (SE in inset map of Tasmania), the

lobster translocation site was at the North Bay Research Reserve (NBRR, NB on this map), and the two control sites were Cape Paul Lemanon (CPL) and Fortescue Bay (FB). Areas where the research was undertaken are shown as heavy dots. (See also Fig. 22 for more details of the ERRR and NBRR sites.)

Monitoring the impact of populations of large lobsters on sea urchins and benthic community structure

An outline of the essential methodology is given below, while details of the approach to statistical analysis of data are presented in Appendix 6.

Study sites and experimental translocations

Lobster translocations and benthic surveys were conducted on widespread *C. rodgersii* barrens in north east Tasmania and in incipient barrens in south east Tasmania as described in the previous section. Both reserves quickly developed elevated populations of large predatory capable lobsters (see Results and Discussion). The research reserve at Elephant Rock (ERRR) and adjacent control sites at St Helens Island and Sloop Rock supported both widespread barrens and kelp bed habitats, which were examined separately, while only kelp bed habitat was surveyed at the three sites (North Bay Research Reserve and associated control sites at Cape Paul Lemanon and Fortescue Bay) in the south east (Table 2). In addition, the seaweed bed / barrens interface was monitored in the NE as any recovery of kelp was anticipated to occur nearby to mature kelp stands where propagule supply would be non-limiting. Similarly, finer scale habitat-level responses were explored in the SE by monitoring changes in the size of individually marked incipient barrens patches.

Monitoring of sea urchins, other benthic macro-invertebrates, and algal community structure

Three monitoring approaches were used to detect changes in benthic communities in response to lobster translocations: (i) *in situ* belt transects in both kelp and barrens habitats (north east reserve and control sites) and in incipient barrens (south east reserve and control sites) to detect broad-scale changes in macro-invertebrates and seaweed cover; (ii) diver operated video belt transects across the kelp/barrens interface to detect fine scale changes (north-east sites only); and (iii) monitoring the size of individually marked incipient barrens patches (south-east sites only). Surveys were conducted over a total of five periods between 2008 and 2011, with surveys occurring both before and after large lobster reintroduction (see Table 2).

On the fixed belt transects (50 * 2 m) were recorded percentage cover of key algal guilds, cover of barrens habitat, substratum type, and densities of sea urchins (*C. rodgersii* and *Heliocidaris erythrogramma*), abalone (*Haliotis rubra*), and rock lobsters (*J. edwardsii*). Assessments were recorded by divers in 5 m long × 1 m wide blocks along each sides of the transects, with the exception of rock lobsters which were recorded in a 2 m swath either side of the 50 m transect line defining the belt transect (i.e. covering 200 m² per transect). Note that potential declines in abalone at control sites were not independent of fishing mortality since control sites were open to commercial and recreational diver harvest over the duration of the study, while both research reserves were closed to abalone fishing.

Algal cover was resolved to species level for dominant species, and to genus or guild level (e.g. encrusting invertebrates and erect/encrusting coralline algae) for other taxa. A full list of algal groups recorded, together with their classification as either canopy formers or understory species, is provided in Appendix 6 (Table A6.1). Percentage cover of algal species / groups, barrens and substratum type, were recorded to the nearest 5%, with cover < 5% recorded as present. *C. rodgersii* individuals were recorded as either cryptic (in crevices with < 90° aperture) or exposed on 'open' reef surfaces where urchins were either occurring on flat rock or positioned against rudimentary vertical structure (> 90° aperture).

Fine-scale monitoring of dynamics at the kelp/ widespread-barrens interface

At sites in the north east, permanent stainless steel eyebolts were drilled into bedrock at the seaweed / barrens interface and flagged with float lines. Video belt transects of total length 40 m by 1 m swath width, centered on the permanent bolt fixtures, were used to monitor advance and/ or retreat of the kelp / barrens boundary and monitor the distribution of habitat types in contiguous 1 by 1 m quadrats. Video belt transects ran perpendicular to the seaweed / barrens boundary, extending 20 m into the kelp bed and barrens habitat from the permanent fixtures. Six replicate fixtures were deployed at each site in 2008, with

surveys conducted annually in 2009, 2010 and 2011 (see Table 2C for survey dates). Videos were taken along the transect line maintaining a constant speed (approximately 3 m.s⁻¹) and a constant height (~1.5 m) from the substratum.

Table 2. Survey design for monitoring changes in sea urchin abundances and associated benthic community structure in response to large predatory lobster enhancement and concomitant protection of reefs from lobster fishing for (A.) widespread *Centrostephanus* barrens in north-east Tasmania; and (B.) incipient *Centrostephanus* barrens in south-east Tasmania.

Location	Site name	Experimental Treatment	Habitats surveyed	Translocation dates (No. translocated lobsters)		
A. North-east	Elephant Rock	Lobster enhancement (Reserved reef + translocation)	Widespread barrens	Apr08 (476)		
				Nov08 (116)		
						Total barrens 592
			Adjacent kelp beds	Apr08 (213)		
				Nov08 (128)		
				Total kelp beds 341		
				Total for NE site 933		
	Sloop Rock	Control 1	Widespread barrens	Nil		
				Adjacent kelp beds	Nil	
			St. Helens Island	Control 2	Widespread barrens	Nil
Adjacent kelp beds					Nil	
B. South-east	North Bay	Lobster enhancement (Reserved reef + translocation)	Kelp beds with incipient barrens	May09 (543)		
						Mar10 (189)
				Total 732		
	Cape Paul Lemanon	Control 1	<i>As above</i>	Nil		
Fortescue Bay	Control 2	<i>As above</i>	Nil			

Displacement of the kelp/barrens interface was extracted from the video footage by stitching together individual images calibrated against 1 m intervals along the transect line using the set scale function within the free-ware program *ImageJ*. Movement of the kelp edge into barrens habitat was recorded as a positive 'advance' while expansion of barrens with destruction of kelp habitat recorded as a negative 'retreat'.

Videos were also analysed to extract the percentage cover of identifiable algal species, barrens, and *C. rodgersii* densities at 1 m intervals along each transect (for a 1 m² area to the left of the transect line). Because sea urchin counts from video transects in kelp habitat were unreliable due to the inability to detect urchins underneath the kelp canopy from video sampling, only *C. rodgersii* densities from barrens habitats are presented.

Dynamics of incipient barrens patches

The density and size of incipient *C. rodgersii* barrens patches were surveyed at NBRR and associated SE control sites using two replicate (independent and non-overlapping) 45 minute geo-referenced swims on SCUBA prior to and post reintroduction of large lobsters. Divers towing a float with GPS (logging the dive track) recorded the time a barrens patch was encountered enabling positional estimates to be obtained by synchronizing the time recorded from the divers watch with the GPS track. The density of patches along the total length of the diver's track was thus obtained. The geo-referenced swims were conducted parallel to the coast within a depth range of ~4-10 m.

Marked incipient barrens

To assess dynamics of individual incipient barrens patches at NBRR and associated control sites, steel pegs (star-pickets) were hammered between crevices centered within randomly selected patches and marked with float lines to enable survey of patches before and after translocation of lobsters to NBRR and at control sites. A 1 by 1 m frame sub-divided into four 0.25 m² sub-quadrats was placed over the central peg for calibration and the area (planar dimension) of the barrens patch assessed by a diver hovering squarely above the quadrat. At NBRR, initially a total of 20 patches were marked and monitored, however only 16 barrens patches were routinely assessed as 4 patches were not re-locatable at the conclusion of the experiment. At each control site, 10 patches were initially marked, with 9 relocated at all sampling times at Cape Paul Lemanon while all 10 were relocated by final sampling at Fortescue Bay.

An explanation of the statistical analysis of data is presented in Appendix 6.

Estimating rates of lobster predation on *Centrostephanus rodgersii* using molecular and other methods

Given temporal variability in lobster foraging (Ziegler et al. 2002, 2003, 2004) and the need to obtain robust estimates of average absolute predation rates across the broad population of lobsters at the experimental sites without removing lobsters from the system or harming them, molecular approaches based on PCR (polymerase chain reaction) amplification of targeted DNA in lobster faeces were developed. The approach develops from relatively recent successful applications of molecular analysis of predator faeces to determine diet composition and quantify relative predation rates (e.g. Symondson 2002; Jarman & Wilson 2004; Deagle et al. 2005, 2009; Deagle & Tollit 2006; Pompanon 2012).

All the work was undertaken at the Elephant Rock Research Reserve (ERRR; extensive *C. rodgersii* barrens) and North Bay Research Reserve (NBRR; incipient barrens) where densities of large lobsters were elevated by translocation from deep water, as described previously. A more detailed account, including more technical aspects, of the methods is given in Appendix 7.

Sampling lobster faecal material

Faecal samples from individual lobsters were obtained by trapping lobsters within the research reserves during winter and summer seasons over two years post translocation of lobsters (see Fig. 22A). Traps were set across the available reef area within the reserves on a regular spaced virtual grid (60 m between grid points). For ERRR, each trap position was assigned to either kelp or sea urchin barrens habitat following intensive video mapping of the benthos at each grid point. As per commercial operations, traps were baited with whole jack mackerel (*Trachurus declivis*) and couta (*Thyrsites atun*) heads, which were deployed on reef in depths of ~3-45 m. Traps were effective at sampling lobsters to a minimum size of approximately 50 mm carapace length (CL; ~60 g fresh weight) while lobsters below this size, while present at the sites, were likely to escape through the mesh of the trap (25 by 25 mm). Each captured lobster was measured for carapace length to the nearest mm with knife-edge callipers and assigned to size categories of small (≤ 110 mm CL, i.e. undersized lobsters); medium (> 110 & < 140 mm CL); and large (≥ 140 mm CL), inclusive of large residents and large translocated individuals. Captured lobsters were then sampled for faecal material, tagged (if they were untagged residents), and released at the site of capture.

Lobster faeces were collected using a 100-1,000 μ L pipette with disposable tips. For each faecal sample a new sterile tip was used to prevent contamination between samples. The tip was inserted directly into the anal pore of the lobster to remove faeces from the hindgut. Rock lobsters which failed to yield a faecal sample were recorded as 'non-feeding' (for proportions of lobster catch deemed to be feeding, refer to Fig. 22B). Water was removed from samples prior to DNA extraction.

DNA extraction and amplification

DNA extraction followed standard protocol (see Appendix 7 for details) using a commercial kit designed for the purpose (The Ultra Clean™ Faecal DNA Kit; Mo Bio Laboratories, Inc.). The manufacturer's protocols were followed, using supplied proprietary buffers and reagents. The procedure proved efficient at processing large batches of samples (96) simultaneously, and the manufacturer's protocol appeared to remove potential PCR inhibitors.

For PCR amplification of sea urchin DNA, care was taken to avoid contamination by extraneous DNA. The PCR primer sets used in this experiment (Table A7.2, Appendix 7) were designed to be specific for *C. rodgersii* and *H. erythrogramma*, and targeted the 16s rDNA region. Real-time PCR reactions were run for 50 cycles to ensure amplification of small quantities of DNA.

Filtering PCR amplifications: determining presence of sea urchin DNA

PCR amplification curves were screened for non-normal amplification curves, including a minimum threshold for fluorescence, and lower and upper *Ct* (the number of reaction cycles) thresholds to minimise effects of false positives as a result of primer dimerization (i.e. reactions that developed unrealistically quickly were indicated by *Ct* values of < 8 cycles; and reactions manifest as normal curves but that took too many cycles to amplify, consistent with primer dimerization, were excluded from consideration). Thus, positive tests for assays of *C. rodgersii* were considered as those $8 < Ct < 40$; and for *H. erythrogramma* as $8 < Ct < 45$ (see Fig. A7.2, Appendix 7).

Where prior feeding regimes are unknown (such is the case for wild-caught lobsters) it is not feasible to estimate even relative quantities of prey consumed using sensitive molecular techniques, so we recorded either presence or absence of urchin DNA for each sample. Thus, instantaneous predation rates of lobsters on sea urchins were scored as the number of individual lobsters in a given catch testing positive to sea urchin DNA, which we assumed could arise from ingestion of urchin DNA at any time over the previous 3-days (earlier work established that *C. rodgersii* DNA is detectable in lobster faecal samples for 7-60 hours after ingestion, so the assumption of 3 days errs on the conservative; Redd et al. 2008).

Analysis of variability in lobster feeding on sea urchins based on assays from field samples

Patterns of variability in the proportion of lobsters positive for sea urchin DNA (as defined by *Ct* thresholds outlined above) were assessed. For ERRR, a 4-way model was assessed to assess the effects of year, season, lobster size and habitat on the proportion of lobsters positive for urchin DNA, in which there were 2 levels of *Year*, 2009 vs. 2010; *Season*, winter vs. summer; *Habitat*, seaweed bed vs. barren; and 3 levels of *Size*, small lobsters (≤ 110 mm CL) vs. medium lobsters (>110 & <140 mm CL) vs. large lobsters (≥ 140 mm CL). For NBRR, where habitat consisted entirely of seaweed bed (albeit supporting small incipient barren patches), the influence of year, season and size on the proportion of positive assays was examined.

Potential passive sources of sea urchin DNA: benthic sediments and excreted sea urchin faeces

Direct observations of large rock lobsters during daylight hours indicate that they sometimes appear to 'taste' and / or consume sedimentary material; a feature also noted occasionally for resident individuals (S. D. Ling *pers. obs.*). It was therefore necessary to assay for the presence of sea urchin DNA in benthic sediments, and to assess the potential for qPCR to detect sea urchin DNA in lobster faeces following ingestion of sediment or cast urchin faeces by rock lobsters. Benthic sediment samples were collected by SCUBA divers at both the ERRR and NBRR sites across a range of water depths and habitats. Distinct habitats at ERRR included both sea urchin barrens and adjacent seaweed dominated areas which were sampled at 10 m (seaweed habitat), and 15, 20 and 25 m (barrens habitat) depth, while at NBRR samples were from the seaweed bed and incipient barren patches within it at a depth of ~8 m.

Feeding lobsters benthic sediment/ sea urchin faecal material

Rock lobsters used in feeding trials were captured by trapping in the Crayfish Point Marine Reserve at Tarooma, Tasmania (42.95 °S, 147.34 °E) in April 2010. Lobsters were collected opportunistically ensuring an even distribution of sexes and a wide range of sizes. The size (carapace length) of all captured lobsters was measured to the nearest millimeter.

For each trial individual lobsters were placed in one section of a 450 L tank separated into three sections with plastic mesh and dividers. Each lobster was provided with a 400 mm x 200 mm concrete block as a shelter. All lobsters were starved for > 3-days prior to each feeding trial to facilitate gut evacuation and to remove any remaining prey DNA from the digestive tract (Redd et al. 2008). For each trial, fresh sea urchin faecal material was obtained from both species by allowing individuals of *H. erythrogramma* and *C. rodgersii* to defecate overnight in aquaria. To prepare gelatine 'food parcels' based on both the sea urchin faecal material and the benthic sediment samples, filtered seawater was heated to 100° C and mixed with

gelatine (Davis, New Zealand), stirred and then poured into 30 ml plastic moulds to which the component of each diet formula (i.e. sediment, or fresh sea urchin faecal pellets, or fresh sea urchin gonad tissue) was added and stirred in once the mixture had cooled to $\sim 25^{\circ}\text{C}$, each time using a new pipette tip to prevent contamination between diet formulas. The mix was then allowed to solidify in a standard refrigerator.

A gelatine ‘food parcel’ (with appropriate dietary element) was introduced to each lobster at 1700 h and individual lobsters were monitored for feeding activity. Only lobsters that fed actively and consumed the entire food sample within the first hour were used in the feeding trials. No additional food was provided to lobsters for the duration of the trial and each lobster was sampled only once in each trial. Lobsters were selected for faecal collection over the next two days at times after commencement of feeding based on results of previous experiments to determine the longevity of dietary signals in lobster faeces (Redd *et al.* 2008). Lobsters were allocated diets randomly to eliminate any systematic ‘tank’ effect. For each sampling time, attempts were made to collect faecal material from at least three lobsters. For each of the individual faecal samples, qPCR assays were performed twice to guarantee the consistency of the result.

Lobster predation rates estimated from decline in sea urchin populations

Independent estimates of lobster predation rates on *C. rodgersii* were obtained by monitoring urchin and lobster populations.

Estimating change in sea urchin abundance

Diver-based counts of abundances of emergent sea urchins (*Centrostephanus rodgersii* and *Heliocidaris erythrogramma*) were performed at both the ERRR and NBRR sites using fixed belt-transects (50 m length by 2 m width) to monitor changes in their density. To distinguish changes in sea urchin density that might be attributable to dynamics unrelated to the addition of lobsters and declaration of the reserves, sea urchin densities were also monitored in the same way at nearby control sites (matched by similar reef types, with one to the north and one to the south of each research reserve). For north east sites where rocky reef habitat exists as seaweed bed or widespread sea urchin barrens, a total of 12 independent fixed belt transects were surveyed to assess change in urchin populations within ERRR and at both control sites, with transects established on both seaweed-dominated ($n=6$) and sea urchin barrens habitats ($n=6$) at each site (Fig. 3; see also Fig. 22). In the south east, 6 independent fixed belt transects were established within the seaweed bed supporting incipient barrens inside the reserve (NBRR) and outside at both control sites (Fig. 3; see also Fig. 22). In both regions, surveys were conducted on 5 occasions (approximately equally spaced) between 2008 and 2011, with one survey before and four after translocation of large lobsters, as outlined previously. However, to quantify change in the populations of both sea urchin species at experimental and control sites in both regions, we compared only the first (pre-translocation of lobsters = ‘before’) and last (= ‘after’) surveys in the study (see explanation below; these two surveys were ~ 2.5 years apart).

Two approaches were used to assess change in urchin populations at the two experimental sites relative to the appropriate control sites (referred to as C1 and C2 in each region). First we compared the change in urchin density between control and experimental sites, pooling across control sites where it was valid to do so (see Appendix 7). For both urchin species and for both the NE and SE regions, the change in density (‘B-A’ = ‘before’ - ‘after’) in the experimental sites and adjacent control sites was compared using 1-way ANOVA. In the second and complementary approach, which addressed a related but distinctly different null hypothesis, because transects were fixed in space it was possible to separate the independent effects of change in urchin density and spatial variability using paired t-tests to determine whether the change in urchin density (‘B-A’) at each site differed significantly from zero (see Appendix 7). For the NE, because predatory lobsters were observed to move freely between adjacent habitats and urchins in both habitats were equally accessible to lobsters, benthic transects were pooled across habitats to give an overall trend of urchin population dynamics at the site level (i.e. $n = 12$ replicate transects for reserve and control sites).

Estimating large lobster abundance

Every translocated and captured resident lobster caught within both ERRR and NBRR was uniquely tagged for individual identification. Trap sampling was performed ~6 monthly at both NBRR and ERRR over the ~2.5 year study, yielding encounter histories for each lobster (individuals were scored as either, 'present and alive' or 'absent' at each re-sampling period). This enabled modelling individual survival estimates for translocated (group 1) and resident (group 2) lobsters using the Cormack-Jolly-Seber (CJS) 'recaptures only' mark-recapture routine (using the MARK[®] software, White and Burnham 1999; see Appendix 7 for details). For translocated lobsters, the estimated apparent 'survival' rate (which reflects both survival and *emigration of lobsters out of the reserve site*) was low immediately post-release of translocated lobsters, but thereafter translocated lobsters demonstrated survival rates similar to resident animals. For translocated lobsters, the best estimate of the number retained within the reserve sites was obtained by projecting daily survival rates (obtained by the best supported CJS model) onto the known number of lobsters released over the duration of the study.

Where the starting abundance was unknown, i.e. for resident lobsters, the POPAN model in the MARK[®] software was used to estimate abundances of resident lobsters by size-class (large, 140mm CL; medium ≥ 110 & < 140 mm CL; small, < 110 mm CL) within each reserve at the time of final sampling. The total abundance of large lobsters ≥ 140 mm CL (translocated plus resident lobsters) capable of preying on emergent size-classes of *C. rodgersii* (Ling et al. 2009a), and of medium- and large-sized lobsters (translocated plus residents) ≥ 110 mm CL capable of consuming emergent *H. erythrogramma* (Pederson and Johnson 2006), were estimated for each reserve.

Estimating predation rates

Independent estimates of mortality rates of emergent sea urchins (i.e. excluding the smallest size classes of sea urchins, approx. < 70 mm test diameter, that are restricted to cryptic habitat within the interstices of the reef and not visible or accessible to divers without them rolling boulders) were determined for comparison with rates of ingestion of sea urchin DNA obtained from molecular analysis of lobster faecal material. Given consistent and statistically significant declines in sea urchin populations at both reserve sites over the duration of the study (significant declines were observed for both *C. rodgersii* and *H. erythrogramma* at NBRR, and *C. rodgersii* within ERRR; see footnotes in Table 23), but relatively small and non-significant changes, and lack of an overall trend, in urchin populations at adjacent control sites, we assumed that urchin population declines at the reserve sites were solely the result of predation by lobsters.

For each reserve site and for each species of sea urchin, we estimated the mean number of sea urchins to which each lobster had access, and fitted an exponential decay model based on a three day time step to preserve the observed density of urchins at the beginning and end of the experimental period (observation periods were 955 days at ERRR and 840 days at NBRR). Exponential decay was fitted on the basis of the pattern of mortality observed in four populations of tagged *C. rodgersii* subject to predation by lobsters inside and outside of two marine reserves (Ling et al. 2009a) and to patterns of urchin decline at the reserve sites themselves. This is ecologically sensible since it captures declining absolute predation by lobsters as sea urchin densities, and thus encounter rates, decline. We also ran a similar exercise but where the initial and final urchin densities at ERRR and NBRR over the experimental periods were taken as the mean densities estimated by fitting an exponential decay through all data from every sampling period. Since the estimated predation rates were within 1% across the two methods, here we report on calculations based only on the observed sea urchin densities at the beginning and end of the study inside the research reserves.

Extensive data on movement of individual lobsters provided by VRAP acoustic tagging technology provided robust estimates of the home range area of individual lobsters (reported earlier) and indicated that lobster densities were sufficiently high that home ranges were overlapping at both study sites. On this basis the mean number of sea urchins to which each lobster had access was estimated as the total number of sea

urchins in each reserve divided by the number of predatory-capable lobsters in the reserves. As outlined earlier, based on extensive empirical and experimental observation of size-specific predation on sea urchins by lobsters, predatory-capable lobsters for *Centrostephanus rodgersii* were deemed as those >140 mm CL (Ling *et al.* 2009a) while lobsters >110 mm CL were considered capable of predating *Heliocidaris erythrogramma* (Pederson & Johnson 2006).

Cross-checking the two independent estimates of predation rates

Rates of DNA-based predation by each lobster size-class were averaged across seasons and years to obtain time-integrated average sea urchin predation within the reserves over the study, with mean values and confidence intervals generated from 10,000 bootstrap simulations of the observed variability between different years and seasons. To cross-check DNA based predation estimates within the research reserves, the rate of instantaneous lobster predation was calculated from the observed decline in urchin abundance using an exponential decay function with a 3-day time step from which we calculated the mean number (over the entire study period) of urchins consumed per lobster per 3-day period. Mean values and confidence intervals for instantaneous 3-day predation rates were estimated from 10,000 bootstrap simulations of the variability in predicted large lobster abundance and variability in the change in urchin abundance across replicate fixed transects surveyed at the start and conclusion of the study within the reserves. Estimating predation rates on urchins based on both the DNA assays and observed declines in urchin densities at the reserve sites assumes that each lobster would not consume more than 1 urchin within any 3-day period. While this assumption may be conservative (deliberately), it is supported by *in situ* remote video surveys of lobsters consuming sea urchins within marine reserves (see Ling *et al.* 2009a) where, particularly for large urchins, on average no more than a single urchin was observed to be consumed by large individually identifiable lobsters within a 3-day period. In addition, as was the case in deriving overall mean-field estimates of predation rate based on DNA assays pooled across years and seasons, in deriving estimates of predation to explain declines in sea urchins we calculated an average across the entire study period.

Large scale – Are there acceptable options to manage the rock lobster fishery to build the biomass of large lobsters sufficiently to control *C. rodgersii* numbers coast-wide?

Consideration of how *Centrostephanus rodgersii* populations might be controlled at a whole-of-coast scale to ensure low risk of overgrazing and barrens habitat formation and/or effect rehabilitation of existing extensive barrens was addressed through modelling. We used two independent approaches, one based on development of a new multi-species model (called 'TRITON') to capture 'ecosystem' dynamics between seaweeds, *C. rodgersii* and lobsters as the key predator of the urchins, and the other focused on separate single-species models of *C. rodgersii* population dynamics and the existing rock lobster stock assessment model that currently provides the basis for management of the fishery. In the single-species approach, the rock lobster stock assessment model was used to assess how potential management strategies that might be employed in the fishery would influence the abundance of predatory-capable lobsters, and the effect of these large predatory lobsters on the sea urchin population determined.

Here we present the approach to the modelling in three sections, comprising (1) the development, calibration and validation of the TRITON ecosystem model, (2) assessment of management scenarios using TRITON, and (3) a single-species modelling approach using a model of *C. rodgersii* population dynamics and the current rock lobster stock assessment model. The technical accounts of this work are presented in Appendices 8, 9 and 10 respectively.

Development, calibration and validation of the TRITON model

We developed a simulation model of shallow Tasmanian rocky reef communities, which we have called TRITON (Temperate Reefs In Tasmania with LObsters and URChINs), to test the ecological consequences of different management scenarios applied to rocky reef systems in eastern Tasmania. If simulation modelling is to assist management of formation of barrens habitat by overgrazing by the urchins, the ability of TRITON to realistically capture the potential for discontinuous shifts between the two alternative states (seaweed bed versus sea urchin barren) is essential. The following subsections describe the structure of the TRITON model, its parameterisation and the empirical data available to calibrate model dynamics. We then introduce the extended Fourier amplitude analysis test (FAST; Saltelli et al. 1999) used to test model sensitivity to parameter values, before specifying both the simulation characteristics and the important output metrics screened for the sensitivity tests.

TRITON: The dynamics of Tasmanian rocky reef communities

TRITON represents the mean community dynamics of an individual patch of rocky reef (area 100 m² - 10 ha; depth 8 - 35 m on open exposed reef habitat where *C. rodgersii* barrens occur in Tasmania) at any point on the east coast of Tasmania. The dynamics of three functional groups or species (Fig. 4) are captured explicitly using difference equations (details of the equations are given in Appendix 8) representing the dynamics of the seaweed bed (SW), the sea urchin *Centrostephanus rodgersii* (CR), and rock lobsters (RLs). Size-structured dynamics of both sea urchin and rock lobster populations are key for TRITON to realistically capture both the effects of size-related fishing regulations (e.g. legal catch size), and the size-structured nature of lobster predation on the urchin (Ling et al. 2009a). Each guild or species is introduced in turn:

Seaweed: The seaweed bed includes all canopy-forming macroalgae (dominated by *Ecklonia radiata* at depth > 6 m, or *Phyllospora comosa* on shallow reef, and including a suite of other large phaeophytes that contribute to the canopy structure, including representatives of the genera *Cystophora*, *Sargassum*, *Sierococcus*, *Carpoglossum*, *Acrocarpia* and *Xiphophora*) and understory algal assemblages (e.g. filamentous and foliose rhodophyta, small foliose chlorophyta and phaeophyta, and corallines and other encrusting red algae). Quantitative information on the dynamics of the different guilds of algae that constitute the seaweed bed is lacking. Thus, in the model, the seaweed bed compartment corresponds to the current minimum realistic representation of temperate algal communities. Seaweed assemblage dynamics follow logistic growth, with parameters derived from monitoring macroalgal recovery from a

barren state over two years after experimental removal of the urchins (Ling, 2008; see details in Appendix 8). Propagule supply is assumed to be constant and independent of the local state of the seaweed bed, as external supply from adjacent macroalgal beds is not limiting (CR Johnson, personal observation). Although a range of herbivorous species rely on macroalgae as part of their diet, only *C. rodgersii* has demonstrated the ability to overgraze Tasmanian seaweed beds on exposed rocky reefs on the open coast (Johnson et al. 2005, 2011). The native purple sea urchin (*Heliocidaris erythrogramma*) also forms barrens habitat (but on a smaller scale than *C. rodgersii*) in relatively sheltered bays in eastern Tasmania (Johnson et al. 2004; Valentine & Johnson 2005; Ling et al. 2010), but TRITON focuses exclusively on the dynamics of exposed inshore reefs where the effect of *H. erythrogramma* is marginal (Johnson et al. 2005). Thus, grazing by the long-spined sea urchin is the only explicit source of seaweed biomass loss in the model.

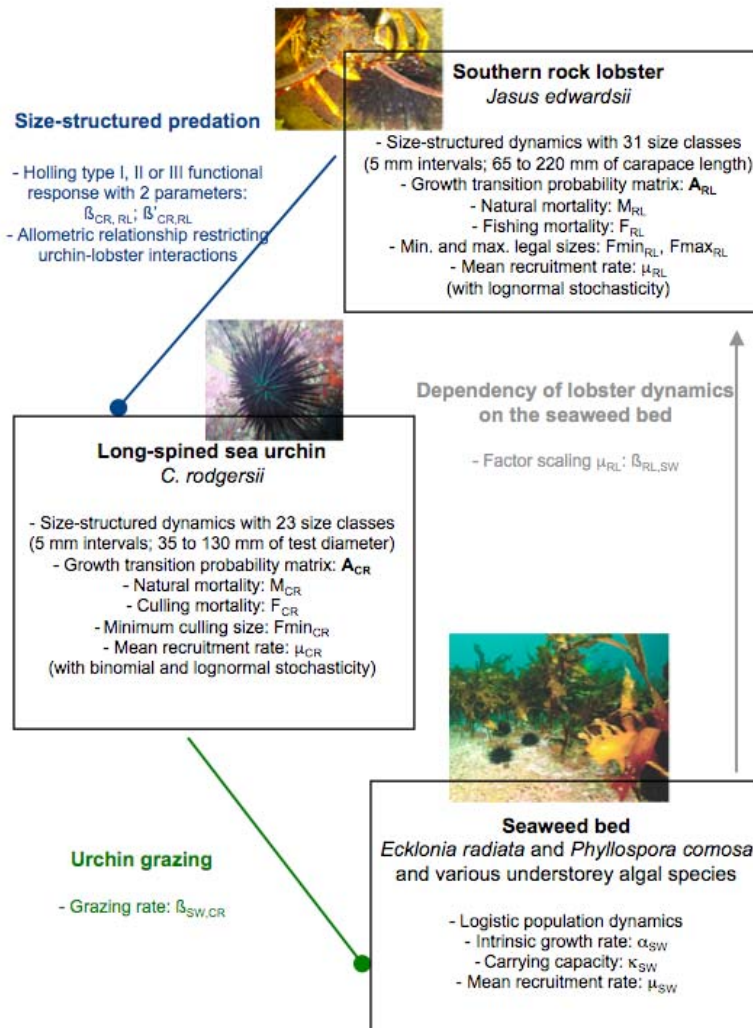


Figure 4. Conceptual diagram of TRITON, a model of local community dynamics on rocky reefs in eastern Tasmania.

The boxes represent the three functional groups or species explicitly interacting in TRITON, namely southern rock lobster, long-spined sea urchin and the seaweed assemblage. Each box lists all the parameters defining the dynamics of each group (see Appendix 8 for details). Interactions between the three groups are represented as arrows, where a full circle at the end of lines indicates a negative effect to the adjacent group while an arrow head points to a group positively affected in this interaction. Photography credits: Scott D. Ling.

Urchin grazing rate is assumed to be constant, dissimilar to northern hemisphere stronglycentroid urchins that destructively graze seaweeds by forming a grazing front once critical density and behavioural thresholds are reached (Lauzon-Guay et al. 2009). In Tasmania there is no evidence of density-dependence of *C. rodgersii* grazing rate, and the effects of individual grazers are additive. We show elsewhere in this report that across incipient and extensive barrens habitat, sea urchin destructive grazing shows a

remarkably consistent ratio of $\sim 0.6 \text{ m}^2$ of grazed area per individual urchin irrespective of the size of the barrens patch (Flukes et al. 2012). Although all size classes of emergent urchins consume seaweed at the same rate for a given biomass of urchins, larger urchin individuals have a higher per capita destructive impact on standing macroalgae in the model since urchin population dynamics capture biomass gain from one size class to the next due to individual growth.

Centrostephanus rodgersii: Population growth of *C. rodgersii* is size-structured and fitted against data from large-scale population surveys on the east coast of Tasmania (Johnson et al. 2005, 2011; and data from the present study). Despite its destructive grazing of seaweed beds, sea urchin population dynamics is independent of seaweed consumption because sea urchins also forage on drift material, ephemeral filamentous algae and microalgae to subsist on barrens habitat in the absence of attached macroalgae (Johnson & Mann 1982; Ling & Johnson 2009). In TRITON, the size structure of sea urchin individuals is distributed across 21 size classes ranging from 40 to 120 mm test diameter using 4.12 mm increments. The effect of habitat complexity on survival of juveniles (provision of crevices to shelter from predation) is implicitly modelled in the Monte-Carlo simulations through changes in mean recruitment rate. Only adult animals of test diameter >70 mm are fully emergent in Tasmania and smaller individuals largely stay cryptic in crevices, with virtually no effect on standing macroalgae through grazing and likely very limited interactions with rock lobster (SD Ling, unpublished data; Ling et al. 2009a). Hence, only these larger urchins have material effects on seaweed and are exposed to lobster predation in the model.

C. rodgersii recruitment is stochastic and independent of local population size given that *C. rodgersii* has a planktotrophic larval stage of *ca.* 3+ months duration that disperses with currents at scales of 10^2 - 10^3 km (Huggett et al. 2005; Banks et al. 2007). The southern rock lobster is the only effective predator of the spiny sea urchin in Tasmanian waters. Because a lobster's ability to handle a given size of sea urchin is determined by the size of its front pair of walking legs (Ling et al. 2009a), predation of *C. rodgersii* by rock lobster is constrained by the relative size of prey and predator. Hence, size-structured predation by lobsters is the only explicit source of natural mortality on sea urchins in the model. In the model we allow for different kinds of density-dependence of predation *C. rodgersii* predation, following any of Holling's Type I, II or III functional responses (Holling, 1966).

Recruitment to the smallest emergent size class of urchins in a given year is determined in part by a binomial term which determines whether a recruitment event will occur *at all* in any given year, which acknowledges that water temperatures in some years are not sufficiently warm to support larval development (Ling et al. 2008). When recruitment does occur, its magnitude is determined with a parameter μ from a uniform distribution ranging between minimum and maximum absolute values (this parameter reflects natural variability between reefs, in which some reefs appear to consistently receive more recruits than others on average), which is then modified by a lognormal scaling quantity to capture inter-annual stochastic variation.

In marine ecosystem models, recruitment rates are often the most uncertain parameters and are commonly used as calibration factors (e.g. Marzloff et al. 2009). We adjusted *C. rodgersii* recruitment to ensure that simulations could achieve realistic sea urchin biomass densities while accurately producing 'forward' shifts from the seaweed bed to the urchin barren state when predation by lobsters was low. In regions where *C. rodgersii* has been present for several decades and where key reef predators have been depleted by fishing (e.g. New South Wales, the Furneaux group and north-eastern Tasmania), about 50% of coastal rocky reef habitat is reported as sea urchin barrens (Andrew & O'Neill 2000; Johnson et al. 2005, 2011). Thus, sea urchin mean recruitment rate was calibrated to meet this observation in Monte-Carlo simulations under historical levels of lobster fishing (see Fig. 38).

Rock lobster: The size-structured rock lobster population component is derived from the Tasmanian rock lobster fishery stock assessment model (see Punt & Kennedy 1997; McGarvey & Feenstra 2001), and so TRITON represents the lobster population across 31 size classes ranging from 65 to 215 mm of carapace length by 5 mm increments. This enables a realistic representation of the effects of size-related fishing regulations. The lobster size-structured population model was closely fitted against the population recovery

observed following protection from fishing (Barrett et al. 2007). There is a term for natural mortality that accounts for sources of mortality that are not explicitly captured elsewhere in the equation, e.g. through predation by sharks or cephalopods (Pecl et al., 2009).

In the model the lobster population relies on the local state of the seaweed bed as an essential source of habitat and food. More specifically, abundances of juveniles are lower on barrens habitat than in adjacent kelp beds, while observations associated with experimental manipulation of large lobsters suggest that abundances of large supra-legal predatory-capable lobsters are largely unaffected by barrens habitat (evidence presented elsewhere in this report). Canopy-forming macroalgae can facilitate both settlement of lobster puerulus by providing a complex three-dimensional structure and (by inference) an appropriate settlement cue, and development of juvenile lobsters by supporting a broad diversity of invertebrate prey species. Therefore, a constant coefficient, ranging from 0 (for no recruitment on barren habitat) to 1 (for no effect of barrens on recruitment), scales lobster recruitment as a function of the state of the seaweed bed

As for the sea urchin, recruitment of the lobsters is a vital process in the model. Lobster recruitment rate is stochastic following a lognormal stochastic function, and independent of the local lobster population given that lobsters have an 18-24 month pelagic larval stage, implying large-scale dispersal (Bruce et al. 2007). For all three modelled groups, larval or propagule settlement occurs over much larger spatial scales than individual reefs, and hence is not limited locally (Banks et al. 2010; Johnson et al. 2011; Linnane et al. 2010; Coleman et al. 2011).

Model time is discrete because it is more computationally efficient than using continuous time, and also more flexible to implement using the object-oriented Python programming language in which TRITON is developed (Python Software Foundation, 2008). A two-week time-step was adopted as a compromise between computational efficiency and adequate convergence between discrete- and continuous-time dynamics (Deng et al. 2008).

Parameterisation

Variables are expressed as fresh weight biomass density with a default parameterisation for a reef area of 200 m² (variables are in g. 200 m⁻²). Biomass density allows for weight-based (rather than abundance-based) trophic interactions and was derived from experimental or other empirical observation (see Appendix 8 for details). All modelled processes were parameterised from *in situ* observations or measurements, or field- or laboratory-based experiments, or well-validated models (details in Appendix 8).

Importantly, none of the parameters is fixed at a single value, and for each run parameter estimates come from the estimated distribution (i.e. mean and standard deviation for normal distributions; minimum and maximum bounds for uniform distributions). In the absence of sufficient empirical data to derive distributions, and to sample extremes as frequently as mean values, we assumed uniform distributions for input parameters within minimum and maximum bounds. For normally distributed parameters, values within the 90% confidence interval (bounded by the 5 and 95% quantiles) were explored during the sensitivity analyses. As well as enveloping uncertainty in modelled processes, these ranges implicitly encompass the span of environmental conditions (e.g. habitat, depth) and anthropogenic forcing (e.g. fishing pressure) encountered on Tasmanian rocky reefs (refer to Appendix 8 for details).

Sensitivity analyses

An important component of the work was to identify the particular parameters to which particular aspects of the output of the model were sensitive. We applied the extended Fourier amplitude sensitivity test (extended FAST) since it provides a robust quantitative and model-independent sensitivity analysis method for models of complex systems dynamics (Saltelli et al., 1999). It is suited to quantitative sensitivity analysis of complex non-linear models because it does not assume linearity or monotony between model inputs and outputs.

The extended FAST computes the relative contribution of each input to the variance in the output. The contribution of each input is reported as a total sensitivity index which includes both the main effect attributable to that parameter and higher degree effects from interactions with other parameters. Higher degree interactions often contribute more than the primary effect of any individual parameter to variance in model output, so these total sensitivity indices are useful to quantify a parameter's overall influence on the dynamics of complex ecosystem models (Saltelli et al., 1999). The extended FAST method was implemented using the sensitivity package of the R software for statistical computing (R Development Core Team, 2010). Preliminary tests of the approach indicated that Monte-Carlo simulations using 500 n runs per 'test' (where n refers to the number of input parameters screened) provided a robust sensitivity test.

Sensitivity analysis was used to assess the influence of model formulation and input parameters on the model's general behaviour and, more specifically, on its ability to shift from seaweed bed to sea urchin barren and back (see following subsections). Model outputs were saved monthly for each 50-year-long simulation, and the extended FAST applied to several output metrics. The first of these was the mean simulated biomass of each modelled group over the last 10 years of simulation. Note that the relative biomass of the seaweed bed is directly convertible to percentage cover of seaweed. We also used the first axis of a Principal Component Analysis on the three normalised biomass densities as a one-dimensional summary of community state (accounting for 73% of the total variance).

The FAST technique was used to test the sensitivity of TRITON's general behaviour to alternative formulations of the lobster predation rate, which was represented as a Holling Type I, II or III functional response (Fig. 33). The effects of alternative formulations of lobster predation rate were also examined by comparing the scores on the first two axes of the PCA of simulation outcomes with each of the Holling Type I, II or III functional responses (Fig. 34).

We also investigated the influence of input factors on the general behaviour of TRITON with a global sensitivity test in which all parameters varied and initial conditions were unconstrained for all three groups (Fig. 35). Monthly outputs from these simulations were used to investigate both model community composition and the dynamics of the TRITON model (Fig. 39a), and to assess the model's ability to mimic observed patterns (Fig. 39b) of seaweed percentage cover and sea urchin density from large surveys of reef habitat and reef species abundance around Tasmania (Johnson et al. 2005, 2011; this study), which we converted to biomass densities directly comparable to model outputs. The frequency of occurrence of community states along the Tasmanian coastline, which encompasses a gradient of local contexts in terms of fishing pressure, habitat complexity and urchin invasion history, could then be compared to the patterns emerging from Monte-Carlo simulations with TRITON (Fig. 39).

Finally, we examined the effect of input parameters on the 'forward' (kelp bed to urchin barren state) and 'backward' (seaweed recovery from the barren state) shifts. In each of these cases, initial conditions were constrained to mimic either an urchin-free seaweed bed (for the forward shift) or a well-established sea urchin population on extensive barrens habitat (for the backward shift). For the sensitivity tests on the forward (Figure 36) and backward (Fig. 37) shifts, we also measured the time for the community to shift to the alternative state as an important feature of model dynamics. A shift to the barren state was defined as seaweed bed cover dropping below 10%, while seaweed bed recovery corresponded to >50% seaweed cover.

Choice and calibration of a minimum-realistic model

No meaningful optimisation could be designed to calibrate the goodness-of-fit of the model against multiple quantitative criteria (e.g. Klepper 1997; Duboz et al. 2010). In particular, because of the occurrence of alternative states in the system (i.e. barrens- and seaweed-dominated configurations), consideration of model mean dynamics to capture mean community composition is not meaningful. Also, because of the model complexity, an interpretable analytical solution could not be derived to formally validate the occurrence of alternative stable states within the estimated parameter space as was achieved, for example, by Fung et al. (2011). Accordingly, we used pattern-oriented modelling, proposed as a means to calibrate

agent-based models (Grimm et al. 2005), as an effective way to validate and calibrate the behaviour of TRITON against the data available for Tasmanian reef dynamics.

We focused initially on the ability of simulations to mimic the dynamics of the forward shift from the seaweed bed to the sea urchin barren state. Prior to applying TRITON to address management questions, fishing mortality was set to mimic historical fishing mortalities derived from the rock lobster stock assessment model for eastern Tasmania (i.e. within 1-1.8 year⁻¹; Klaas Hartmann, pers. comm.), and size-structured predation of lobsters on sea urchins was set based only upon field observations and ignoring information from tank predation experiments in which starved lobsters were 'artificially' induced to predate sea urchins by making a small hole in their test and where urchins were unable to behave normally (Ling et al. 2009a).

As mentioned above, we also calibrated *C. rogersii* recruitment to ensure that simulations could achieve realistic sea urchin biomass densities in the 'forward' shift from the seaweed bed to the urchin barren state when predation by lobsters was low, and that under these conditions the model would predict that about 50% of coastal rocky reef habitat is sea urchin barrens under historical levels of lobster fishing, in line with observation (Andrew & O'Neill 2000; Johnson et al. 2005, 2011).

Application of the TRITON ecosystem model: Identifying thresholds in community dynamics and assessing management intervention to limit destructive grazing of sea urchins

Having developed, calibrated and validated the TRITON ecosystem model, here we apply the model using Monte-Carlo simulations to address several important questions focused on management of Tasmanian reef communities:

1. What are the characteristic thresholds in community dynamics? Identifying the tipping points is critical for sound management, but they cannot easily be observed empirically. The simulation-based estimates of these thresholds from TRITON are intended to help define essential reference points for the Tasmanian rock lobster fishery so as to minimise the risk of barren formation or facilitate the recovery of seaweed beds from a state of extensive barrens.
2. What are the merits and overall effectiveness of alternative management scenarios to either prevent the establishment of sea urchin barrens habitat, or restore dense seaweed beds from sea urchin barrens? Here we test, both independently and in combination, the effectiveness of available management levers: reducing lobster fishing, implementing a maximum legal size to protect large lobsters as key predators of the sea urchins, and culling of sea urchin populations and translocating large lobsters from deep reefs to shallow reefs that are exposed to sea urchin destructive grazing.
3. How do the different management scenarios affect the performance of the rock lobster fishery in eastern Tasmania (as estimated from simulated catches with TRITON and overlain with a version of the current Tasmanian rock lobster stock assessment model)? Over the last two decades, fisheries scientists have increasingly emphasised the need to account for the ecosystem effects of fishing, and to shift management practises away from a traditional single species focus towards an ecosystem-based approach (Smith *et al.* 2007; Smith *et al.* 2011). It is in this context that this question is addressed. With this simple example in which lobsters play an important ecological role as predators of sea urchins, we illustrate some of the misleading assumptions of a single-species focus when 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 ecological services delivered by commercial species, and suggest that these targets may need to be revised to maintain ecosystem functioning. This will be particularly important for ecological systems in which the dynamics are characterised by alternative community states with hysteresis, i.e. where phase shifts are particularly difficult to reverse.

These questions are addressed using the TRITON model outlined in the previous section, and presented in detail in Appendix 8. Below is outlined (1) characteristics of the different sets of Monte-Carlo simulations and model outputs examined; and (2) some specifics about alternative management scenarios tested through simulations. A detailed account of the technical aspects of the approach is given in Appendix 9.

Simulation characteristics and model outputs

To account for prediction uncertainty, all model results are reported as mean outcome (+/- standard error) across Monte-Carlo simulations (please refer to the outline of the TRITON model in the previous section). These sets of simulations fully explore parameter space by both comprehensively sampling values within the 90% confidence interval of each parameter's distribution (Table A9.1; see also Appendix 8), and including the effects of interactions between all input parameters (Saltelli *et al.* 1999 for details about the sampling design; see also Appendix 8). The simulations also account for environmental variability encountered from reef to reef in eastern Tasmania (e.g. across variability in habitat, depth, exposure to urchin larvae). For each scenario tested, the total number of runs in each Monte-Carlo simulation is equal to 500 times the number of input parameters (Saltelli *et al.* 1999; see also Appendix 8). The extended FAST

technique (Appendix 8) was used to provide a robust model-independent assessment of the relative contribution of input parameters to variance in model outputs (Saltelli *et al.* 1999), including those parameters associated with the different management levers (e.g. fishing mortality; see Figs. 42a and 43a).

The results presented rely on two types of model outputs, *viz.* standing biomass density (in g 200 m⁻² fresh weight) and annual lobster catches as fresh weight, i.e. biomass loss from the system due to fishing mortality (in g 200 m⁻² y⁻¹). Although the time step in TRITON is two weeks to overcome any artefacts due to discrete-time modelling (Deng 2008), model outputs were saved monthly for each 50-year-long simulation, which proved adequate to monitor the shift in the modelled community.

The scenarios explored through Monte-Carlo simulation either focussed on the ‘forward’ shift (from dense productive seaweed-dominated habitat to extensive sea urchin barrens), or the ‘backward’ shift (regrowth of dense macroalgal beds on sea urchin barrens). Simulations examining the ‘forward’ shift were initiated in a seaweed-dominated state characterised by low densities of sea urchins and high seaweed cover, while simulations to examine the ‘backward’ shift were initiated in a state of extensive sea urchin barrens state characterised by low seaweed cover and high densities of sea urchin (Table A9.2, Appendix 9). Using the subset of simulations that demonstrated a shift in state, we also recorded the time (in months) for the community to shift to the alternative state as a function of input parameters.

The sampling design for parameter settings across Monte-Carlo simulations was fixed to enable assessment of each scenario under identical conditions (Saltelli *et al.* 1999 provides details about the sampling design; see Appendix 8). The exceptions, of course, are those parameters related to the management levers themselves, namely lobster and sea urchin fishing mortality (F_{RL} and F_{CR}), lobster maximum legal size and lobster ‘initial condition’ (which can effectively be interpreted as the level of translocation of lobsters to an area). Table A9.1 (Appendix 9) summarises the parameters specific to each of the separate management scenarios considered, which included (i) culling sea urchins (ii) under a range of lobster fishing mortality, (iii) implementing a maximum legal size, or a combination of all three. We also tested the effects of culling or harvesting sea urchins under different lobster recruitment levels given establishment of a fledgling *C. rodgersii* harvest industry in Tasmania and that lobster recruitment in the region may decline with ongoing climate-driven changes in large-scale oceanographic features in eastern Tasmania (Pecl *et al.* 2009; Johnson *et al.* 2011).

Finally, for comparison, we simulated lobster population dynamics as a single population (Equation A9.1’ in Appendix 9) with a model derived from the current stock assessment model used in the Tasmanian southern rock lobster fishery in the central east coast of Tasmania (Punt & Kennedy 1997; Hartmann *et al.* 2012). We compared fishery performance (annual catch) under a suite of different management scenarios predicted by the single species model that does not account for the risk of sea urchin barrens formation, and by the TRITON model which does take this into account.

Thresholds in community dynamics and critical biomass densities

A primary aim is to inform management about the dynamics of the ‘forward’ shift and the ‘backward’ shift in Tasmanian rocky reef communities. Specifically, we use model simulations to (1) estimate thresholds in community dynamics, i.e. the tipping points beyond which model community shifts to the alternative state, and (2) define critical reference community states, which correspond to either a ‘limit not to cross’ (so as to minimise the risk of extensive sea urchin barrens formation), or a target to reach so as to facilitate seaweed recovery from extensive sea urchin barrens. All reference points are expressed as biomass densities of both sea urchins and large predatory-capable rock lobsters (of carapace length ≥ 140 mm; cf. Ling *et al.* 2009a).

All monthly biomass outputs were considered in investigating the thresholds for the model community to shift from the seaweed-dominated state to sea urchin barrens habitat (e.g. Fig. 40b) or back (e.g. Fig. 41b). When focusing on the long-term effects of alternative scenarios (cf. following section) in terms of the probability of extensive sea urchin barrens forming or seaweed bed restoration, we computed mean values of monthly outputs over the last 10 years of the simulation (e.g. Fig. 40a) to minimise effects of interannual

stochasticity. We examined TRITON's mean behaviour across Monte-Carlo simulations (See Fig. 39a) to define presence (1) or absence (0) of a shift to the alternative state at the end of a simulation. A persistent shift to sea urchin barrens is assumed if the seaweed bed drops below 10% cover, while recovery of seaweeds corresponds to the seaweed bed re-growing above a 50% of cover (Table A9.2, Appendix 9). These values are used to define the presence or absence of a shift in the long-term (defined by the mean value over the last 10 years of a 50-year simulation). They were chosen based on the mean behaviour of TRITON (Fig. 39a previous section) so that they reflect whether the model state has shifted towards the end of the simulation.

Using R's generalised linear model (GLM) routine (R Development Core Team 2010), we fitted logistic binomial models to relate seaweed cover or the probability of community shift (i.e. extensive barren formation or restoration of the seaweed bed) to the standing biomass density of different model groups. We define tipping points, beyond which the model community shifts to the alternative state, as associated with $p = 50\%$ seaweed cover (i.e. with both declining and increasing seaweed cover, the tipping point at $p = 50\%$ cover is the same). This corresponds to the inflection point of the fitted GLM, i.e. the point at which the change in seaweed percentage cover is the greatest. Critical biomass densities, identified as the reference points for management, were arbitrarily defined as either the point where the risk of extensive sea urchin barrens formation is marginal ($p = 5\%$), or the point where the probability of long term seaweed bed recovery is $p = 75\%$ (given the high stability of the model community once extensive sea urchin barrens have established, a 95% likelihood of seaweed bed recovery is almost unachievable).

Assessing management strategies using population models of *Centrostephanus rodgersii* and rock lobsters

We adopt two broad and complementary approaches, based on the population dynamics of *Centrostephanus rodgersii* and rock lobsters, to address the feasibility of managing the rock lobster fishery to affect the abundance of large predatory-capable lobsters and control *C. rodgersii* populations in eastern Tasmania. In the first approach, long term dynamics are modeled to identify the level of mortality from predation by large lobsters that is necessary to achieve particular target densities of urchins associated with different levels of risk of formation of extensive *C. rodgersii* barrens. This work is focused on intact seaweed beds and incipient urchin barrens, and preventing their transition to extensive barrens.

In the second approach the question is reversed and the level of urchin barrens we can expect in eastern Tasmania for a given density of large predatory capable lobsters is estimated. In addressing this question, we first consider the general case and predict expected barrens cover in the long term for a given density of predation capable lobsters, and then address the outcome of specific rock lobster management scenarios over short (10 years) and medium (21 years) terms. Given the strong hysteresis¹ in dynamics, outcomes of specific management scenarios are considered separately for intact seaweed beds or incipient urchin barrens, and for extensive barrens. In the case of incipient barrens the expected distribution of barrens cover in 2021 (10 year prediction) and 2032 (21 year prediction) is estimated for each management scenario. In addressing extensive barrens, for each management scenario the probability density profile across a range of *C. rodgersii* densities is estimated and compared with the target density of urchins necessary to realize regrowth of seaweeds.

While analysis of the consequences of specific short- and medium-term approaches to managing the rock lobster industry are of most immediate interest, the general case provides a context for interpretation of specific scenarios, and the combined approach provides a comprehensive assessment of the likely short and long term state of shallow reefs in eastern Tasmania given an 'acceptable' level of risk of barrens formation. All approaches rely on the same underlying model of *C. rodgersii* population dynamics.

Preliminaries – identifying target densities of *Centrostephanus rodgersii*

To identify target densities of large rock lobsters, target densities of *C. rodgersii* first need to be defined. Given the nature of the hysteresis in the dynamic between sea urchins and seaweed cover, two different target densities for *C. rodgersii* are required, *viz.* one which applies to extensive barrens and that will allow some reasonable probability of recovery and regrowth of seaweeds, and one which applies to seaweed beds and which ensures low risk of ongoing formation of extensive barrens in intact seaweed beds or in early stage incipient barrens.

Target density: Recovery of extensive C. rodgersii barrens

It is clear that the overall interaction between the sea urchin and seaweed cover is characterized by hysteresis and therefore that lower densities of sea urchins are necessary to maintain a *C. rodgersii* barren than to create one. However, the density at which the urchins' grazing capacity is overwhelmed by seaweed 'propagule pressure' such that seaweed recovery commences is not known precisely. The so-called 'reverse shift' (i.e. seaweed recovery) has never been observed, either in Nature or in experiments, unless most of the urchins have been removed (Andrew 1991; Andrew & Underwood 1993; Ling 2008). In experimental work, recovery of seaweeds at low urchin densities reflects attempts by researchers to clear experimental plots of all urchins (Andrew & Underwood 1993; Ling 2008; Strain & Johnson 2013). Notably, experiments in NSW in which 66% of urchins were removed did not achieve regeneration of seaweeds on barrens (Andrew & Underwood 1993).

¹ Hysteresis in these dynamics means that the outcome of different scenarios of lobster density will depend on what has already happened at a particular reef; the outcome will be different depending on whether an area has been extensively overgrazed or whether it has healthy macroalgal cover.

Until experiments are undertaken on extensive barrens to examine the response of seaweeds to a range of lowered urchin densities, the best estimate of the threshold density at which regrowth of seaweeds will commence is that from the ecosystem model TRITON presented earlier. This model well represents the broad set of observations made in eastern Tasmania, and indicates that recovery of seaweeds commences when urchin density reduces to $\sim 15,000 \text{ g.urchins.200 m}^{-2}$ (Fig. 5 Appendix 8). Assuming a mean size of *C. rodgersii* on barrens approaching $\sim 100 \text{ mm TD}$ (Ling & Johnson 2009; Ling et al. 2009b), this is equivalent to a density of $0.24 \text{ urchins m}^{-2}$; here we round this to 0.25 m^{-2} .

Target density: Preventing widespread overgrazing of seaweeds by C. rodgersii

Defining an upper target density for *C. rodgersii* below which risk of barrens formation is acceptably low equates with defining an acceptable level of cover of barrens habitat in seaweed beds. Clearly, the target density of urchins will be lower if no amount of barrens habitat is tolerable, while target densities will be higher if some level of incipient barrens is deemed an acceptable state of the system.

Determining this target is informed by the relationship between the extent of barrens habitat and sea urchin density at local scales across a variety of reefs in eastern Tasmania. The relationship between the extent of barrens habitat and density of *C. rodgersii* at local scales (10^1 - 10^2 m^2) is statistically significant, but noisy (e.g. Johnson et al. 2005). Given the scale of patch sizes of incipient barrens, this relationship is also influenced by the spatial scale of observation. As the scale of observation is reduced from hundreds or thousands of m^2 to something less than or equal to the mean patch size of incipient barrens, the amount of barrens related to a given density of sea urchins will increase. In the context of setting an upper target density of urchins, data based on spatial scales of the order of 10^2 m^2 are most appropriate. In addition, at a given spatial scale of observation, the relationship will also depend on the time since establishment of the sea urchins, i.e. on the stage of maturity of the urchin-seaweed dynamic. This is evident in the different relationships between the extent of barrens and sea urchin density in the Kent Group in Bass Strait (where *C. rodgersii* first established in Tasmanian waters), in north-east Tasmania (where the urchins first established on the coast of mainland Tasmania), and in the south-east (where urchins have most recently established; see Johnson et al. 2005, 2011; this study) (Table 3).

As might be expected, the data collected from the east coast of Tasmania in 2000 are within the spread of data from the more intensive (but less spatially extensive) surveys in the St Helens and Tasman Peninsula region conducted in this study (2008-2011). However, for a given urchin density, and particularly for densities $< 1.0 \text{ m}^{-2}$, the extent of *C. rodgersii* barrens in the Kent group is much greater than for the corresponding urchin density further south on the east coast of Tasmania. We interpret the situation for the Kent group in 2000, where *C. rodgersii* had been long established and urchin barrens cover $\sim 50\%$ of the reef surveyed (Johnson et al. 2005), to represent a 'mature' urchin-seaweed system in which (because of the hysteresis) extensive barrens, once formed, are readily maintained by relatively low densities of sea urchins which can arise through natural fluctuation in local *C. rodgersii* populations (see section below on *C. rodgersii* recruitment). For this reason, this relationship between extent of barrens and urchin density is unlikely to represent a situation where urchin barrens are *forming* in response to a given density of *C. rodgersii*, and so we ignore these data in deriving estimates of target densities of urchins. Thus, we posit that the most robust information defining this relationship is our most recent data from the east coast sites in the St Helens and Tasman Peninsula region (this study).

Table 3. Best fit relationships, and upper boundary of the 75% and/or 95% prediction intervals, describing the extent of urchin barrens habitat as a function of density of *C. rodgersii* for different locations in space and time in Tasmanian waters. Separate relationships are shown for the Kent group of islands in Bass Strait (data collected 2000; region of long established urchin barrens), and the east coast of Tasmania (data collected in 2002 when, over much of this region, urchins were only recently established; and in 2008-2011 when populations of urchins were well established at the study sites). Data derive from transects 100-200 m²; transects with no sea urchins were excluded from the analysis to prevent large numbers of 'zero-zero' observations with no urchins from dominating the fit. The relationship for the east coast of Tasmania described for 2002 is within the spread of data from 2008-11. In deriving target densities to minimise risk of development of urchin barrens, we use the data from the present study (see text; Fig. 5).

Relationship	adj R ²	Source
$y = 21.82\ln(x) + 48.37$ (logarithmic) *Upper boundary, 75% PI: $y = 21.82\ln(x) + 62.36$	0.635	Kent group, 2000 survey (Johnson et al. 2005)
$y = 47.31x^2 - 4.96x + 0.20$ (2 nd order polynomial) *Upper boundary, 75% PI: $y = 47.93x^2 - 5.18x + 1.45$	0.969	East coast Tasmania, 2002 (Johnson et al. 2005)
$y = 20.68x^{1.31}$ (power) *Upper boundary for 95% PI: $y = 92.85x^{1.31}$, and for 75% PI: $y = 49.84x^{1.31}$	0.810	East coast Tasmania, 2008-2011 (this study)

y = percentage barrens, x = urchin density as numbers m⁻²

*equation defines upper boundary of 75% or 95% (as specified) prediction interval (PI; the interval within which 75% or 95% of future observations are expected to lie)

Given the scatter about the relationship between the extent of urchin barrens and urchin density (Fig. 5), and acknowledging the difficulty in rehabilitating extensive barrens and consequences of barrens formation, it is prudent to be conservative in defining target densities of the urchins. Considering the 95% prediction interval provides a conservative approach, in that it anticipates that only 2.5% of future observations will lie above the upper limit of this envelope, while 12.5% of future observations are expected above the upper limit of the 75% prediction interval.

Target densities of *C. rodgersii* for selected levels of barrens habitat based on the upper boundaries of the prediction intervals show a considerable range depending on the level of barrens cover and prediction interval that is deemed acceptable (Table 4). On the basis of these relationships, we suggest that a target density for *C. rodgersii* of not more than 0.2 m⁻² reflects acceptable risk, while 0.1 m⁻² represents a more conservative (lower) risk strategy.

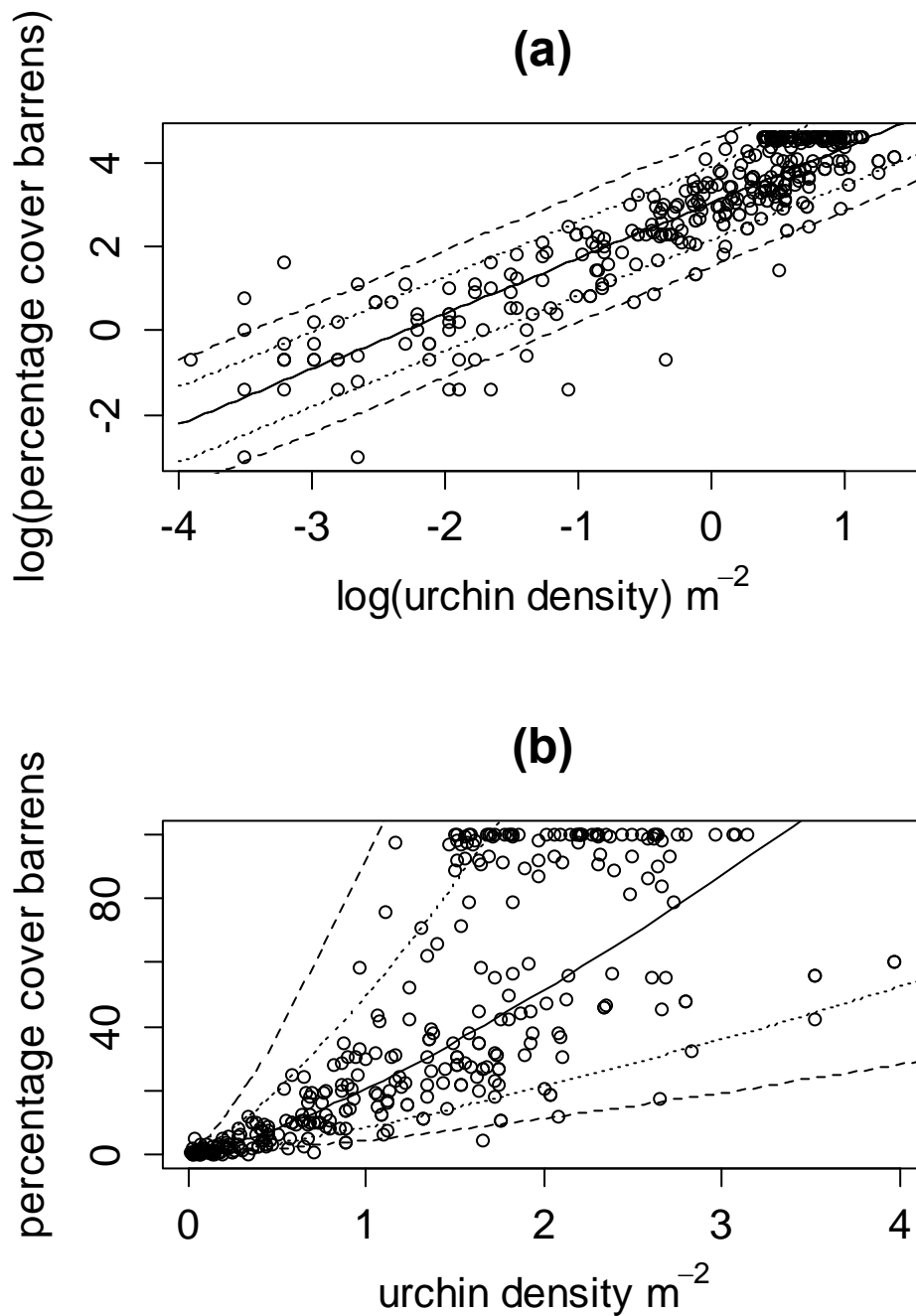


Figure 5. Relationship between average extent of *C. rodgersii* barrens (as percentage cover) and mean *C. rodgersii* density (per m²) on the east coast of Tasmania determined at scales of 10² m² (2 x 50 m transects), observed April 2008-January 2011, and presented on (a) natural log and (b) linear scales (a small number of observations with low densities of urchins and zero barrens were excluded given high leverage). Solid black line is fitted power curve, $y = \exp(3.029)x^{1.309}$, adjusted $R^2 = 0.81$; dashed lines denote 95% prediction interval (upper limit is given as $y = \exp(4.531)x^{1.305}$, lower limit as $y = \exp(1.527)x^{1.313}$, while light dotted lines denote 75% prediction interval (upper limit is given as $y = \exp(3.909)x^{1.307}$, lower limit as $y = \exp(2.149)x^{1.312}$).

% cover barrens acceptable	Target <i>C. rodgersii</i> density (m ⁻²)	
	based on 75% prediction interval	based on 95% prediction interval
0.1	0.009	0.005
1	0.050	0.031
2	0.085	0.053
5	0.172	0.107
10	0.293	0.181
20	0.497	0.308

Table 4. Target densities of *C. rodgersii* for selected levels of barrens habitat based on the upper boundaries of the 75% and 95% prediction intervals of the observed relationship between extent of barrens cover and urchin density on the east coast of Tasmania (see Fig. 5).

A model of population dynamics of *C. rodgersii* on the east coast of Tasmania

Given the nature of data available for *C. rodgersii* populations in eastern Tasmania for which there is robust information on densities and age and size structure, a simple and appropriate model is based on a stochastic projection matrix. The inherent stability of this kind of model (in which predictions inevitably converge to an asymptote) allows greater insight to be obtained in our application, and suggests the approach as 'fit for purpose'. In this approach age-specific survivorship and recruitment are parameters of critical importance. A general outline of model development and parameter derivation is presented below, while a more technical outline is given in Appendix 10.

Key elements of population dynamics are survivorship and recruitment, estimates of which are outlined below prior to introducing the model *per se*.

Annual survivorship and mortality of C. rodgersii

Survivorship is expressed as age-specific survival (transition) probabilities. The proportion of each age class surviving to the next year is estimated from the age-frequency pattern for eastern Tasmania obtained from pooling population age-structure data from all sites for which these data are available (see Ling et al. 2009b; Johnson et al. 2011). These data show an exponential decay over age classes 8-50 years (Fig. A10.1), indicating a remarkably constant decay rate of 0.1103 y^{-1} , or annual survival rate of 0.8897, irrespective of age class. We assume that this describes the background mortality rate in fished areas outside of reserves that, given the scarcity of large lobsters (>140 mm CL) on shallow reefs (<25-30 m depth) in eastern Tasmania, is largely independent of predation by lobsters. Notably, this estimate is identical to the estimate of overall annual *C. rodgersii* mortality (of 0.11 y^{-1}), derived in developing the TRITON model, based on fitting a logistic growth model to the relationship between sea urchin population biomass density and the 90th quantile of the population age distribution (used as a proxy for the time elapsed since settlement of the urchins) as observed for populations in eastern Tasmania. That these two quite different approaches based on two different data types yield the same result gives us confidence in the estimate. Note however that while available data provides an estimate of *annual* mortality, the model is implemented in *daily* time steps (see below). Thus in the model daily mortality is scaled to yield the estimated annual mortality rate.

Recruitment

Recruitment in the model is defined as recruitment to the emergent size class. Although small individuals (e.g. 40 mm TD) are occasionally found emergent on reefs, and 50 mm TD animals can be observed in non-cryptic habitat at night, size-frequency distributions of emergent animals from the Kent Group (Johnson unpublished data, $N=298$ animals) and east coast of Tasmania (Ling et al. 2009b) are consistent in showing the smallest emergent sizes as predominantly 75 mm and 70 mm TD respectively. Given the large spatial

extent over which these data were obtained (i.e. several 100 km of coastline), this result is unlikely to represent development of a single cohort. Assuming emergence at 70 mm TD equates with an expected modal age of emergence of 7 years (Johnson et al. 2005, 2011; Ling and Johnson 2009; Ling et al. 2009b).

Recruitment rates of *C. rodgersii* to any size or age class have not been monitored directly, so it is necessary to estimate this critical population parameter. We follow the basic procedure used for the TRITON model in determining recruitment as the combination of a binomial and lognormal distribution (details in Appendix A.10), although in the projection model we consider recruitment to the emergent 7+ age class, not the 3+ age class as in TRITON. This approach combines several elements that allow for observed space-time variability in recruitment at different spatial and temporal scales. First, it allows for the possibility that in some years recruitment will not occur at all because water temperatures will be too cold to support larval development (Ling et al. 2008). In the period 1946-2007 only 4 in 10 years achieved water temperatures sufficiently warm to support larval development, or 3.9 in 10 years over the last 40 years 1967-2007 (Ling et al. 2008). While the frequency of favourable years is likely to increase into the future (Johnson et al. 2011), this is not considered in the model, and we assume that water temperatures will, on average, support larval development for 4 in 10 years. The approach to estimating recruitment also allows for spatial variation from reef-to-reef (some reefs are likely to consistently receive better recruitment than others; Ling et al. 2009b), and for stochastic annual variability.

The projection model of C. rodgersii population dynamics

The model simulates population dynamics on a hectare of reef, reflecting an appropriate spatial scale for the ecological and management questions to which the model is applied.

The projection commences from an initial population of *C. rodgersii*, which may contain zero individuals. Initial populations that are non-zero are structured to the age distribution averaged for the east coast (Fig. A10.1). There are 45 age classes representing ages 7-50 years, while the oldest age class represents individuals 51+ and older. Choice of the oldest age class to model is to some extent arbitrary, however the model is not sensitive to a sensible range in this choice. Note also that the model converges to the asymptotic density irrespective of the initial population density.

Variability in population size is driven largely by recruitment, which is annual. Accordingly, population dynamics from run to run can vary significantly depending on recruitment. We emphasise again that in simulating recruitment, each run accounts for (1) variability in the large scale oceanographic environment (in some years winter temperatures are too cold for larval development), (2) spatial variation from reef-to-reef (some reefs have consistently better recruitment than others), and (3) stochastic annual variability. Note that while it is straightforward to also introduce stochastic variation into the background mortality term, since the standard error of this estimate is so small, it makes little difference to model behaviour and so for simplicity background mortality is treated as constant.

Projection matrix models, by definition, use a finite time step. To avoid bias leading to inflated urchin numbers, particularly as mortality due to lobster predation increases, it is necessary to use a sufficiently short time step. Thus, mortality takes place with a daily time step such that estimated total annual mortality rates (determined as the sum of 'background mortality' m_b and mortality due to predation by large lobsters m_l) are preserved (Appendix A10).

For scenarios focused on extensive urchin barrens, predation rates are scaled linearly to that observed within the Elephant Rock Research Reserve which, over the entire study period, averaged 18.55 large (>140 mm CL) lobsters ha^{-1} , resulting in a mean instantaneous annual mortality rate on the *C. rodgersii* population of 0.0394. For scenarios focused on incipient barrens or fully intact kelp beds, predation rates are scaled linearly to that observed within the North Bay Research Reserve which, over the period of the study, averaged 37.66 large (>140 mm CL) lobsters ha^{-1} imposing a mean instantaneous annual mortality rate on the emergent *C. rodgersii* population of 0.4919. The linear scaling assumes that, at the densities of urchins and lobsters encountered in Nature, lobsters do not interfere with each other in foraging. (At this point we

remind that constant mortality rates will result in exponential decline in the prey population).

Predation mortality is applied equally across all age classes, i.e. it assumes that large lobsters in the system are large enough to tackle any urchin they encounter, that emergent urchins are distributed randomly at the scale of a lobster's home range, and that lobsters do not select urchins on the basis of their age. A constant *rate* of mortality is consistent with observations from *in situ* experiments showing exponential decline of tagged urchins subject to lobster predation (after Ling et al. 2009a; Ling & Johnson 2012). These data indicate that the time taken by a lobster to encounter a sea urchin, and the absolute number of urchins consumed by a fixed population of lobsters in a year, depends on the density of sea urchins; this is ecologically sensible.

Given the underlying management imperative, what is required from a particular parameterization of the model is the overall likely 'steady state' population size and density (i.e. the mean asymptotic population) of the urchins, which is given as the mean of a Monte Carlo simulation of 1,000 runs ($\pm 95\%$ confidence interval); results of a typical run are shown in Fig. 6. Since the asymptotic mean density is invariably reached within 30 years irrespective of the starting density of *C. rodgersii*, each run simulates 100 years of population development, and the asymptotic density is calculated as the mean of the last 70 years of the averages of the Monte Carlo. Given variability in recruitment, and the consequences for management of loss of seaweed beds with widespread barrens development, the mean asymptotic density defined by the upper 95% confidence interval is also calculated as an important quantity to consider in a management context.

Estimating predation rates of lobsters on *Centrostephanus rodgersii* and target densities of predation-capable lobsters

Given target densities of urchins necessary to realize low risk of extensive barrens formation or to rehabilitate extensive barrens (see above), and knowledge of predicted (asymptotic) densities of urchins for a given mortality rate, annual mortality rates from lobster predation necessary to achieve particular target densities of urchins can be ascertained (see above). By scaling this with known predation rates of large lobsters on urchins it is possible to estimate the target density of large (>140 mm CL) lobsters necessary to, on average, achieve particular long term urchin target densities. In other words, by defining urchin target densities from which associated levels of lobster predation can be inferred, it is possible to identify long term target densities of lobsters necessary to either maintain *C. rodgersii* populations in healthy seaweed beds at sufficiently low densities to provide low risk of incipient barrens developing into extensive tracts of barrens habitat, or to rehabilitate extensive *C. rodgersii* barrens. Thus, to achieve this, it remains only to estimate absolute rates of predation of large lobsters on *C. rodgersii*.

There are three ways to estimate absolute predation rates of large lobsters on urchins based on observations at the two experimental reserves: (1) from fitted models of change in urchin abundance related to lobster abundance at the experimental reserve sites, taking into account all data from all surveys of urchin abundance during the study, (2) from the change in urchin abundance related to lobster abundance but based only on the initial and final estimates of the study period, and (3) from results of screening lobster faecal pellets for evidence of *C. rodgersii* DNA. The first two approaches are justified on the basis that the observed changes showed a statistically significant decline in *C. rodgersii* densities at the North Bay Research Reserve, a notable decline in urchin density at the Elephant Rock Research Reserve², while at control sites there was no consistent trend either up or down in urchin numbers and changes in density were not statistically significant.

² Paired t-tests showed the decline in *C. rodgersii* at ERRR between the initial and final samplings, but not the corresponding changes at control sites, as statistically significant (after controlling level to maintain an overall Type I error rate = 0.05), while ANCOVA across all sampling dates indicates the change at ERRR was not significant although this approach has low power given 5 sampling occasions. See earlier section on estimating predation rates.

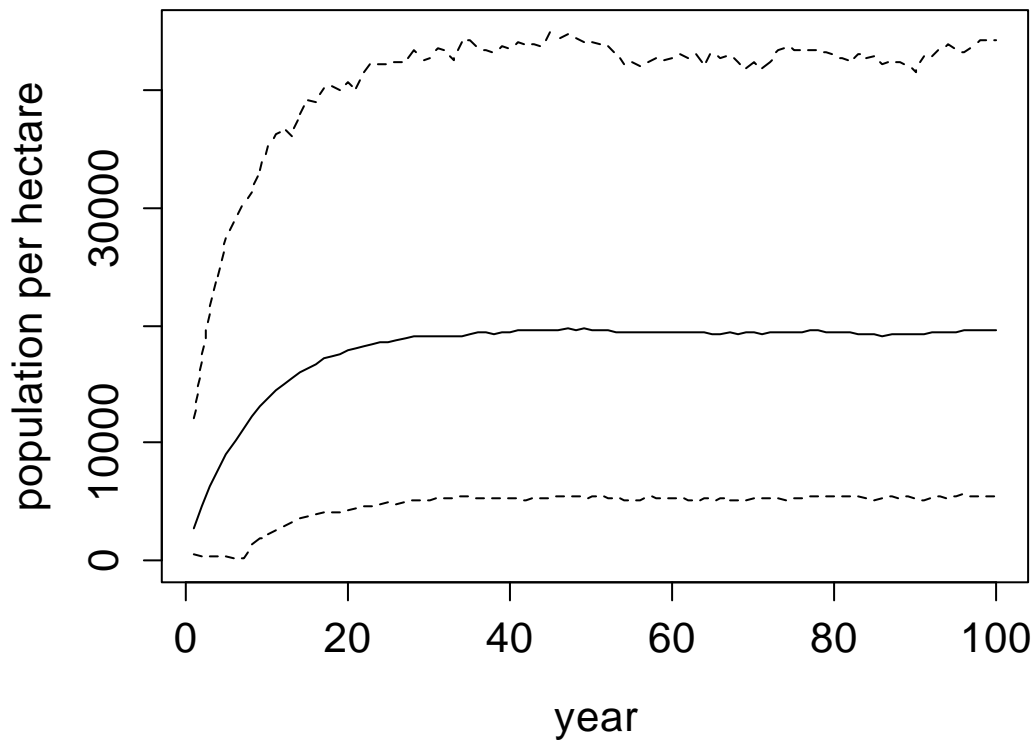


Figure 6. Example of output of the projection model showing changes in the *C. rodgersii* population through time, in this case simulating conditions on the east coast of Tasmania 2002-2005 where we assume that predatory control of urchins by large (>140 mm CL) lobsters is insignificant (i.e. observed background mortality of urchins is not materially influenced by lobsters). The estimated trajectory is given as the mean (black solid line) \pm 95% CI (dashed lines) of a Monte Carlo of 1,000 runs, and is consistent with observations in the Kent Group and NE Tasmania, and with the projections of the TRITON model, that it takes \sim 2-2.5 decades for the urchins to build to a point where extensive barrens form. A predicted mean density of \sim 2 sea urchins m^{-2} and maximum of \sim 4 m^{-2} is also consistent with observations on extensive barrens in eastern Tasmania (e.g. see Fig. 5). The initial population density in this particular simulation was 0.05 m^{-2} , but the model converges on the asymptotic density in 2-2.5 decades irrespective of the initial density.

For the first two approaches we assume exponential decline in urchin numbers based on observations at the experimental sites and our earlier work with predation on a population of tagged urchins (Ling et al. 2009; Ling & Johnson 2012). Thus, within habitat types, we assume that a given lobster density will exert a constant annual mortality rate on *C. rodgersii* across the range of urchin densities likely to be encountered on the east coast of Tasmania and that the absolute encounter rate of lobsters with urchins depends on urchin density, i.e. a fixed density of lobsters will consume greater numbers of urchins as urchin densities increase. Similarly, we assume that lobster predation scales linearly with lobster density over the range of densities likely to be realized on the east coast of Tasmania (e.g. that twice as many lobsters in a given location will consume on average twice as many urchins at a given density at an instant in time). Effectively, this assumes that lobsters do not interfere with each other in prey capture and feeding over the densities encountered on east coast Tasmania.

Of the three approaches, the first is most robust in utilizing all available data – thus providing the greatest precision of the trend – to describe changes in *C. rodgersii* density at the two experimental sites. However, for completeness, and because the modelling approaches also require assumptions, we present results based on all three. For the model based estimates, there is risk of underestimating predation rates because, in the absence of site-specific data, it is necessary to assume zero recruitment of urchins to the emergent

population over the study period; and in the other direction there is risk of overestimating predation rates because we assume sources of mortality other than from lobster predation are negligible (on the basis of no trends or significant changes in urchin density at the control sites). As discussed earlier in this report, of the three approaches, the DNA based estimates are most problematic given the likelihood of inflated positive assays as a result of lobsters ingesting urchin DNA from scavenging or from ingesting urchin faecal pellets in the sediments. Detection rates of urchin DNA in faeces of lobsters from North Bay indicates ingestion other than through direct predation since the *C. rodgersii* population at that site could not sustain the predation rate indicated from the DNA-based approach. Lobster target densities for extensive barrens and incipient barrens are developed separately since it cannot be assumed that the same dynamics apply to both habitats.

The inverse problem – estimating urchin density and extent of barrens cover for given lobster density

General case – long term dynamics

Assuming that lobster predation rates observed at the North Bay and Elephant Rock Research Reserves (in incipient barrens and extensive barrens respectively) scale linearly over the range of densities of lobsters and urchins likely to occur in eastern Tasmania, then the projection model can be run to estimate asymptotic urchin densities (and the 95% CI) for a given lobster density. Using this approach we first examined the general case of long term dynamics (based on asymptotic behaviour), in which long term mean urchin density, and the upper 95%CI of the mean, is predicted dependent on lobster density. By considering the observed relationship between urchin density and the extent of urchin barrens (Fig. 5), this is readily converted to an estimate of barrens cover. Using this approach, four different relationships describing the expected cover of urchin barrens dependent on lobster density are derived. These consist of all four possible combinations of the urchin-lobster density relationships (using the asymptotic mean and upper 95% confidence interval) and the urchin density-barrens cover relationships (based on median and upper 95% prediction interval). Management might be guided by any of these four relationships depending on the level of risk of barrens cover deemed acceptable.

Specific management scenarios

While predicted long term dynamics can provide an overall context and guidance for management, key decisions are more usefully informed by reference to specific scenarios. In consultation with managers and industry, several potential scenarios for management of the rock lobster fishery were considered. Initially, the Tasmanian rock lobster stock assessment model (Hartmann et al. 2012) was used to canvas a range of management scenarios to increase the population of large 140+ mm CL lobsters on the east coast of mainland Tasmania (defined as areas 1-3 in the rock lobster fishery; Fig. 7). Different management strategies were defined as various combinations of (1) spatial management (implemented as a cap on the total allowable commercial catch (TACC) from fishery areas 1-3 combined), (2) introduction of an upper size limit to areas 1-3 (but not elsewhere), beyond which lobsters could not be harvested, and (3) measures to reduce the harvest of the recreational fishery, which is most intensive on the east coast. All strategies were examined in the context of a statewide total allowable commercial catch (TACC) of 1103.2 tonnes, which is a reduced TACC implemented in 2011. The effects of further reductions in TACC as a management strategy were not examined as it was considered that the TACC was appropriate for the statewide fishery, and that within this overall constraint regionally focused measures were required to address the problem of barrens formation unique to the east coast region. A further strategy, referred to as 'no cut', was included. This used the TACC from 2010 (1323.9 t) and no regional measures to illustrate the effect of the implemented TACC cut.

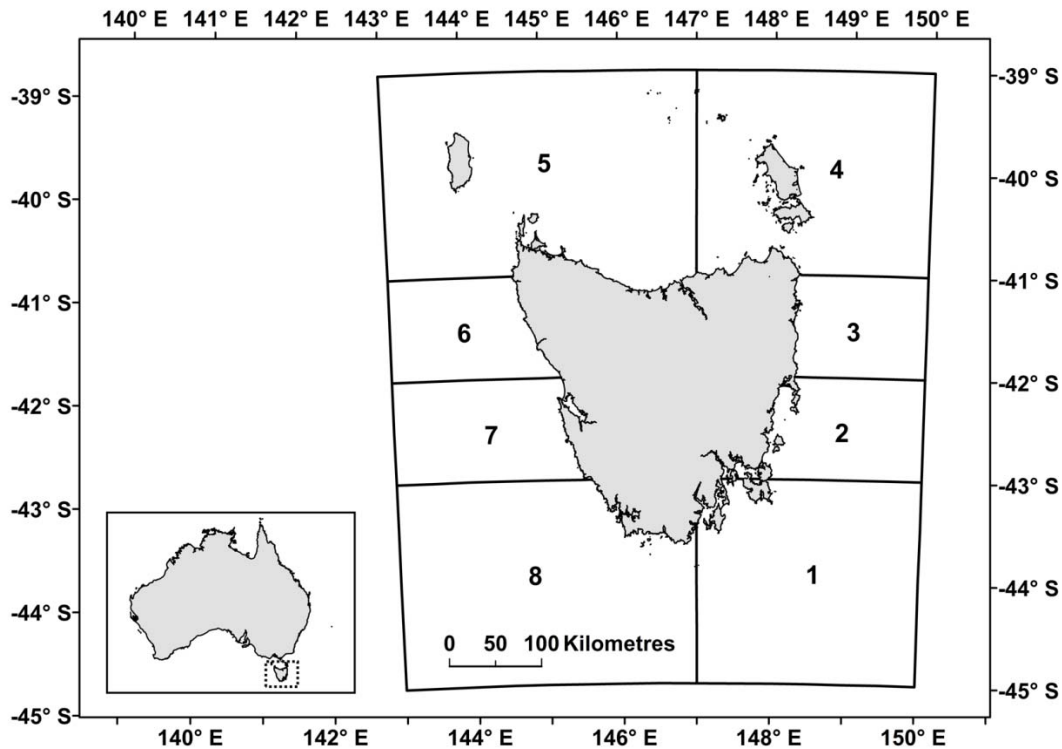


Figure 7. Map of management areas in the Tasmanian rock lobster fishery. Alternative management strategies in the fishery were assessed to identify the most cost effective approach to build biomass of large (140+ mm CL) lobsters, capable of predating emergent *Centrostephanus rodgersii*, in areas 1-3 on the east coast.

Comparing and selecting among the management strategy options was largely on the basis of their effect on (1) net present value (NPV) of the fishery in areas 1-3, (2) statewide NPV, (3) catch per unit effort (CPUE) across all size classes for the east coast component (areas 1-3), (4) CPUE across all size classes statewide, and (5) the biomass of 140+ mm CL lobsters in areas 1-3. NPV provides a measure of future cash flows from the fishery and was calculated over 20 years with a 6.5% real discount rate. These various metrics were compared with the 'no cut' strategy as a reference point.

Assessment of the suite of alternative management strategies identified reduction in the total allowable catch (TAC) of lobsters in areas 1-3 as the most cost effective means to increase the biomass density of large lobsters in this region (see Results and Discussion). Accordingly, the effect of implementing a range of TACs on abundances of large lobsters, and ultimately on *C. rodgersii* densities and the likelihood of barrens formation, in this region was assessed using the stock assessment model. For each TAC scenario, the biomass trajectories of large (140+ mm CL) rock lobsters in areas 1-3 (combined) over two decades (to 2032) were predicted and compared with the extreme scenarios of status quo management and closing the fishery entirely. Scenarios invoking a cap on catch referred to total catch across both the commercial and recreational sectors (thus TAC, not TACC), and ranged between 160-240 t pa. For each scenario the mean biomass density of 140+ mm CL lobsters is predicted to increase until 2032 (the model time horizon), but the increase occurs at different rates (Fig. 8). In the simulations to predict the effects of management scenarios on urchin numbers and extent of barrens cover, biomass density of lobsters was converted to density in terms of numbers of large predatory capable lobsters per hectare of reef.

The projection model was modified to include an annual change in mortality from rock lobster predation as the density of 140+ mm CL animals changed over the simulation period 2012-2032. The change in density of large lobsters is described as annual increments, consistent with a circumscribed period for their annual moult. For scenarios with incipient barrens, lobster densities are converted to an annual predation mortality rate on the urchins based on the observed impact of large lobsters on *C. rodgersii* at North Bay (from the present project) and assuming linear scaling, i.e. that lobsters do not interfere with each other's feeding over the range of lobster densities considered.

All scenarios are explored through Monte Carlo simulation ($n = 5000$ runs). For each scenario, simulations for incipient barrens (and intact seaweed beds) predict changes in urchin density over the simulation period, and the probability density of urchin barrens in 2021 and 2032. These distributions are most appropriately interpreted as the likely distribution of extent of barrens at local scales (10^2 - 10^4 m²) across the east coast. In the case of extensive barrens, the predicted probability distribution of urchin density in 2021 and 2032 is related to the maximum target density of *C. rodgersii* ($= 0.25$ m⁻²) at which recovery of seaweed cover is expected to commence.

All modelling and analysis, excepting the rock lobster assessment model, was undertaken using the *R* package, version 2.14.1.

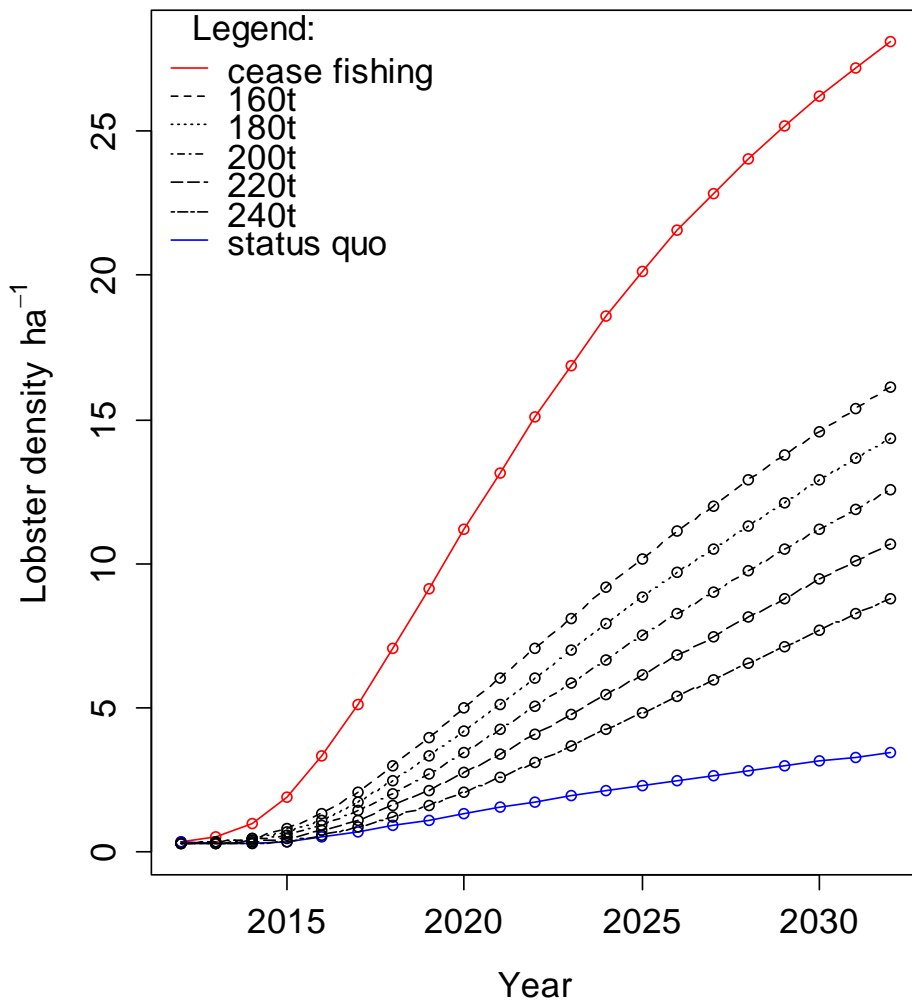


Figure 8. Projected density (number per hectare) of large rock lobsters (140+ mm CL) in east coast fishery areas 1-3 under various scenarios of annual total catch (160-240 t pa) from areas 1-3 between the 'extreme' scenarios of the status quo (blue line) and complete cessation of fishing (red line). The projections were made using the current rock lobster stock assessment model assuming average recruitment to the fishery. Initial predictions were of biomass density, which was converted to density of individuals (on the basis of predicted average size of animals >140 mm CL) to enable direct extrapolation from data obtained from the Elephant Rock and North Bay Research Reserves.

7 RESULTS and DISCUSSION

As was the case for the Methods section, given the scale, complexity and interdisciplinary nature of the project, the Results and Discussion are also presented separately addressing potential management responses at small, medium and large spatial scales.

Small spatial scales – Can abalone divers effectively control *Centrostephanus rodgersii* densities at local scales by culling them while fishing for abalone?

Recall that there were two steps required to address this question, namely a detailed analysis of *Centrostephanus rodgersii* behaviour to establish that areas largely cleared of the sea urchins by divers would not be recolonised quickly from the surrounding population, and then an assessment of the effectiveness of divers at culling the urchins while they fished for abalone.

Fine scale behaviour

A total of 368 sea urchins were tracked across the three barren habitat types, each of which contained a similar density of sea urchins (Table A3.1, Appendix 3). Movement of *C. rodgersii* was strongly nocturnal with peaks in velocity occurring immediately following sunset and just before sunrise (Fig. 9A). This broad pattern was common to all habitat types, although sea urchins consistently moved fastest on flat-rock surfaces and slowest in incipient barrens patches on boulder habitat (Fig. 9B). Differences among habitat types in the distribution of movement patterns across hourly time intervals during the night were not significant.

A total of 189 sea urchins remained within the field of view of the camera for the entire duration of filming and, importantly, approximately equal proportions of the 179 excluded transitory animals moved into (44%) and out of (56%) the field of view. The total nightly distance travelled by sea urchins on widespread flat-rock barrens (5.1 ± 0.3 m) was significantly greater than that of animals on either widespread boulder (3.5 ± 0.2 m) or incipient (2.8 ± 0.2 m) barrens habitat on a boulder substratum (Fig. 10A). Similarly, sea urchins on flat-rock were significantly further from their starting position at the end of the night, and their overall homing tendency to their site of origin at the beginning of the night was weaker relative to animals on incipient or widespread boulder barren (Fig. 10B). The net displacement of sea urchins on incipient barrens was not significantly different to that of animals on widespread boulder barrens, however 98% returned to within 0.8 m of their starting position compared with 84% in widespread boulder barren and just 24% on widespread flat-rock barren habitat. Sea urchins in incipient barrens also spent significantly less time moving than their counterparts on widespread boulder or flat-rock barrens. While many foraging animals display classic Lévy flight movements (i.e. local random movement with occasional large 'jumps' to new sites), we found no evidence to suggest that *C. rodgersii* exhibits this mode of behaviour. This is also supported by very high recovery rates of tagged urchins from circumscribed sites after 12-14 months (Ling & Johnson 2009). Using this evidence, combined with a moderate to strong homing tendency across all habitats (average net displacement < 0.6 m) (Fig. 10B, and below), we are confident that exclusion of animals leaving the camera field of view did not influence our estimates of total distance moved and net displacement.

Our detailed observations of nocturnal behaviour of *C. rodgersii* are consistent with previous observations in situ (Jones & Andrew 1990) and evidence of light sensitivity in other diadematid sea urchins (Millott 1954, 1968; Gras & Weber 1983). Aside from subtle differences in the timing of peak velocity, time-related patterns in foraging were similar across habitats indicating a common response to ambient light levels and an inherent circadian cycle (e.g. Ogden et al. 1973; Bernstein et al. 1981; Hereu 2005). The subtle habitat-specific patterns can be attributed to features of the substratum rather than the extent of barrens formation. For example, sea urchins on widespread flat-rock barren moved faster and over greater distances than their counterparts on boulder substratum (whether widespread or incipient barrens), and had a greater net displacement over the nightly foraging period. This may be explained by more rapid locomotion of sea urchins across flat-rock substrata in the absence of crevices and vertical surfaces (Laur et al. 1986).

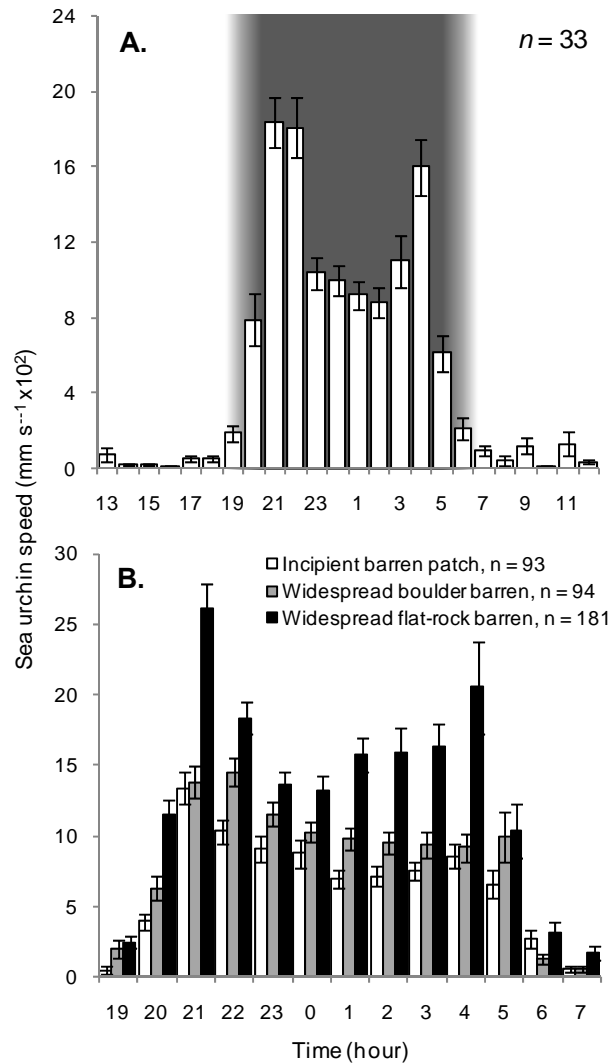


Figure 9. Mean (\pm SE) time-dependent velocity of *Centrostephanus rodgersii* on incipient, widespread boulder and widespread flat-rock barrens as recorded using time-lapse photography. Time is given in 24-hour format. (A) Movement over the entire diel cycle and pooled across habitat types. Shading indicates estimated relative light levels based on the timing of sunset (20:38) and sunrise (05:27) averaged across recording dates. (B) Movement over nocturnal period separated into habitat types.

Of all the sea urchins tracked, 292 paths were composed of at least three moves and were thus appropriate for use in the random walk analysis. The average length of moves varied significantly between habitats, with sea urchins on flat-rock barren travelling approximately 50% further in a single move than those on widespread boulder barren, and more than twice as far as the average length of move in incipient barren patches. The random walk model significantly overestimated net movement of sea urchins (determined as net squared-displacement) in all habitats (Fig. 11), consistent with stronger homing behaviour than is evident from a random walk. Despite variation in individual movement parameters (see Table A3.1, Appendix 3), the relationship between observed and predicted net squared-displacement was similar across habitats. The observed net squared-displacements of pooled paths was within or close to the 95% confidence limits of model predictions for the first and second move of a path, but displacement increased very little beyond these two initial moves. The value at which the observed mean net squared-displacement stabilised varied from $\sim 1 \text{ m}^2$ in flat-rock barrens to ~ 0.35 and $\sim 0.15 \text{ m}^2$ in widespread boulder barrens and incipient barrens habitats, respectively (Fig. 11). The smaller stabilising value for animals in incipient barrens relative to widespread boulder barrens reflects a shorter average move length and less frequent movement overall (see Fig. 10, Table A3.1, Appendix 3). The majority of movement within each

habitat was local due to active homing or movement of short distances within a restricted area, although individuals in incipient barrens patches showed a greater tendency for homing or localised movement relative to that observed on widespread flat-rock or boulder barrens (Table A3.2, Appendix 3).

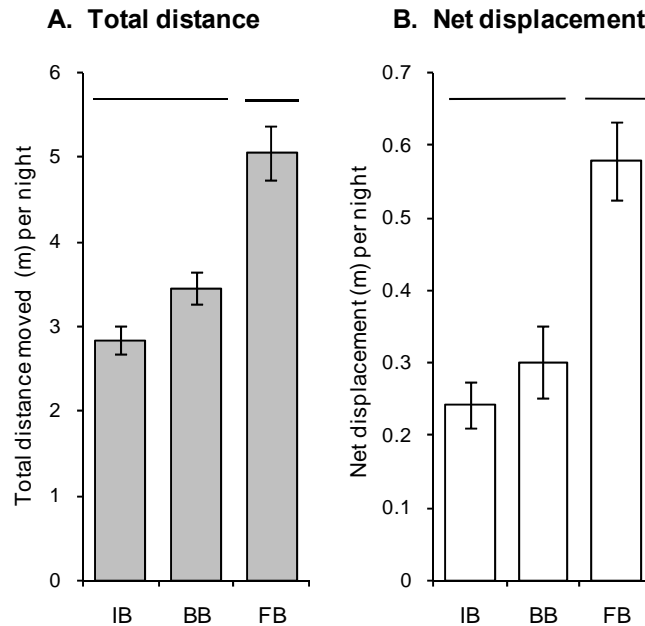


Figure 10. Movement of *C. rodgersii* on incipient, widespread boulder and widespread flat-rock barrens between 19:30 and 07:30 hours as determined by time-lapse photography (data are means \pm S.E.). Only sea urchins remaining within the field of view for the duration of filming were considered; $n = 54, 51, 85$ for incipient (IB), widespread boulder (BB) and widespread flat-rock barrens (FB), respectively. Horizontal bars above indicate statistically significant differences between habitat means. (A) Total distance moved throughout the recording period. (B) Net displacement (i.e. straight line distance) of sea urchins from their starting position after a night of foraging.

In summary, movement of *C. rodgersii* is highly localised relative to the predictions of the random walk model. This suggests either that animals move in a restricted fashion remaining in close proximity to a particular focal point (i.e. a 'home site') or, alternatively, that they move predominantly randomly but with the addition of a distinct 'outwards' and 'inwards' phase away from and returning to a home crevice (i.e. homing behaviour). A homing strategy is the more parsimonious explanation of the observed behaviour, with the observed net-squared displacement only deviating from the predictions of the random walk following the second move of a path. Homing behaviour has been well-documented in conspicuous marine invertebrates such as limpets (e.g. Underwood 1977; Ruiz Sebastián et al. 2002), as has the alternation between random and homing 'phases' of movement within an overall strong homing pattern (Mackay & Underwood 1977).

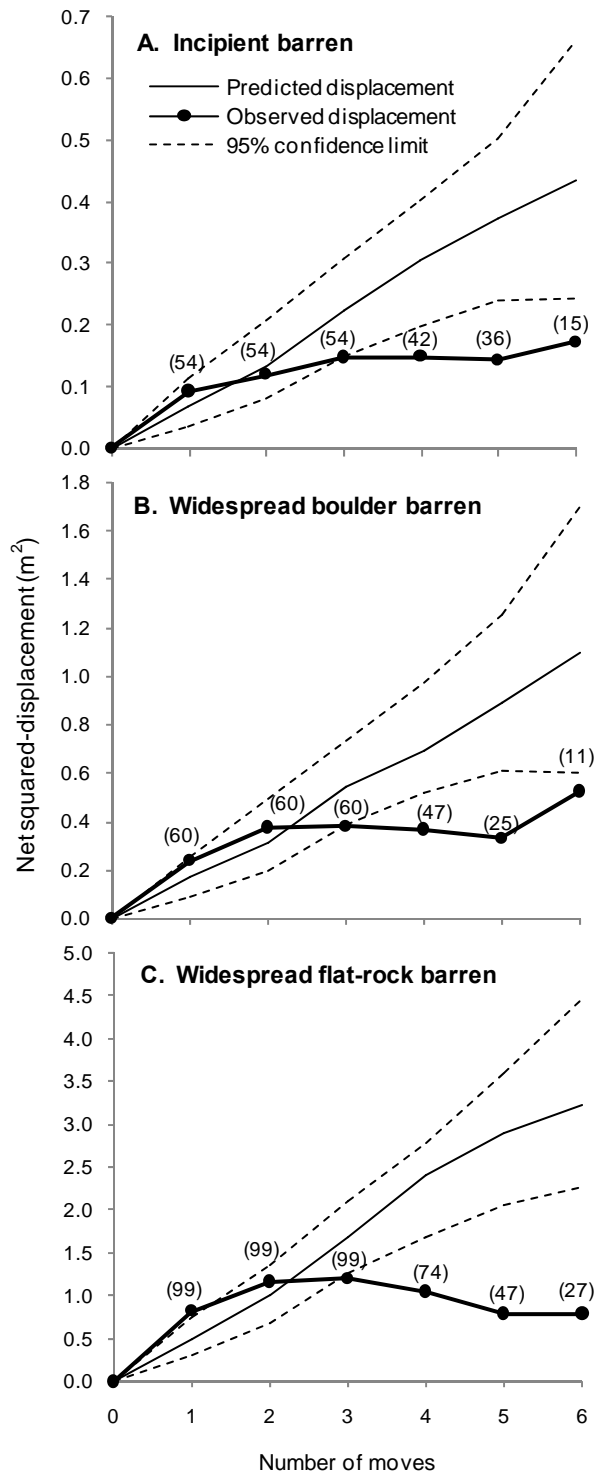


Figure 11. Examination of *Centrostephanus rodgersii* movement across habitats relative to predictions of a correlated random walk model. Mean net squared-displacement is calculated over six consecutive moves from predicted (solid line) and observed (closed circles) movement paths in three habitat types. Dashed lines are 95% confidence limits for the predicted net squared-displacement based on a random walk. Numbers in parentheses indicate the number of individuals observed.

Shelter-oriented homing behaviour has previously been observed and quantified in the diadematid sea urchins *Centrostephanus coronatus* (Nelson & Vance 1979) and *Diadema antillarum* (Carpenter 1984). In general, a homing strategy is thought to be advantageous when predation pressure is reduced by occupying a shelter site, and when the availability of such sites is limited (Cook 1979; Nelson & Vance 1979; see also Ling & Johnson 2012). Shelter-centric homing is frequently observed in conjunction with nocturnal patterns of activity as a defence against predation during daylight hours (Ogden et al. 1973; Nelson &

Vance 1979; Bernstein et al. 1981; Hereu 2005).

The homing behaviour of *C. rodgersii* we observed contrasts with the predominantly random movement observed in *Strongylocentrotus droebachiensis* (Lauzon-Guay et al. 2006; Dumont et al. 2007), a prominent barrens-forming species in the North Atlantic. While neither of these studies examined habitat-specific movement characteristics per se, movement was found to be random on both barrens habitat and in grazing fronts, suggesting an inherent difference in foraging dynamics between *S. droebachiensis* and *C. rodgersii*. In this context it is worth noting that there were no major differences in movement between incipient and widespread barrens as might be expected if *C. rodgersii* exhibited the kinds of behavioural shifts demonstrated in strongylocentrotid sea urchins (Mattison et al. 1977; Dean et al. 1984; Lauzon-Guay & Scheibling 2007a; Scheibling & Hatcher 2007).

These results show clearly that over time scales of 24 h, *C. rodgersii* shows strong homing behaviour to their crevice region or patch, particularly when they occupy a barrens patch within a seaweed bed. This suggests good potential for strong fidelity to particular sites or patches, and is consistent with our observations of high levels of site fidelity over much longer time scales, as evident from up to 45% recovery of chemically tagged individuals within unfenced 8 x 8 m areas on extensive barrens over a 14 month time period (Ling & Johnson 2009).

Fidelity to incipient patches

Of the 42 tagged sea urchins, 71.4% were recovered from within or immediately adjacent their respective incipient barren patches after three months of monitoring. Every individual was resighted on at least one occasion (i.e. they 'disappeared' but 'reappeared' on subsequent visits), suggesting that it is likely that the 12 urchins not recovered at the end of the study were present in the reef matrix but simply not found by divers on the last dive of the study. The cumulative distance moved by animals between the 5 consecutive sampling periods was much greater than their net displacement (even with relatively infrequent sampling), indicating that while local movement and reshuffling of shelter sites continued to occur within patches over the monitoring period, most individuals remained within their particular patch over the three month observation period (Fig. 12A). Indeed, the mean net displacement of sea urchins over the monitoring period did not exceed 2.5 m from the position of initial tagging, although this metric was clearly influenced by the physical dimensions of the patch with animals in larger patches showing greater net displacement than animals in smaller patches (Fig. 12B). These results show clearly the tendency of individuals within incipient barrens patches to remain within the confines of their patch. This is further supported by the observation that no more than six individuals were observed outside incipient patches on any one occasion, five of which were on the periphery of an incipient grazed patch following a seasonal flush of small ephemeral algae.

Observations of marked incipient barren patches in eastern Tasmania have indicated long-term persistence (2001-2011) of patches (*S. Ling unpub. data*), but it was previously unknown whether these patches were maintained by transitory animals from the surrounding kelp bed and neighbouring patches, or by sea urchins that largely remain resident within a given patch, as is shown by our results. Our observations reveal that while individuals are readily able to cross the macroalgal boundary at the perimeter of patches, i.e. substratum discontinuities or abrasion by kelps sweeping the substratum (Andrew 1993; Konar 2000; Konar & Estes 2003) do not prevent movement of sea urchins across the border of barren patches, they tend not to move into the seaweed. The tendency of sea urchins to remain within patches therefore suggests strong fidelity to patches is explained by attraction to characteristics of the patch site rather than inhibition of movement beyond patch boundaries. In the context of efforts to remove urchins from local patches, this high patch fidelity is important since it effectively renders each incipient barren patch an isolated system independent of other patches. This circumstance provides high likelihood of recovery of seaweeds in barrens patches cleared of urchins at local spatial scales.

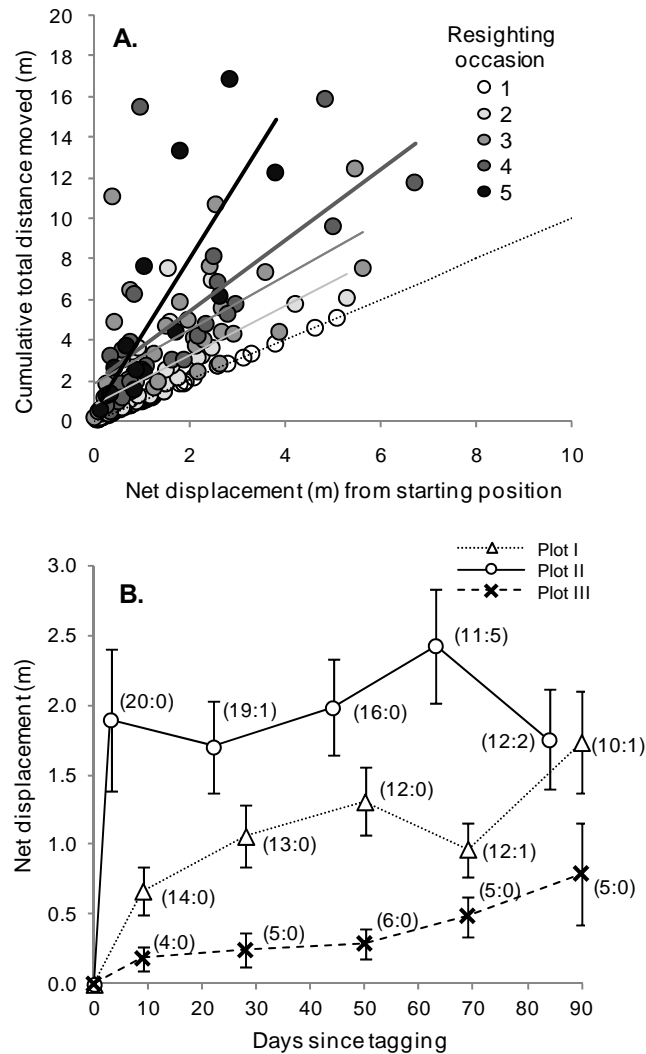


Figure 12. Movement of tagged *C. rodgersii* over a three month monitoring period. (A) Cumulative total distance moved by individuals between sightings vs. net displacement from initial tagging position. Dashed line indicates perfect directional movement (1:1) away from the initial position, while perfect homing is represented by a vertical line passing through the origin. Gray scale of points and fitted lines darken with successive sighting occasions at 10, 28, 50, 69, 90 days since commencement of the experiment. Increasing slope of lines with successive sightings indicates persistent fidelity to incipient barren patches. (B) Mean (\pm SE) displacement of sea urchins from initial tagging position over time across monitored plots (barren patch plus surrounding kelp area). Numbers in parentheses indicate the number of individuals sighted on each monitoring occasion (inside patch : outside patch). Barren patch (plot) areas I-III are 2.41, 3.85 and 1.27 m², respectively.

Response to chemosensory cues and relationship to aggregative behaviour

A choice, either towards or away from either a food or conspecific stimulus, in Y-maze trials was made by approximately 70% of all sea urchins tested. However, there was no trend in the pattern of choices so that the number of animals moving towards or away from each stimulus did not differ significantly for any of the stimuli trialled ($P > 0.5$ for all sets of trials, Table 5) indicating no directional movement in response to olfactory stimuli.

Table 5. Movement responses of *C. rodgersii* to stimuli in Y-maze trials, indicating neither attraction to nor repulsion from waterborne cues from food or conspecifics. The number of trials conducted for each stimulus set (*n*) is given in parentheses. The 'not choosing' response indicates individuals that did not move up the trunk of the maze and into either branch arm. Probabilities indicate likelihood of choices differing from 'no directional choice' (i.e. ratio of 1:1 responses to both stimuli) by chance, estimated using the χ^2 statistic.

Pairs tested	(n)	No. of sea urchins		χ^2 probability of observed choices
		choosing	not choosing	
Blank	(24)	9	8	$P = 0.617$
<i>E. radiata</i> (fresh)		7		
Blank	(24)	9	7	$P = 0.808$
<i>E. radiata</i> (decomposing)		8		
Blank	(25)	7	8	$P = 0.532$
Conspecifics		10		

The absence of locomotory responses of *C. rodgersii* to food cues in the laboratory trials is consistent with *in situ* observations by divers and from our time-lapse photography that urchins do show directional movement towards or aggregation around attached kelps. Sea urchins may stop at a high-quality food patch whilst foraging, but they appear either not to detect chemosensory stimuli from macroalgae, or else do not respond to detected food cues with directional movement. This contrasts strongly with established models of strongylocentrotid foraging which involves strong attraction to food and subsequent formation of aggregations, as has been demonstrated in both laboratory (Bernstein et al. 1983; Mann et al. 1984; Prince & LeBlanc 1992) and field (Mattison et al. 1977; Lauzon-Guay & Scheibling 2007a) experiments. The absence of a clear aggregation response of *C. rodgersii* to attached macroalgal food, in combination with their homing-like behaviour within patches and thus fidelity to particular patches, confers stability to incipient barren patches, since feeding by sea urchins on macroalgae at the periphery of patches will arise only through random encounters.

C. rodgersii was similarly unresponsive to stimuli from conspecifics despite obvious contagious dispersion in the field. While attraction to conspecifics as a potential mechanism by which formation of incipient barrens is initiated cannot be ruled out, nonetheless chemosensory detection of conspecifics does not appear to induce a locomotory response in *C. rodgersii*. Thus, the common observation of aggregated distributions around crevices in the field may instead be mediated via direct contact or, more likely, attraction to optimal local shelters, the importance of which has already been emphasized (Andrew 1993; Ling & Johnson 2012). The high frequency of sheltering behaviour of *C. rodgersii* in the field is consistent with the overriding tendency of large individuals in Y-maze experiments to remain stationary under laboratory conditions when their spine canopy spans the diameter of the apparatus, mimicking a concave shelter (large individuals able to span the apparatus were excluded from our experiments).

Patch fidelity, patterns of overgazing, and opportunity for local control

The behaviours of *C. rodgersii* revealed in this study, coupled with our general observations made over thousands of person hours of diving in the system, indicate the likely mechanisms of barrens habitat formation. Similarities in foraging behaviour on reefs across eastern Tasmania and thus across all stages of barren development from incipient to widespread barren on all substratum types suggest no evidence of a distinctive behavioural shift leading to overgrazing as has been described in other barren-forming sea urchins (e.g. Dean et al. 1984; Harrold & Reed 1985; Vadas et al. 1986). The fidelity of individual *C. rodgersii* to their particular incipient patch is strong, macroalgal cues do not appear to stimulate movement across the kelp-patch interface and, in particular, the aggregative behaviour thought to precipitate formation of feeding fronts in strongylocentrotid sea urchins (Mann et al. 1984; Dumont et al. 2007; Lauzon-Guay &

Scheibling 2007a) is conspicuously absent. As a result, individual incipient barren patches are highly stable and each patch effectively behaves independently.

The detailed behavioural observations and patch size dynamics presented here are consistent with broad-scale data from our general observations over several 100 km of coastline which suggest that the size of individual barrens patches increases as a linear function of sea urchin abundance and that density within patches is remarkably consistent at ~1 urchin per 0.6 m² of barrens area (Fig. 13A). Beyond individual barrens patches, the percentage cover of reef that is barrens across entire kelp beds also shows a strong linear relationship with *C. rodgersii* density (Fig. 13B), suggesting a fixed grazing impact that is a simple function of the local density of *C. rodgersii* at any given site. Thus, it seems clear that eventual widespread barrens occur through the simple process of patch formation, expansion and eventual coalescence of multiple patches. This mechanism of barrens formation differs fundamentally from the more widely studied stronglycentrotid species in the northern hemisphere that form active grazing fronts (e.g. Breen & Mann 1976; Chapman & Johnson 1990; Scheibling et al. 1999; Lauzon-Guay & Scheibling 2007a).

The position and size of any particular *C. rodgersii* barrens patch is dictated by the individual grazing efforts of sea urchins contained within it and, for a given overall density, the local spatial distribution of the urchins is strongly influenced by the availability of shelter. Similarly, the likelihood of initial patch formation is also a direct consequence of local sea urchin density, and thus the distribution of sheltering sites. It appears that increases in population density of *C. rodgersii* across a reef manifest as an increased number of discrete incipient barren patches which, as they grow by the recruitment and grazing activity of additional urchins, eventually coalesce to form widespread barrens habitat from the 'inside-out'. This pattern, underpinned by high fidelity to patches and a homing tendency irrespective of habitat, sea urchin density or stage of barrens formation across the range-extension region, suggests that regulation of urchin density at the spatial scale of individual patches will reduce the likelihood of widespread barrens formation. Moreover, given the independent nature of patches, removal of urchins from individual patches is likely to be an effective means of local control.

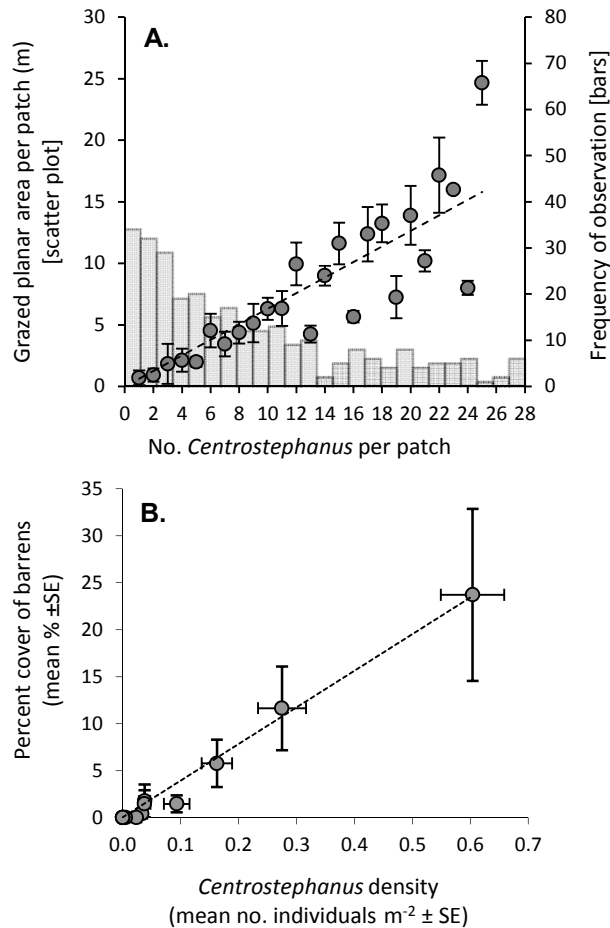


Figure 13. (A) Relationship between the grazed planar area of *C. rodgersii* barrans patches and number of *C. rodgersii* per patch (data are means \pm S.E.) as assessed by timed geo-referenced diver swims ($n = 284$ individual patches). Linear regression given by $y = 0.631x$, $R^2 = 0.901$, $t(24) = 15.1$, $P < 0.0001$. Grey bars represent the observed frequency of each data point. (B) The percent cover of sea urchin barrans and *C. rodgersii* density across sites spanning the entire range-extension region in eastern Tasmania, as assessed by $n = 156$ diver belt-transects (data from Johnson et al. 2005). Data expressed as means \pm S.E. Linear regression given by $y = 39.2x$, $R^2 = 0.99$, $t(12) = 37.5$, $P < 0.0001$. Note that because sea urchin barrans habitat on exposed coast in eastern Tasmanian is caused exclusively by *C. rodgersii* with negligible contributions from grazing by the native *H. erythrogramma* (see Johnson et al. 2005), the intercept for the linear regression was set to 0.

The effect of abalone divers culling *C. rodgersii* while fishing for abalone

A total of seven 'cull' dives were conducted by abalone fishers at Trumpeter Bay (region 2), and there were four at Bunker Bay (region 3) and three at St Helens Is. (region 1). The total numbers of *Centrostephanus rodgersii* culled at each site, based on counts from the divers, were 1,460, 1,447 and 830 for 'cull' sites in regions 1-3 respectively (Table 6). The number of sea urchins culled in a dive was linearly related to the time spent culling (note that these data were not obtained for all dives; Fig. 14a, $R^2 = 0.93$, $P < 0.005$), demonstrating a mean culling rate of 10.7 urchins per minute. Across dives, the urchin cull rate was significantly negatively related to abalone catch rate (Fig. 14b), indicating that in locations where fishing was good, divers killed fewer sea urchins. Notably, the total number of sea urchins culled per dive declined with increasing dive time (Fig. 14c), reflecting that long dives occurred when fishing for abalone was good, while most sea urchins were killed on shorter dives that were truncated when fishing was poor.

Table 6. Summary of *Centrostephanus rodgersii* cull effort by divers while undertaking otherwise normal commercial harvesting of abalone at the three eastern Tasmanian cull sites. (*Survey areas determined from GPS dive tracks, ARC mapping software and SeaMap Tasmania benthic habitat maps).

	*Survey area (m ²)	<i>C. rodgersii</i> density (no. m ⁻²)	Estimated population in survey area	Urchins culled	% popn. culled
Cull Region 1	20,991	0.708	14,868	1,460	9.8
Cull Region 2	25,673	0.766	19,640	1,447	7.4
Cull Region 3	27,436	0.382	10,471	830	7.9

Responses to culling – belt transects

Sea urchins, cover of barrens, and abalone

Overall *C. rodgersii* densities (determined from the 50 m belt transects; Fig. 15) and cover of *C. rodgersii* barrens habitat (Fig. 16) at each site showed little change over the experimental period, even at the cull sites. Changes in *C. rodgersii* density and in cover of barrens habitat over the experimental period were small and did not depend on either 'region' or 'treatment' (i.e. whether sites were subject to culling or not; Table 7). The control site at Sloop Rock (Region 1) supported higher densities of *C. rodgersii* than at any other site, which is also reflected in the higher percentage cover of barrens habitat at this site (Fig. 16). Densities of the native sea urchin *H. erythrogramma* were uniformly low at most sites, and where they were more abundant (control sites in regions 1 and 2; Figs. 17, 19b), changes in abundance were unrelated to culling of *C. rodgersii*. This pattern is reflected as a significant region*treatment interaction for *H. erythrogramma* (Table 8).

Changes in abalone densities were somewhat enigmatic. Cull sites in Regions 1 & 2 and the control site in Region 1 supported the highest densities of abalone in the study (Fig. 18), but at both cull and control sites in Regions 1 and 2, abalone densities declined over the study period, while overall densities in Region 3 were uniformly low and little affected by the culling (Fig. 18). Not surprisingly, these patterns also yield a significant region*treatment interaction (Table 8).

Community Structure

Analyses of the macroalgal and invertebrate communities using CAP shows notable differences in seaweed community composition between regions and between sites within regions (Fig. 19). Region 2 (Freycinet Peninsula) is distinguished by macroalgal species characteristic of moderately exposed waters, e.g. *Caulerpa* spp. and *Cystophora* spp. at the control site (Wineglass Bay), *Acrocarpia paniculata* at the cull site (Trumpeter Bay), while *Sargassum* spp. was common at both sites (Fig. 19a). Regions 1 and 3 support algal communities typical of high wave exposure, with canopies dominated by *Phyllospora comosa* and *Ecklonia radiata*. *E. radiata* was the dominant macroalgal canopy species at all sites.

The 2-dimensional CAP analyses of the invertebrate community distinguishes the control site in Region 2 (Freycinet), and to some extent the control site in Region 1, as supporting higher densities of *H. erythrogramma* (Fig. 19b; see also Fig. 17). It also distinguishes the control site in Region 1 as having higher numbers of cryptic *C. rodgersii*, and the cull site in Region 2 with higher numbers of exposed *C. rodgersii*, relative to other sites. Differences in the relative amounts of cryptic and exposed *C. rodgersii* at the sites likely reflects the nature of the substratum, since we observed a greater proportion of cryptic sea urchins at sites with higher substratum rugosity.

While the ordination plots clearly reveal spatial differences in community composition, over the time period of the experiment there was little evidence of change in community structure associated with fishing abalone or culling sea urchins (Fig. 19, Table 9). This was the case even for the invertebrate community of which *H. rubra* and *C. rodgersii* were important components (Fig. 19b), indicating that,

relative to spatial variation in invertebrate densities, neither fishing abalone nor culling *C. rodgersii* at these sites had a great effect on overall population sizes of these species at scales of 10^2 - 10^3 m.

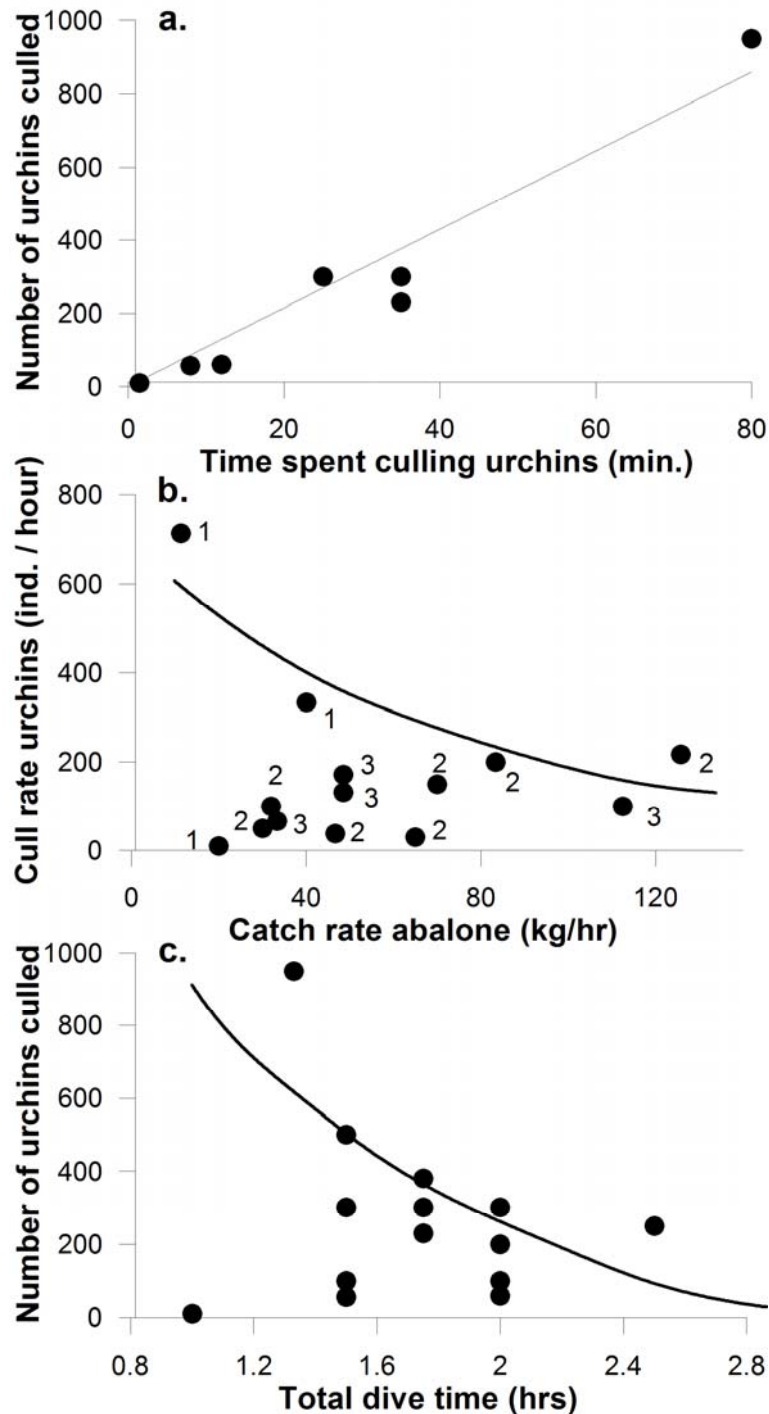


Figure 14. Summary of behaviour of abalone divers culling sea urchins (*Centrostephanus rodgersii*) while fishing for abalone. (a) the number of urchins smashed relates linearly to the time spent culling, 'Urchins Culled' = $11.74 \times \text{'Dive Time'}$ (in minutes), $R^2 = 0.931$, $P < 0.001$. (b) The cull rate of sea urchins declines significantly with abalone catch, curve fitted to data ceiling, $y = -230 \cdot \ln(x) + 1200$, $R^2 = 0.823$. (c) The number of sea urchins culled decreases with total dive time ($R^2 = 0.352$, $P < 0.05$), reflecting that long dives were devoted largely to fishing abalone while short dives indicate divers' quitting the dive early when fishing for abalone is poor and the urchin cull rate is high.

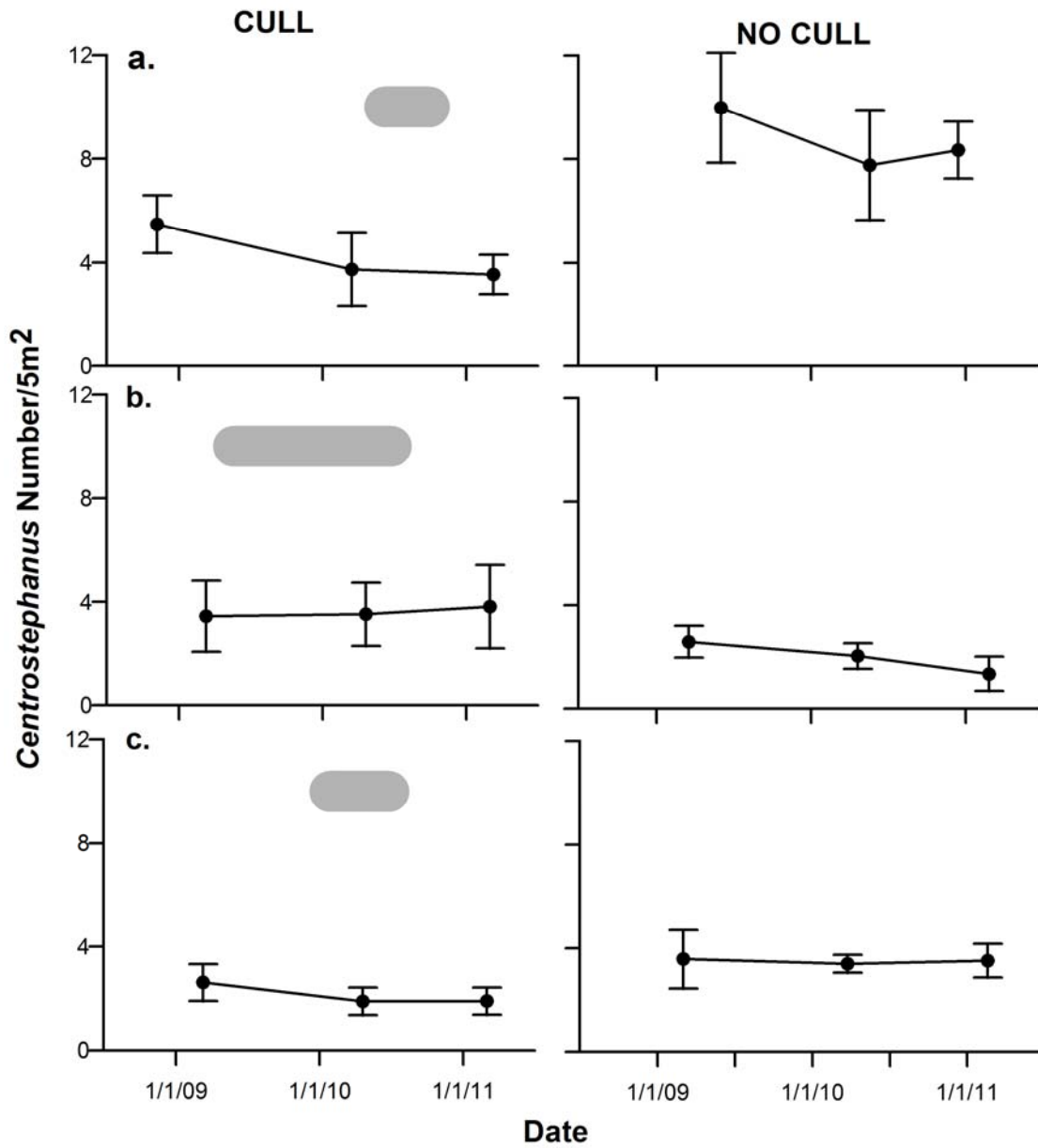


Figure 15. Change in mean abundance (\pm SE) of *Centrostephanus rodgersii* at cull sites and associated control sites in regions (a) 1 = St Helens, (b) 2 = Freycinet Peninsula, and (c) 3 = Maria Is ($n = 6$ replicate transects). Grey bars indicate the period of *C. rodgersii* culling at each site.

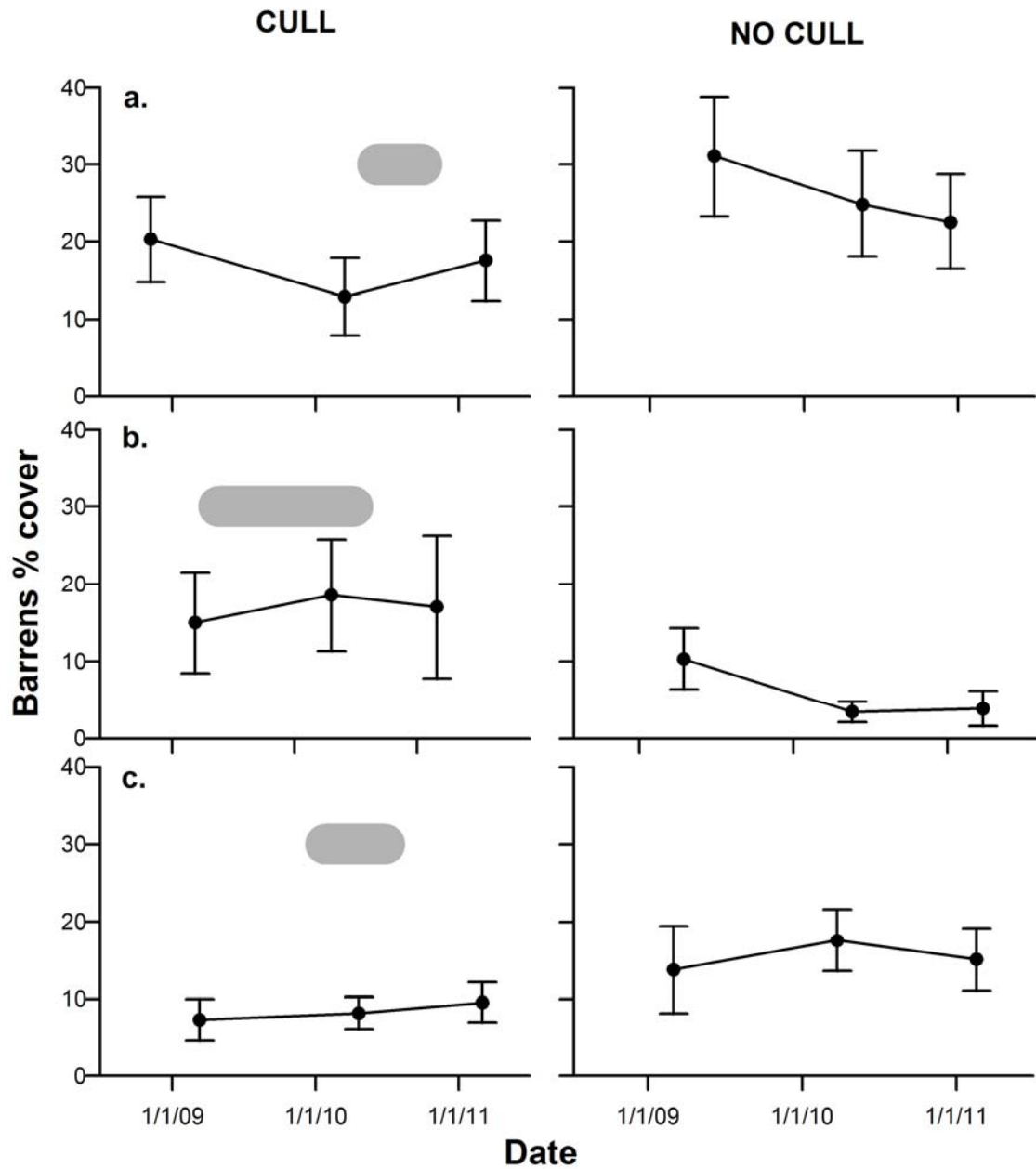


Figure 16. Changes in extent of barrens habitat (mean percentage cover \pm SE) at cull sites and associated control sites in regions (a) 1 = St Helens, (b) 2 = Freycinet Peninsula, and (c) 3 = Maria Is ($n = 6$ replicate transects). Grey bars indicate the period of *C. rodgersii* culling at each site.

Table 7. Results of 3-way ANOVA testing the effect of culling sea urchins (by abalone divers while they fish for abalone) on (A.) the density of *Centrostephanus rodgersii*, and (B.) percentage cover of barrens. 'Treatment' = cull vs. no cull; 'Period' = initial (before culling) vs. final survey times. *C. rodgersii*, transformation = $(Y)^{0.5}$; % barrens cover, transformation = $(Y)^{0.3}$. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

	SOURCE	F Value	Pr(>F)
A. <i>Centrostephanus rodgersii</i>	Region (random)	14.538 _(2,60)	<0.001***
	Treatment (fixed)	0.825 _(1,2)	0.459
	Period (fixed)	15.029 _(1,2)	0.060
	Region*Treat	4.891 _(2,60)	0.011*
	Region*Period	0.126 _(2,60)	0.882
	Treatment*Period	0.000 _(1,2)	0.986
	Region*Treatment*Period	0.797 _(2,60)	0.456
	SOURCE	F Value	Pr(>F)
B. % Barrens cover	Region	6.586 _(2,60)	0.003**
	Treatment	0.668 _(1,2)	0.500
	Period	13.761 _(1,2)	0.066
	Region*Treatment	2.639 _(2,60)	0.080
	Region*Period	0.139 _(2,60)	0.871
	Treatment*Period	0.011 _(1,2)	0.927
	Region*Treatment*Period	1.464 _(2,60)	0.239

Table 8. Results of mixed effects 3-way ANOVA testing the effect of abalone divers culling *C. rodgersii* on (A.) cover of canopy forming algae (*Ecklonia radiata* & *Phyllospora comosa*), (B.) density of *Heliocidaris erythrogramma*, (C.) density of abalone (*Haliotis rubra*) as assessed along fixed belt transects 13-18 months prior to and 6-9 months after the culling effort. 'Treatment' = cull vs. no cull; 'Period' = initial (before culling) vs. final survey times. Canopy forming algae, no transformation required; *H. erythrogramma* and *H. rubra*, transformation = $\ln(Y+0.01)$. ** $P < 0.01$, *** $P < 0.001$.

	SOURCE	F Value	Pr(>F)
A. Canopy algae forming algae	Region (random)	6.82 _(2,60)	0.002**
	Treatment (fixed)	12.53 _(1,2)	0.071
	Period (fixed)	1.79 _(1,2)	0.313
	Region*Treat	0.05 _(2,60)	0.947
	Region*Period	0.94 _(2,60)	0.398
	Treatment*Period	7.74 _(1,2)	0.109
	Region*Treatment*Period	0.249 _(2,60)	0.780
B. <i>Heliocidaris erythrogramma</i>	Region	13.65 _(2,60)	<0.001***
	Treatment	6.57 _(1,2)	0.124
	Period	0.653 _(1,2)	0.504
	Region*Treatment	5.00 _(2,60)	0.010**
	Region*Period	0.53 _(2,60)	0.589
	Treatment*Period	0.281 _(1,2)	0.649
	Region*Treatment*Period	2.01 _(2,60)	0.143
C. Abalone	Region	0.665 _(2,60)	0.518
	Treatment	0.480 _(1,2)	0.560
	Period	6.238 _(1,2)	0.130
	Region*Treatment	5.688 _(2,60)	0.005**
	Region*Period	1.535 _(2,60)	0.224
	Treatment*Period	0.007 _(1,2)	0.942
	Region*Treatment*Period	0.438 _(2,60)	0.647

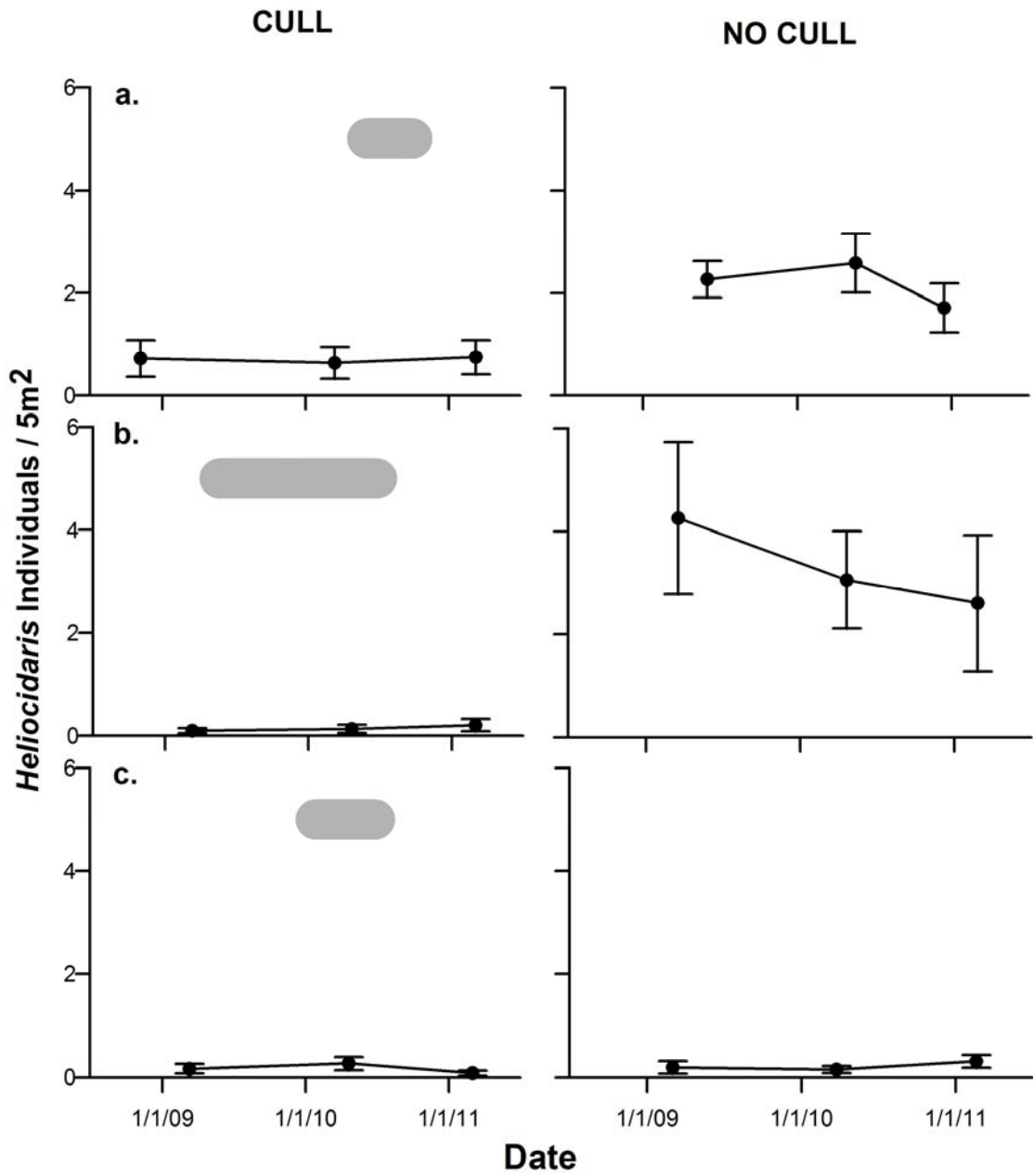


Figure 17. Change in abundance (\pm SE) of *Heliocidaris erythrogramma* over the monitoring period at *C. rodgersii* cull sites and associated control sites in regions **(a)** 1 = St Helens, **(b)** 2 = Freycinet Peninsula, and **(c)** 3 = Maria Is ($n = 6$ replicate transects). Grey bars indicate the periods of *C. rodgersii* culling at each site.

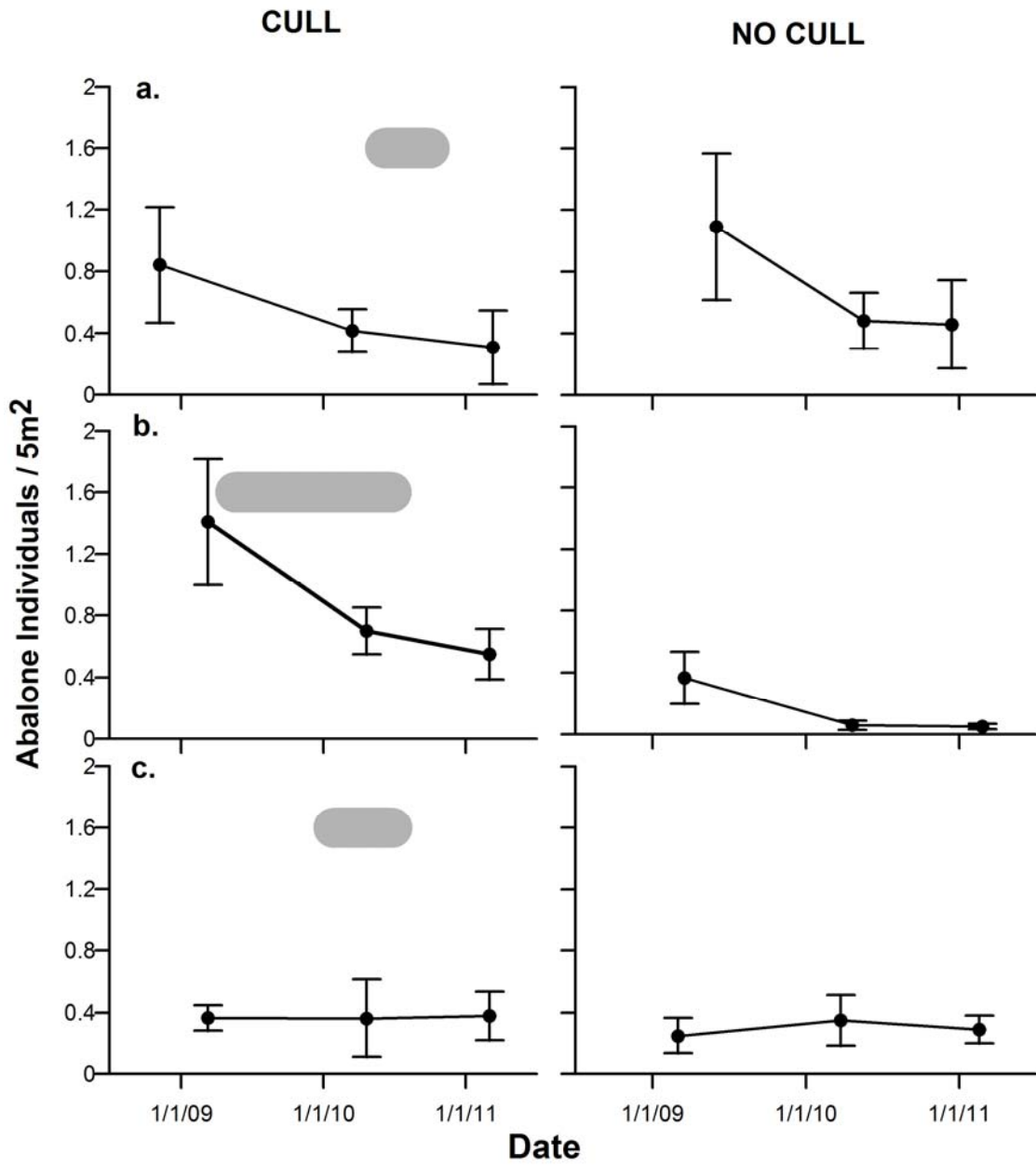


Figure 18. Change in abundance (\pm SE) of abalone (*Haliotis rubra*) at cull sites and associated control sites in regions **(a)** 1 = St Helens, **(b)** 2 = Freycinet Peninsula, and **(c)** 3 = Maria Is ($n = 6$ replicate transects). Grey bars indicate the periods of *C. rodgersii* culling at each site.

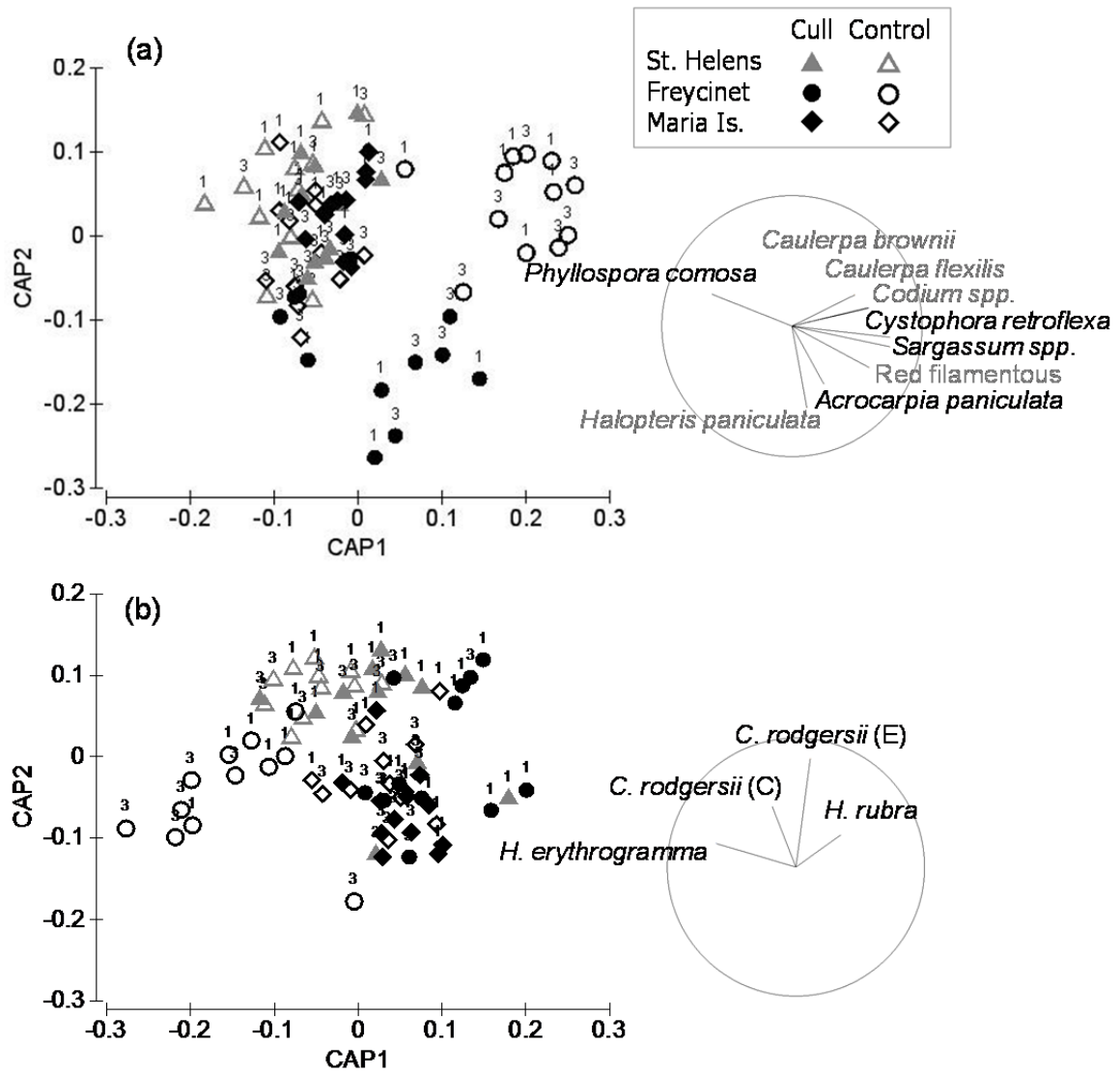


Figure 19. Two-way CAP ordinations of (a) algal and (b) invertebrate community composition for transects at cull and control (no-cull) sites in the 3 regions (St Helens, Freycinet Peninsula and Maria Is) at the beginning (1) and end (3) of the experiment (see Methods for survey dates). Pearson correlations between variables and ordination axes are shown to the right of ordination plots (in (a) only correlations > 0.4 are shown). In (a), canopy species are shown in black text, while understory species are shown in grey. In (b), *C. rodgersii* (C) and *C. rodgersii* (E) refer to densities of cryptic and exposed *C. rodgersii*, respectively. While there were distinct differences in community composition between regions (and sometimes sites within regions), at any one site there was little change in community composition over the duration of the experiment (2009-2011) irrespective of efforts to cull sea urchins.

Table 9. Results of 3-way PERMANOVA testing the effectiveness of culling *C. rodgersii* (= 'Treatment' effect, fixed) by abalone divers during otherwise normal abalone harvesting on (A.) macroalgal, and (B.) benthic invertebrate communities in 3 eastern Tasmanian regions (= 'Region' effect, random), at times 'before' and 'after' urchin culls (= 'Period' effect, fixed). The period 'after' culling was the final sampling session at the conclusion of the experiment (i.e. 2nd 'post cull' survey).

Analysis	Effect	PERMANOVA			PERMDISP		
		df	Pseudo-F	P(perm)	df	F	P(perm)
A. Algal community	Region	2	23.21	<0.0001			
	Treatment	1	0.54	0.601 [†]			
	Period	1	8.08	0.099 [†]			
	Region*Treatment	2	5.75	<0.0001	5	6.76	0.0002
	Region*Period	2	0.77	0.655			
	Treatment*Period	1	2.54	0.218			
	Region*Treatment*Period	2	0.90	0.529			
B. Invertebrate community	Region	2	7.14	<0.0001			
	Treatment	1	2.58	0.162			
	Period	1	3.67	0.190			
	Region* Treatment	2	3.15	0.003	5	1.70	0.354
	Region*Period	2	0.67	0.711			
	Treatment *Period	1	Negative				
	Region* Treatment*Period	2	0.62	0.747			

[†] Based on only 38 unique permutations

Incipient barrens patches

Characteristics of incipient barrens patches based on timed swims were initially conducted in 2008 prior to any culling, with follow up surveys in summer for the next two years and in early spring of the second year (Table 1). On average, each 30 minute swim covered a straight-line distance of 291 m (\pm 43 m). Mean patch density was 23.6 (\pm SE = 1.5) per linear 500 m of benthos, with no significant difference between regions or as a result of the culling treatment (Table 10). There was little change in the size frequency distribution of patches (where the number of urchins per patch was used as a proxy for patch size) over the course of the study, irrespective of culling (Fig. 20; Table 11). Indeed, the only significant change was seen at Sloop Rock (the control site in Region 1), in which there were fewer mid-sized patches but more large ones at the end of the experiment than at the beginning (Fig. 20., top right panel; Table 11), suggesting expansion and coalescence of patches at this site over the course of the study.

Note that the number of sea urchins per patch is a good proxy for patch size since the density of urchins in patches is remarkably consistent; for all incipient barrens patches of ≤ 100 urchins, the density of urchins in the patches was 2.08 m⁻² (\pm SE = 0.06, n = 634 patches assessed), with no significant differences between treatments (i.e. cull vs. no cull sites) or regions (unbalanced 2-way ANOVA using Type III SS, 'Treat' $F_{1,2}$ = 4.603, P = 0.165; 'Region' $F_{2,628}$ = 1.315, P = 0.269; 'T*R' $F_{1,2}$ = 0.791, P = 0.269). This is similar to the mean density of *C. rodgersii* on extensive urchin barrens in eastern Tasmania (e.g. 2.1 \pm SE = 0.1, Ling & Johnson 2009; 2.31 \pm SE = 0.19 for Elephant Rock in eastern Tasmania, CR Johnson unpublished data). Similarly, for each site and irrespective of the culling effort, changes in the density of patches (i.e. number encountered in 500 m) between the first and last surveys were not significant (Table 10). Only patches with ≤ 100 sea urchins were included in this analysis because in censusing large patches with >100 urchins per patch, divers were unable to count sea urchins individually and so these counts are unlikely to have the same accuracy as those based on direct counts in the smaller patches.

Incipient barrens patches in which *C. rodgersii* individuals were culled by abalone divers, and randomly selected barrens patches in associated control sites, were identified, marked, assessed and photographed in Spring of 2010 in two of the three regions, and resurveyed late in the summer of 2011 (after \sim 6 mo).

Over this period, individual culled patches reduced in size on average by ~70% reflecting regrowth of seaweeds in the patches, while monitored 'control' patches not subject to culling did not change size over the same period (Table 12, Fig. 21).

Table 10. Three way ANOVA comparing the density of patch barrens (assessed as number of patches found per 500 m based on timed swim transects) 'before' and 'after' (at time of last survey) urchin culls. 'Treatment' = cull vs. no cull; 'Period' = initial (before culling) vs. final survey times. Transformation = $\ln(Y+0.01)$. * $P < 0.05$.

Response		F	Pr(>F)
Patches/500 m	Region	6.689 _(2,12)	0.011
	Treatment	0.839 _(1,2)	0.456
	Period	0.146 _(1,2)	0.739
	Region*Treatment	1.636 _(2,12)	0.235
	Region*Period	1.037 _(2,12)	0.384
	Treatment*Period	0.881 _(1,2)	0.447
	Region*Treatment*Period	1.281 _(2,12)	0.313

Table 11. Results of paired Kolmogorov-Smirnoff comparisons testing for significance of differences in sea urchin barrens patch-size frequency distribution before and after the culling effort at 'cull' and 'non-cull' (control) sites in the 3 regions in eastern Tasmania.

Region 1	Cull "After"	Control "Before"
Cull "Before"	D = 0.188, P = 0.694	D = 0.190, P = 0.708
Control "After"	D = 0.706, P = 3.134e-05	D = 0.637, P = 3.347e-04
Region 2	Cull "After"	Control "Before"
Cull "Before"	D = 0.202, P = 0.439	D = 0.525, P = 0.0001
Control "After"	D = 0.412, P = 0.003	D = 0.213, P = 0.398
Region 3	Cull "After"	Control "Before"
Cull "Before"	D = 0.200, P = 0.531	D = 0.523, P = 7.10e-05
Control "After"	D = 0.679, P = 8.522e-06	D = 0.310, P = 0.111

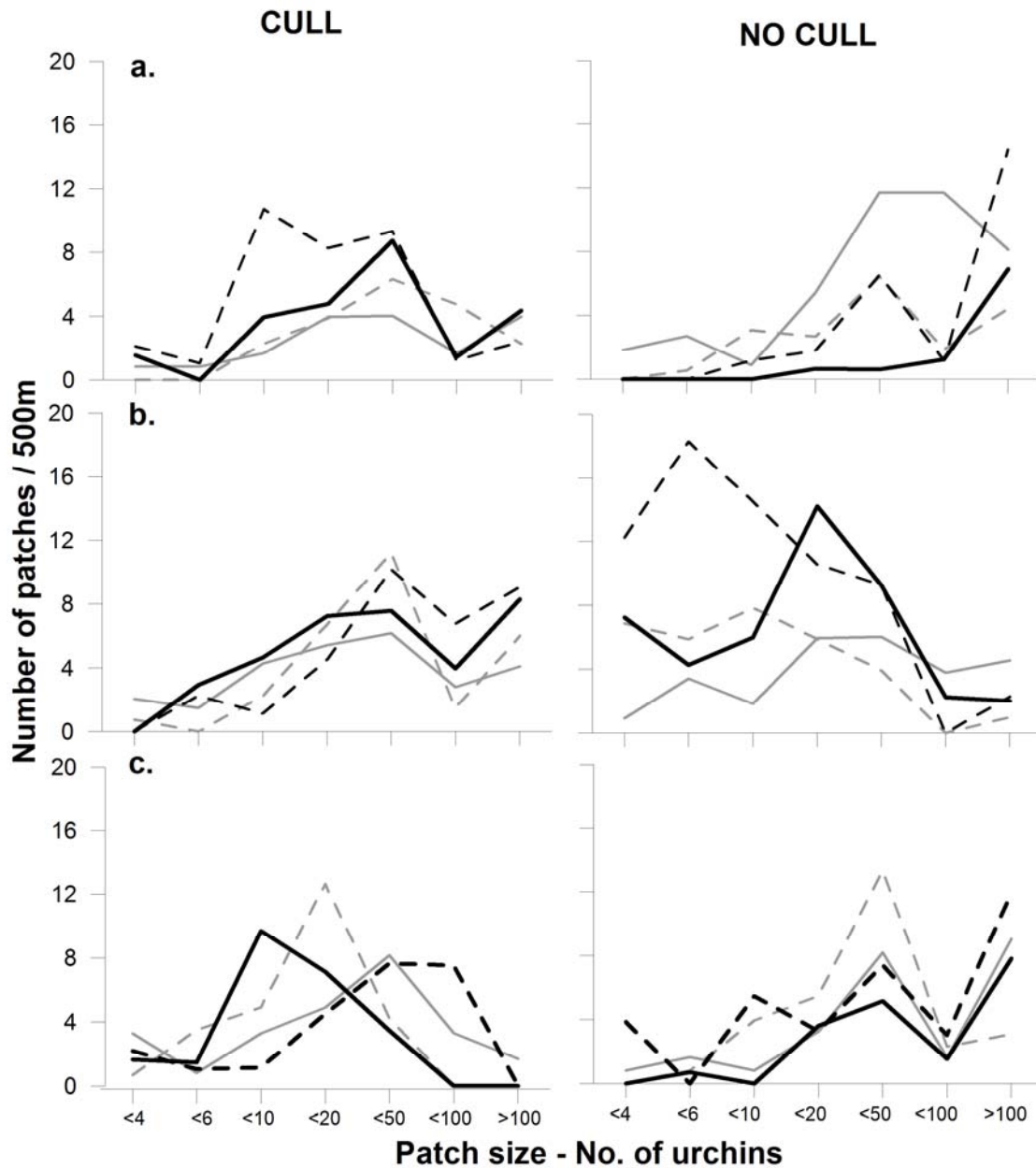


Figure 20. Change in the size frequency distribution of barrens patches at *C. rodgersii* cull sites and associated control sites in regions (a) 1 = St Helens, (b) 2 = Freycinet Peninsula, and (c) 3 = Maria Is. Patch size here is defined in terms of the number of sea urchins per patch. Initial survey = grey dashed; 2nd survey = grey solid; 3rd survey = black dashed; final survey = black solid (see Table 1 for survey dates).

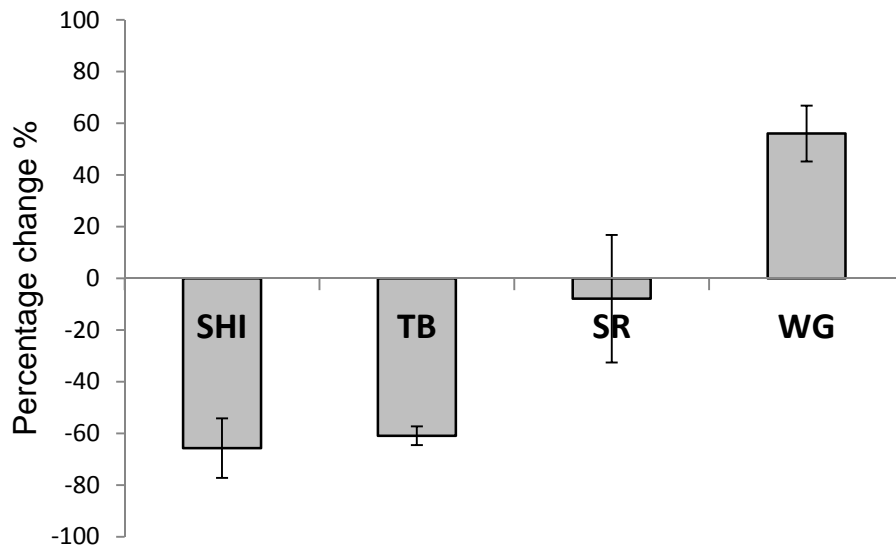


Figure 21. Mean percentage change (\pm SE) in the size of incipient barrens patches determined from photographs taken immediately after culling (cull sites only) and again ~6 months later at cull and control sites in regions 1 (St Helens) and 2 (Freycinet Peninsula) ($n = 6$ in all cases). Cull sites are the two left-hand bars (St Helens Is [SHI] = region 1, Trumpeter Bay [TB] = region 2); respective control sites are the two right-hand bars (Sloop Rock [SR] = region 1, and Wineglass Bay [WB] = region 2).

Given the scale of the *Centrostephanus rodgersii* problem in eastern Tasmania (Johnson et al. 2005, 2011; Ling et al. 2009b), and the social and economic value of the two principal fisheries – abalone and rock lobster – that depend on intact, properly functioning seaweed-based systems (e.g. Babcock et al. 1999, Steneck et al. 2002, Tegner and Dayton 2000), there is considerable pressure on managers to respond to the problem decisively and effectively. This includes a call by abalone fishers to be permitted to cull *C. rodgersii* while they fish for abalone. The results of this study suggest that other than at a very local scale – at the scale of individual patches – this is unlikely to be an effective means to control *C. rodgersii* numbers. While divers were effective at culling sea urchins in the individual patches they encountered to the extent that seaweed cover within these culled patches began to redevelop, in line with experimental work (Andrew and Underwood 1993; Ling 2008; Strain & Johnson 2013), within the overall cull sites (~ 500 m of shoreline) only a very low proportion of the total population at the site was culled (Table 2) such that changes in population size were not detectable. This was also reflected by community composition estimated from belt transects (which sample 600 m² of seafloor at each site on each occasion), and on characteristics of the incipient barrens patches based on timed swims through the site, neither of which detected any effect of the culling effort. Moreover, the divers who participated in the experimental culling were paid an ‘incentive fee’ to participate in the exercise, and were coached on the importance of the culling, so we might expect that their motivation would be higher and ‘dive quitting times’ longer than would be observed in the general population of abalone divers.

When diving for abalone, a fisher’s principal reason for being in the water is for financial return. In Tasmania, abalone quota is nowadays not usually owned by the divers, so that in the majority of cases divers are catching for quota holders at a defined rate of return. While divers in this fishery recognise clearly that *C. rodgersii* is a threat to abalone habitat, they are candid in indicating that their principal concern is to ensure adequate financial return on the day. In this study, where the importance of culling was strongly exhorted, it was clear that highest cull rates were on relatively poor yielding dives for abalone, and that divers quit these poor yielding sites (for abalone) relatively quickly. We interpret diver motivation underpinning this behaviour as reflecting a primary desire to ensure financial return. Thus, abalone catch rates on short dives were relatively low primarily because abalone abundances were low at these sites (perhaps related to the negative relationship between abalone and *C. rodgersii* abundance; Andrew and Underwood 1992; Johnson et al. 2005, 2011; Strain 2010; Strain and Johnson 2009), not because divers

were busy smashing sea urchins and thus devoting little time to fishing. Conversely, divers stayed in the water longer when catch rates (of abalone) were high, but whether low urchin cull rates on these dives reflected high opportunity for productive fishing or low abundances of sea urchins is moot. Either way, the data indicate that divers tend to stay in the water at catch rates of $\sim \geq 40$ kg per hour (e.g. Tarbath & Gardner 2011). It seems clear that at dive sites where *C. rodgersii* is relatively abundant there are also relatively few abalone (see also Johnson et al. 2005, 2011; Strain 2010) and so divers, while able to cull at higher rates, are not prepared to spend long periods of time culling given their need for financial return. From casual conversation with divers, we suggest that those catching abalone for others are least likely to spend time culling urchins.

Table 12. Results of 2-way ANOVA on the percentage change in size of barrens patches (i.e. size of patch at last survey subtracted from initial size, expressed as a percentage of initial size) dependent on effects of 'Region' and 'Treatment' (= 'cull' vs. 'no cull'). Given lack of any effect of 'Region', post-hoc pooling across regions (to improve power) shows a highly significant effect of 'Treatment', 1-way ANOVA, $F_{1,22} = 18.68$, $P = 0.0003$. Mean change in size of patches in which urchins were culled showed a reduction of size of 68.9% ($\pm SE = 11.2$) ~ 6 months after culling, while 'control' patches not subject to culling declined by 3.5% ($\pm SE = 10.17$). Not surprisingly, the decline in size of the culled patches is highly significantly different from 'no change' (=zero; $t_{11} = 3.538$, $P = 0.002$, 1-tailed test), while change in size of the control patches does not differ from zero ($t_{11} = 1.780$, $P = 0.738$, 2-tailed test).

Response	Effect	$F_{(df)}$	P
Δ Barrens planar area (m^2)	Treatment	63.53 _(1,1)	0.079
	Region	1.949 _(1,22)	0.178
	Treatment*Region	0.298 _(1,22)	0.591

Divers may also have limited motivation to devote resources to culling urchins if they perceive that they may not benefit personally from the investment. The abalone fishery in Tasmania is managed by a total allowable catch, but divers are largely unrestricted in where they can fish. Thus, a diver clearing urchins from an area might not see the benefit since he has no control over who fishes in the area subsequently.

Irrespective of motivation, divers are likely to have little overall impact culling sea urchins except at recognised high yielding sites (i.e. where site visitations are likely to be relatively frequent) because they are usually unwilling to return to a site soon after it has been fished, preferring to enable uncaught abalone sufficient time to emerge and/or grow into the fishery. This behaviour combined with requests from processors for abalone from particular areas (depending on where pickup trucks are operating and/or dependent on market demand) ensures that divers are unlikely to return to the same section of coastline more than 2-3 times in a year. In combination, the relatively small impact of divers undergoing normal harvesting activities, as demonstrated in the present study, and low frequency of visitation to particular stretches of coastline, suggest that abalone fishers culling sea urchins while they are fishing is unlikely to have a significant effect at controlling sea urchin numbers other than at very local scales (10^0 - 10^1 m). However, it is likely that particular spatially circumscribed and valuable sites recognised for their consistent and high yield to the fishery may attract particular efforts of divers should it become evident that *C. rodgersii* densities were increasing to the point where incipient barrens patches were appearing and the ultimate threat of widespread barrens perceived to be real. A consistent effort by divers in a locally circumscribed area may well provide critical control at key sites.

Anthropogenic intervention to control 'outbreaks' of sea urchins (Andrew et al. 2002; Bernstein & Welsford 1982; Wilson and North 1983) and other echinoderms (e.g. *Acanthaster planci*, Moran 1986; Great Barrier

Reef Marine Park Authority 1995; Reef Research Centre 2003; Lassig 1995) around the world has challenged managers for decades. Nowhere has intervention by users divers for direct culling been successful in dramatically reducing population numbers, despite massive and widespread effort in some circumstances, other than to provide tactical control in a limited area at specific sites (Lassig 1995). Application of quicklime to reduce urchin densities has been used with some success at intermediate spatial scales in California (Wilson and North 1983), and in an experimental setting at small scales in Nova Scotia (Bernstein & Welsford 1982). In contrast, harvesting of sea urchins associated with fisheries for a commercial product (i.e. sea urchin roe) has been successful in limiting urchin numbers over large spatial scales, and there are numerous examples worldwide of collapse of sea urchin fisheries through overfishing (Andrew et al. 2002). Our evidence leads us to conclude that encouragement of the fledgling diving-based fishery for *C. rodgersii* in eastern Tasmania is likely to play a more useful role in controlling urchin numbers than culling by abalone divers engaged in fishing. Nonetheless, an adequate response to the challenge posed by *C. rodgersii* in eastern Tasmania will require a multiplicity of approaches, and engagement of abalone divers should be a part of the arsenal and can make a contribution, particularly at local sites of particular interest where sea urchins are at low abundance. However, definitive control at scales of 10^2 m by divers is unlikely to be effected while fishing for abalone. This will require targeted intervention, either by divers mobilised for the purpose, and / or through application of technologies such as quicklime, and / or which may be associated with commercial harvesting of *C. rodgersii* for human consumption.

Meso scale – Can translocating large lobsters to shallow reefs control *C. rodgersii* numbers at meso scales?

In this section is presented analysis of the local effects of translocation of large predatory-capable lobsters and closing reefs to fishing of lobsters, and an assessment of predation rates of large lobsters on sea urchins that is necessary to inform the modelling work that is the focus of the work addressing management questions at large (whole-of-coast) scales.

The results are presented in three parts. In the first is examined (i) the extent to which translocated lobsters remained located, and established home ranges, at the site of their release, (ii) whether large lobsters inhabit and forage on extensive *C. rodgersii* barrens given existing data from fished areas (and thus based largely on small lobsters) showing that lobsters are rare on extensive barrens, and (iii) the effect of establishment of research reserves closed to fishing on lobster populations. Having demonstrated establishment of an elevated population of large lobsters at the two experimental research reserves in this first part, the second part examines the impact of these lobsters on the sea urchin populations at the translocation sites closed to fishing relative to the control sites (without added lobsters and open to fishing), and any flow-on effects on seaweed community structure and benthic invertebrates. Finally, we analyse the two methods of determining absolute rates of lobster predation on *C. rodgersii*, which is required as a critical component of the modelling work to assess management scenarios at the whole-of-coast scale.

Lobster translocations: Lobster dispersal, population dynamics and behaviour

Will lobsters reside on extensive barrens habitat?

Acoustic tracking revealed that large predatory lobsters translocated to ERRR were frequently located on widespread sea urchin barrens (Fig. 22A). Of 22 individual lobsters tracked at ERRR, the home ranges of only 6 individuals were observed to be centred on kelp beds, while 12 individuals established home ranges on the extensive sea urchin barrens, with the remaining 4 lobsters establishing home ranges in deeper water where the reef is dominated by sessile benthic invertebrate assemblages (i.e. 'sponge gardens') (Fig. 22A; for full summary see Table A5.3). Home ranges of large lobsters were located on barrens in both winter ($n=12$ tracked individuals, over 3 months) and summer ($n=10$ tracked individuals, over 2 months; Fig. 22A, Table 13A). Summing the time intervals between successive positional estimates in each habitat type showed that large predatory lobsters (140+ mm CL) spent more time on sea urchin barrens than in adjacent kelp beds. Analysis of acoustic tracking across seasons at ERRR indicates that lobsters spent on average 48% (bootstrapped mean; 95% CI = 34 – 60%) and 29% (16 - 44%) of time on barrens and in kelp habitats respectively (Table 13B), and spent the remainder of time split between sessile invertebrate dominated habitat (sponge gardens) on the deeper margin of the reef (~16%) and on the soft sediment adjacent to the reef edge (~10%). At NBRR, acoustic tracking of large lobsters in kelp beds containing incipient barrens patches, which comprised 1.03% of the reef by area, revealed that on average large lobsters spent 1.2% (bootstrapped mean = 1.2%; 95% CI = 0.6 – 1.7%) within these barrens patches (Table A5.4).

Movement rates estimated as total daily displacement of lobsters from an original point of detection were similar for lobsters tracked on urchin barrens and kelp beds at ERRR (means of $4.26 \text{ m.day}^{-1} \pm \text{SE}$ & $5.43 \text{ m.day}^{-1} \pm \text{SE}$ for barrens and kelp respectively; 2-way unbalanced ANOVA, Type III SS; transformation = $\log(\text{displacement})$, effect of 'Habitat'; $F_{1,18}=0.0003$; $P=0.99$); however, overall displacement was greater in summer than winter, averaging 8.15 and 1.7 m.day^{-1} respectively (effect of 'Season'; $F_{1,18}= 5.83$; $P=0.027$), with this seasonal effect evident for both habitats ('Habitat*Season'; $F_{1,18}=0.07$; $P=0.79$).

Within a 24 hour period, examination of movement (velocity) across the night/day cycle at ERRR revealed that the effect of diel phase on lobster movement depended on season (2-way unbalanced ANOVA; transformation = $\sqrt{\text{velocity}}$; 'Diel phase*Season'; Type III SS; $F_{1,220}=7.44$; $P=0.007$), with higher nocturnal

activity evident in summer than in winter (Fig. 23). A slight increase in nocturnal activity was also observed for large lobsters at NBRR during summer (Fig. 23), although an overall nocturnal effect (pooling all night periods vs. all day periods) was not evident at this site (1-way ANOVA, $F_{1,64}=0.004$, $P=0.95$).

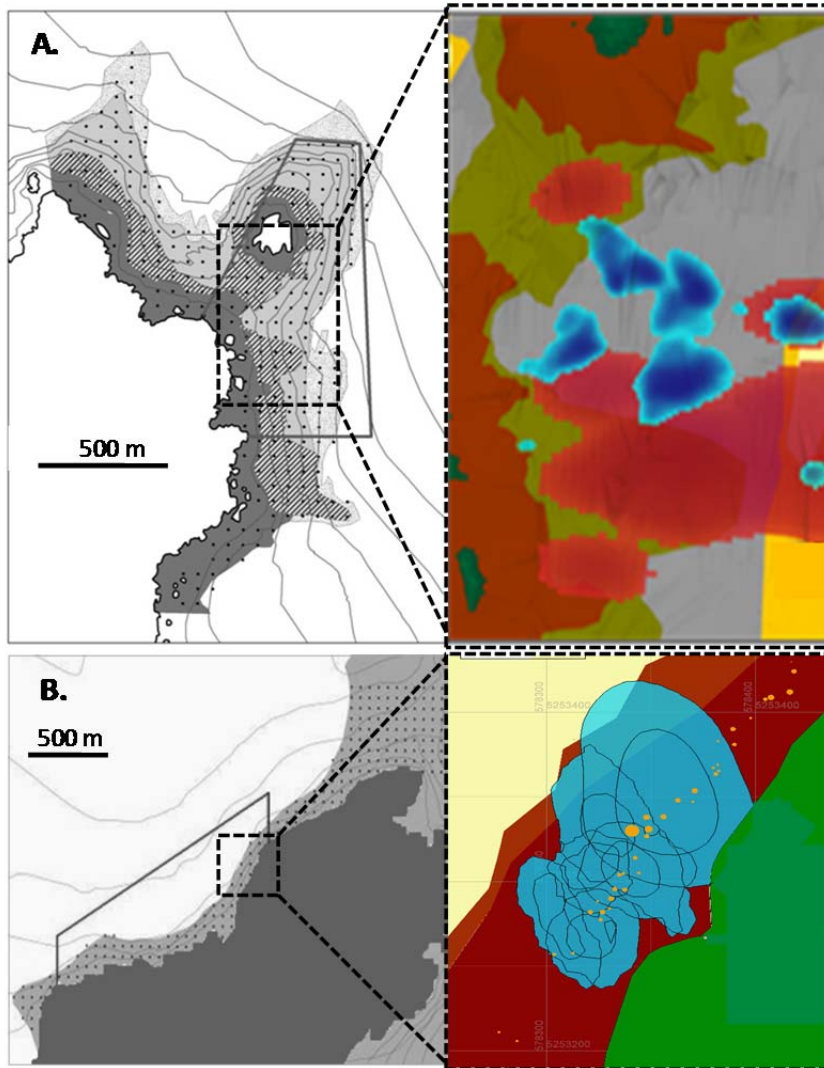


Figure 22. Map of eastern Tasmanian Research Reserves. A. Elephant Rock Research Reserve (ERRR, 41°15'13S; 148°20'24E) showing trapping grid (dots) overlaid on the reef inside the research reserve (defined by grey solid line); dark grey and hashed zones indicate kelp bed habitat (hashed is where urchins effect localised overgrazing of largely understory species), light grey shows widespread *Centrostephanus rodgersii* barrens). Expanded dashed-box indicates the central portion of ERRR where large lobsters were tracked using acoustics; green is land, grey is barrens, kelp is brown, kelp with overgrazing of the understory is khaki, yellow is sand on reef edge; blue and red regions are home ranges (HR95) for lobsters tracked in winter and summer 2008/09 respectively. B. North Bay Research Reserve (NBRR, 42°52'19S; 147°57'14E), showing extent of trapping grid (dots) and kelp dominated reef (with scattered incipient *C. rodgersii* barrens patches – shown as orange dots in expanded dashed-box); in LH figure dark grey is land, light grey is low profile reef, and white is sand. Expanded dashed-box (RH figure) shows overlapping home ranges of large lobsters tracked in summer 2010/11; green is land, brown and burgundy is reef, blue indicates lobster home ranges with boundaries as dark lines. Depth contour lines show 5 m depth intervals.

Table 13. A. Mean proportions of lobster Home Ranges (showing 95CI of 10,000 bootstrap samples in parentheses) comprising urchin barrens vs. kelp beds across seasons (I.); and proportion of acoustic tracked time that lobsters spent in urchin barrens and kelp beds (II.). B. Two-way unbalanced ANOVA results (using Type III SS) testing for effects of *Habitat* (barren vs kelp, fixed effect) and *Season* (winter vs summer, fixed effect) on the distribution of (I.) speed of lobster movement ($m \cdot day^{-1}$); and (II.) lobster displacement, for large acoustically tracked lobsters in the Elephant Rock Research Reserve - transformations required to stabilize variance for each response variable are shown in far LHS column, *indicates significant effects at $\alpha = 0.05$.

	Habitat	% of reef Area at ERRR	Mean Percentage (95% Confidence Interval)		
			Winter	Summer	All Seasons
A. Proportion of Home Range area	Barrens	43.2	54.6 (34.0–73.5)	39.0 (22.7–55.)	47.5 (34.5–60.4)
	Kelp bed	40.0	24.8 (6.2–46.9)	34.3 (18.5–53.2)	29.1 (16.1–43.6)
B. Proportion of tracked time	Barrens	43.2	58.3 (38.1–77.5)	32.6 (17.4–50.7)	46.6 (33.6–59.6)
	Kelp bed	40.0	24.2 (8.0–44.7)	29.4 (9.4–52.4)	26.5 (13.4–41.5)

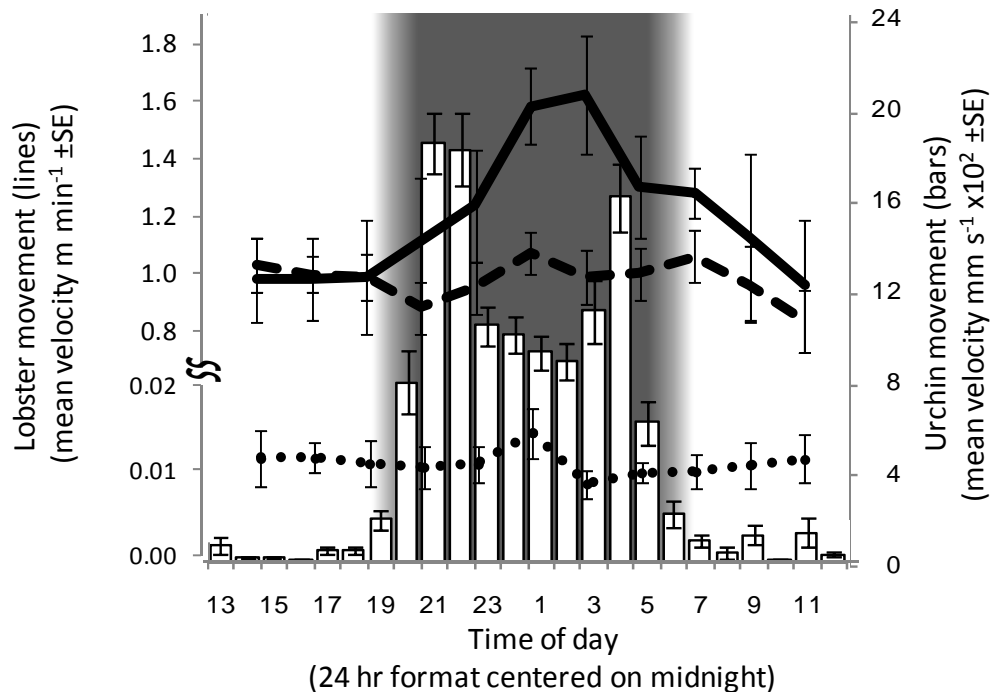


Figure 23. Diel patterns of lobster movement at ERRR (solid line, summer; dashed line, winter) and NBRR (summer, dotted line). Lobster movement patterns are overlaid on the strongly nocturnal movement of the sea urchin *Centrostephanus rodgersii* at ERRR (redrawn from Flukes et al. 2012). Note that the lobster movement axis is split to show the much lower overall rates of movement described for NBRR, which was a function of greater positional accuracy obtained for the VRAP system at this site, thus movement is a relative measure comparable only within sites.

Residency of lobsters on sea urchin barrens is size-dependent

Concordant with observations from the acoustic tracking, displacement of large translocated lobsters between release and location of first recapture in traps were similar across habitats (Kolmogorov-Smirnov test; $D = 0.263$, $P = 0.132$), with displacement distances averaging 358 m ($\pm 21SE$, $n=91$) and 308 m ($\pm 44SE$, $n=25$) for lobsters inhabiting barrens and kelp beds respectively (Fig. A5.2; the magnitude of displacement of translocated lobsters at NBRR was not significantly different to that of lobsters released into kelp beds at ERRR). Also consistent with the acoustic tracking, habitat use by trap caught lobsters (Table A5.5) also showed that large translocated lobsters frequented barrens ground and that overall catch of large lobsters on barrens was greater than in kelp beds (Fig. 24A(i); Table 14). Furthermore, large resident lobsters also showed this pattern of higher catches on extensive barrens (Fig. 24A(ii); Table 14). In contrast, there was no effect of habitat type evident for medium sized lobsters (Fig. 24A(iii); Table 14), while catch trends for small lobsters showed the reverse pattern, with catches of small lobsters greater in kelp beds than on sea urchin barrens (Fig. 24A(iv); Table 14). Strong seasonality in catch, with catch rates higher in summer than in winter, was particularly apparent for medium size-class lobsters (containing many mature females) regardless of reef state but was less pronounced for small (inclusive of immature individuals) and larger size-classes (dominated by males) inclusive of large translocated lobsters (Fig. 24A cf. i-iv).

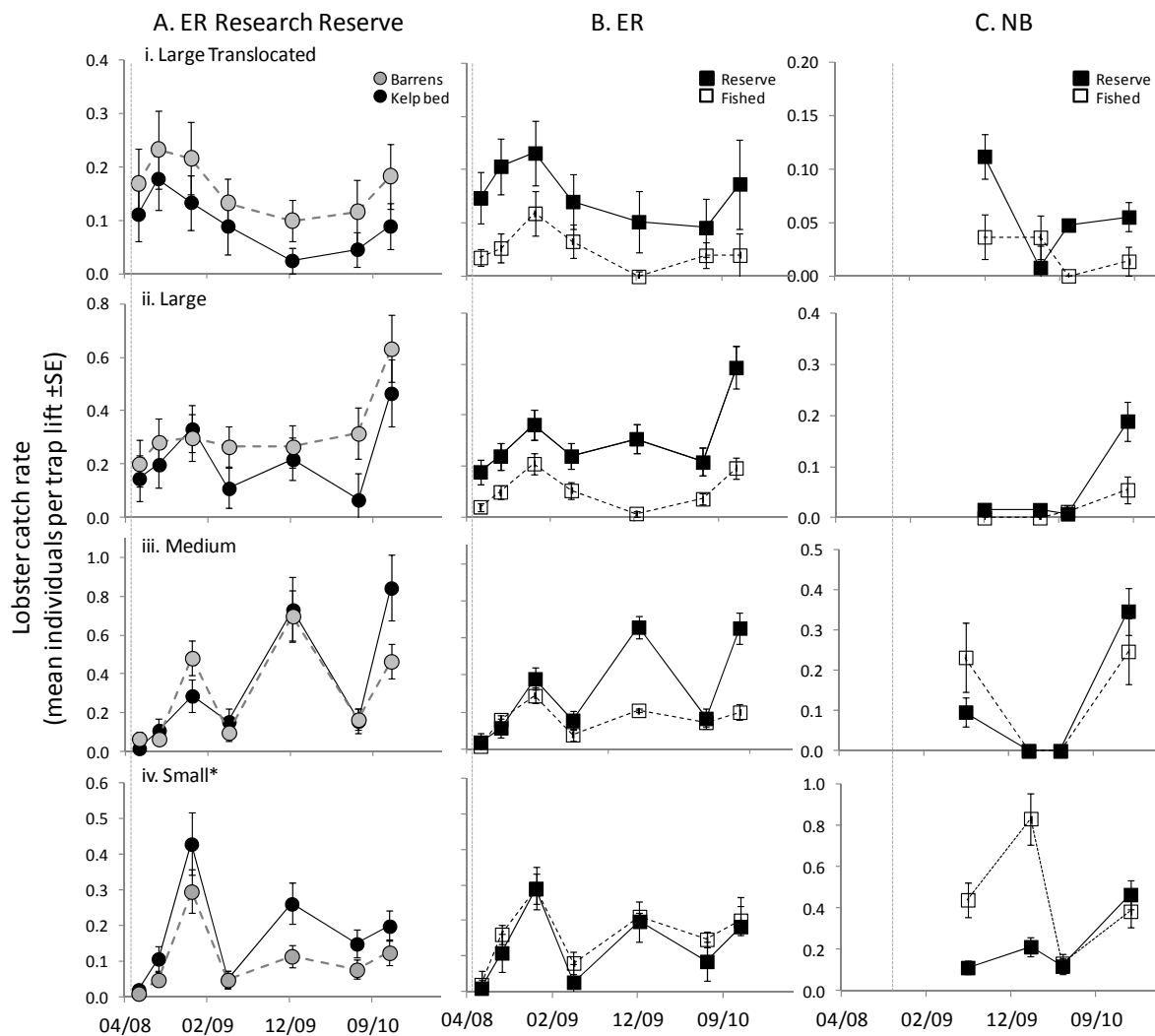


Figure 24. Size-specific patterns in lobster catch-rates on sea urchin barrens and in kelp beds as sampled by traps within the Elephant Rock (ER) and North Bay (NB) Research Reserves, and on adjacent reef open to fishing that is contiguous with the reserve sites. (i.) Large lobsters ≥ 140 mm carapace length (CL) translocated to ERRR; (ii.) large lobsters resident at the site; (iii.) medium lobsters ($110\text{mm} < \text{CL} < 140\text{mm}$); (iv.) small sub-legal lobsters < 110 mm CL. *Note that because small lobsters (undersized individuals) are not taken by the fishery, habitat patterns for this size class were pooled across the entire region inclusive of the research reserve at Elephant Rock and adjacent contiguous fished reef, thus allowing for a more robust comparison between habitat types.

Table 14. Analysis of deviance table for GLM fitted to poisson distribution and using log link function for terms added sequentially (first to last) testing the effect of period (1-7) and habitat type (kelp beds vs. urchin barrens) on the abundance of different lobster size-classes (a.-d) as sampled by trapping within the Elephant Rock Research Reserve, June 2008- Dec 2011. Levels of significance are coded by ***= $P < 0.0001$; **= $P < 0.01$; *= $P < 0.05$; ns=not significant. For significant effects, parameter estimates are shown as a multiplier of the abundance of lobsters in kelp habitat (including 95% confidence intervals shown in parentheses), thus values >1.00 indicate higher lobster catch rate in kelp beds relative to sea urchin barrens and values <1.00 indicate higher abundance on barrens.

Lobster size-class	Source	Df	Deviance	Resid. Df	Resid. Dev	P(> Chi)	Parameter estimate
Large Translocated lobsters	null			737	443.44		
	period	6	11.62	731	431.82	0.07	ns
	habitat	1	6.52	730	425.29	0.01	** 0.68 (0.51-0.91)
	period*habita	6	1.63	724	423.66	0.95	ns
Large lobsters	null			737	697.01		
	period	6	33.72	731	663.29	<0.0001	**
	habitat	1	7.01	730	656.28	0.01	** 0.59 (0.38-0.89)
	period*habita	6	7.69	724	648.59	0.26	ns
Medium lobsters	null			737	732.24		
	period	6	155.86	731	576.38	<0.0001	**
	habitat	1	0.76	730	575.62	0.38	ns
	period*habita	6	10.44	724	565.18	0.11	ns
Small lobsters* (inside + outside ERRR)	null			1549	899.91		
	period	6	115.13	1543	784.78	<0.0001	**
	habitat	1	14.51	1542	770.27	<0.001	** 1.75 (1.31 - 2.34)
	period*habita	6	4.32	1536	765.95	0.63	ns

*Note that because the abundance of small lobsters (individuals below legal size) is not influenced by the fishery as for larger size-classes, habitat patterns for small lobsters were examined by pooling data across the entire Elephant Rock site inclusive of sampling within the research reserve and adjacent fished reef, thus allowing for a more robust comparison of abundance across habitat type.

The depth distribution of kelp beds was generally shallower than barrens at ERRR (Fig. A5.1; see also Fig. 22) although depth frequency distributions of trap caught lobsters were broadly consistent across lobster size-classes within ERRR (Fig. A5.1b-e, but large vs. medium size-classes were different; see Table A5.6a). Consistency in depth distributions between lobster size-classes was also observed for NBRR (Table A5.6b). Moreover, the habitat effects on catch rates observed within ERRR appeared largely independent of depth as no trends in catch rate were detected across depth for any lobster size-class (min. P -value = 0.33; Fig. A5.1).

Density estimates of lobsters from *in situ* counts by divers on sea urchin barrens and within kelp beds (~12-18 m depth) corroborate the habitat-specific patterns in lobster catch. At ERRR large lobsters were more abundant on urchin barrens than small lobsters. At both ERRR and fished sites (beyond the immediate adjacent fished areas at ER, see *Materials & Methods*), small lobsters were more abundant within kelp beds than on urchin barrens (Fig. A5.3). Across the total lobster count, the effect of habitat was significant on fished reefs in the north east (Table A5.7) reflecting the scarcity of large lobsters on these reefs (Fig. A5.3).

The response of lobsters to closing reefs to fishing – the ‘reserve’ effect

While the translocation of large lobsters immediately enhanced the number of predatory capable lobsters within ER and NB Research Reserves, there was also a clear and ultimately large positive effect of closing these areas to fishing on the size and abundance of local resident lobsters relative to adjacent contiguous reef that remained open to fishing (Fig. 24B&C). Despite spill-over from the reserves, the net reserve effect on the abundance of resident lobsters was striking, with catch rates increasing by 2.2 times for legal lobsters, and 18.5 times for large predatory resident lobsters inside ERRR following 2.6 years (945 days) of reef closure relative to reef exposed to fishing (Table A5.8a-b). At NBRR, catch rate increased by 1.8 times for legal lobsters, and 3.5 times for large resident lobsters inside NBRR relative to adjacent contiguous reef exposed to fishing following 2.3 years (823 days) of closure (Table A5.8c-d). While translocation instantly increased the local abundance of large lobsters, which largely remained within the reserve boundaries (Fig. A5.4), this effect was clearly overtaken by the positive ‘reserve effect’ on growth of local resident lobsters to the large predatory capable size-class by the time of final sampling at ERRR & NBRR respectively (Fig. 24B&C).

Analysis of mark-recapture data (CJS – summarised in Table A5.9) and model reduction revealed that ‘survival’ of translocated lobsters was not different to resident lobsters within the reserves except for an initial period post release. For ERRR, the best supported CJS model indicated that survival of translocated lobsters was the same as resident lobsters in all except the immediate post-translocation period, in which ‘survival’ was low reflecting an initial emigration of lobsters from the reserves immediately post translocation. No hypothesis containing differences in survival and recapture probability by lobster size-class was supported (Table A5.10; see also Table A5.12 for best estimate of large lobster abundance within ERRR). For NBRR, the top ranked CJS model indicated that survival of translocated lobsters was not different from that of large resident lobsters, however the next ranked model (which was not significantly different to the top-ranked model, likelihood ratio test, Chi-sq. = 2.075, $P=0.15$; and of lower deviance) indicated that survival (and recapture probability) of translocated lobsters was different immediately post-release after which survival and recapture of translocated animals was not detectably different to that of residents. Again, there was no support for differences in survival and recapture probability across lobster size-classes (Table A5.11; see also Table A5.13 for best estimate of large lobster abundance within ERRR). Pooling across all lobster sizes within ERRR, the best supported model did not differentiate survival or recapture probability based on habitat type (see Table A5.14). However, capture probability, as averaged across the top 10 ranked models, was slightly higher on average for lobsters on sea urchin barrens than in kelp beds, with 4.90% ($\pm 0.17SE$) of the legal-sized lobster population occurring on barrens estimated to be catchable within a trapping session, compared with 4.40% ($\pm 0.17SE$) of the legal-sized lobster population within kelp beds (Table A5.14). In absolute terms, this equates to a 10% higher rate of catch-ability of lobsters on barrens, suggesting that the trap fishery is relatively more effective at harvesting remaining lobsters once barrens form.

Following estimation of total lobster population size (Jolly-Seber mark-recapture model; see Tables A5.15 & A5.16 for ERRR & NBRR respectively) and factoring for the proportion of total lobsters in each size-class at final sampling (assuming even catch-ability among size-classes as indicated by CJS model outputs), absolute densities of different size classes of lobster (Table A5.17) were calculable by dividing the abundance of lobsters in each size-class by the available reef area (see Table A5.2). Comparison of lobster density inside vs. outside the research reserves revealed a total lobster density 1.57 times higher within ERRR 2.6 years after declaration of the reserve, but ranged from 1.5, 3.1, 9.5 and 12.7 times higher inside the reserve relative to fished reef for medium, legal, large residents, and all large lobsters (i.e. including translocated) size-classes respectively (Table A5.18A). Notably, density of small lobsters within ERRR was approximately half (0.55 times) that observed on the adjacent fished reef. For NBRR, overall lobster density was 3.4 times higher, but ranged from 2.3, 7.3, and 9.4 times higher inside the reserve relative to fished reef after 2.3 of protection from fishing for medium, legal, large residents, and all large lobsters (i.e. including translocated) respectively (Table A5.18A). Allometric conversion using the average lobster CL for each size-class inside and outside reserves ($[\text{biomass (g)} = 0.0005 * ((\text{CL})^{2.9976}]$, after S. Frusher unpub. data), revealed that by final sampling the biomass of large predatory lobster biomass (independent of translocated large lobsters) was

1.92 times higher inside ERRR (35.90 kg hectare⁻¹) relative to fished reef (18.73 kg hectare⁻¹), while the biomass of legal-sized resident lobsters inside ERRR (57.60 kg hectare⁻¹) was 2.02 times higher than adjacent fished reef (28.53 kg hectare⁻¹; see Table A5.15B for all size-classes). For NBRR, the biomass of large predatory capable lobsters was 7.32 times higher inside NBRR (59.96 kg hectare⁻¹ vs. 8.19 kg hectare⁻¹ for adjacent fished reef; see Table A5.18B for all size-classes), while biomass of legal-sized lobsters was 3.81 times higher than that on adjacent fished reef (Table A5.18B).

Back-calculating initial biomass estimates from the factors-of-increase inside the research reserves (relative to fished reef, see Table A5.8), the net increase in biomass of large predatory lobsters as a result of the 'reserve effect' (exclusive of large lobster translocations), was 33.96 kg hectare⁻¹ (from 1.94 to 35.90 kg hectare⁻¹ from start to end of the study) and 42.83 kg hectare⁻¹ (from 17.13 to 59.96 kg hectare⁻¹) for ERRR and NBRR respectively. Occurring over 2.6 yrs (945 days) and 2.3 yrs (843 days) of protection at ERRR and NBRR, this equates to respective biomass gains within each reserve site of 13.06 and 18.62 kg of large predatory capable lobsters per hectare of protected reef per year. Increasing from 26.18 to 57.60 kg hectare⁻¹ at ERRR and 56.39 to 101.51 kg hectare⁻¹ at NBRR over the duration of the study, respective net biomass gains for legal-sized lobsters were 12.08 and 19.62 kg per hectare of protected reef per year.

Interpretation of results

Broad-scale surveys spanning 330 kilometres of eastern Tasmanian coastline indicates that lobster abundance is positively associated with seaweed cover (Fig. 25a), and negatively correlated with cover of sea urchin barrens (Fig. 25b). While these correlative patterns are useful to help understand the effects of barrens formation on the fishery and for generating hypothesis about species-habitat associations, they do not provide critical tests of the nature of such associations (e.g. reviewed by Elner & Vadas 1990). Here our combined lines of evidence from large scale manipulations indicate clearly that large lobsters are relatively scarce on barrens grounds not because the barrens represent less desirable habitat, but because of ongoing and intensive fishing of such reefs. Our manipulative approaches - protecting barrens reef from fishing in combination with reintroduction of large predatory lobsters - demonstrated that lobsters can reside on sea urchin barrens completely devoid of canopy-habitat forming seaweeds. That is, lobster populations were observed to set-up home ranges on *Centrostephanus rodgersii* barrens (Fig. 22A), and spatial trends in catch rates confirmed local distribution of lobsters on widespread sea urchin barrens ground (Fig. 23A). In addition, acoustic tracking of large lobsters in kelp beds at NBRR indicated lobster excursions to incipient barrens patches within the kelp bed.

Countering the broad-scale correlative evidence, these findings outwardly provide little support for the hypothesis that urchin barrens represent less suitable habitat for lobsters than intact kelp beds (Fig. 25a). However, a strong size-specific nature to this habitat association was revealed. Catch rates of small sub-legal sized lobsters (<110 mm CL) were indeed lower on sea urchin barrens than in the adjacent kelp bed habitat. This suggests an ontogenetic shift in habitat associations across lobster size-classes as large lobsters were generally observed in higher densities on barrens grounds whereas smaller size-classes of lobsters were observed to show the exact opposite pattern to be relatively more abundant in kelp beds (Fig. 23). Given that the broad-scale correlative data was sampled across fished reefs in eastern Tasmania (Fig. 25) - where the lobster population is dominated by small undersized individuals - it is the small size class of lobsters that largely defines this correlative relationship. Thus our cumulative data across reserve and fished reefs show that correlative patterns described from fished reefs are likely to give a poor indication of habitat-related patterns if fishing were to cease. These data provide a pertinent example, albeit on a rapidly warming coast, of the utility of no-take marine reserves as a tool capable of re-establishing otherwise unknown ecological baselines (e.g. Dayton et al. 1998).

Closure of reef rapidly demonstrated a strong 'reserve effect' on abundances of both legal-sized and large predatory capable lobsters in both kelp and extensive barrens habitat. That is, reef denuded of seaweeds and of low productivity can, providing fishing ceases, allow the rebuilding of lobster populations relative to reefs continually exposed to intense levels of fishing pressure. However, significantly higher catch rates of

small lobsters in kelp beds (corroborated by *in situ* abundance estimates using dive transects, Fig. A5.3 and Table A5.7) suggests that the overall process of rebuilding lobster populations on sea urchin barrens, starting with settlement of lobster puerulus larvae, recruitment into the fishery and ultimately growth to large ecologically important size-classes, may indeed be mediated by the availability of kelp bed habitat. We cannot rule out the possibility that the capacity lobster populations to rebound on extensive barrens habitat post-cessation or reduction of fishing may be compromised by lower overall levels of recruitment to juvenile stages relative to reef dominated by intact kelp beds.

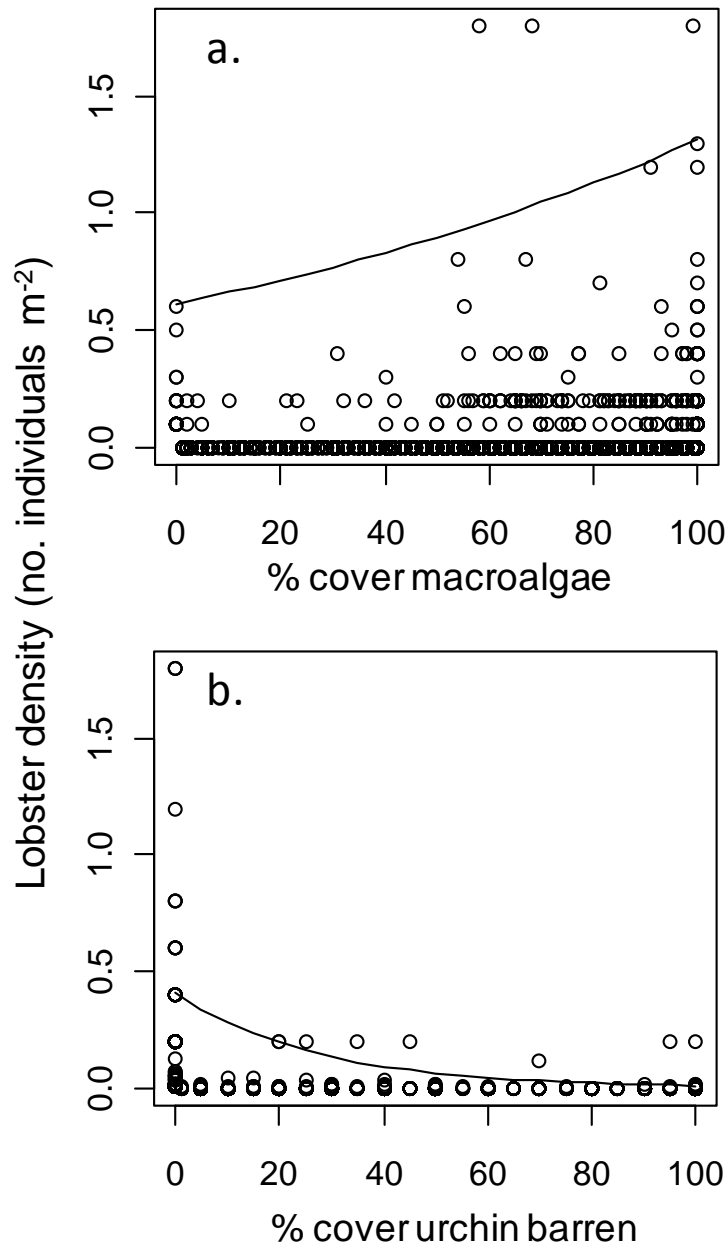


Figure 25. Relationship between spiny lobster density (all size-classes) and (a.) cover of macroalgae, and (b.) cover of urchin barrens formed by *Centrostephanus rodgersii* in eastern Tasmania; $n = 11,455$, 5 m² quadrats assessed *in situ* by divers between 6 and 18 m depth (data from Johnson et al. 2005, 2011, this study). Trend lines defining ceilings of each relationship were fitted to 99th quantiles. The 'factor ceiling' relationship suggests that several factors influence abundances of *J. edwardsii*, but that kelp habitat cover (as in (a.)), or lack of habitat owing to sea urchin overgrazing (as in (b.)) sets an upper limit to abundances of lobsters.

Higher abundance of small lobsters within kelp beds relative to sea urchin barrens suggests that kelp beds have higher carrying capacity for small lobsters, perhaps as a result of increased structural complexity and for sheltering and/ or availability of food (e.g. Wahle & Steneck 1992). Primary production is of the order of a 100-fold less on barrens than intact seaweed beds (Chapman 1981), and diversity and abundance of small invertebrates that are potential prey for small lobsters (approx. ≤ 20 mm diameter) is about an order of magnitude lower on *C. rodgersii* barrens in eastern Tasmania than on intact reefs (Ling 2008). This is consistent with observations elsewhere indicating that juvenile lobsters prefer kelp habitat over sea urchin barrens (e.g. Johns & Mann 1987; Miller 1989) and that kelp beds provide a diversity of small prey items for early post-settlement lobsters < 35 mm CL (Edmunds 1996). Kelp beds may also be important for settlement as artificial puerulus collectors adorned with kelp realised relatively high settlement rates (S. Ibbott, pers. comm.), however effects of urchin-driven kelp loss on puerulus settlement at the reef scale remains speculative.

As lobsters grow in size, our data indicates that migration from kelp beds to sea urchin barrens can occur as lobsters seemingly undergo ontogenetic shift in habitat utilisation as they grow through to larger size-classes (≥ 140 mm CL & ≥ 1.36 kg). Upon reaching such size, habitat structure appears less important as such individuals can be observed roaming across reef habitats offering low or intermediate shelter, consistent with having outgrown most of their natural predators (e.g. Wahle & Steneck 1992; Wahle 2003). Consistent with this notion, our observations of behaviour of large lobsters using acoustic tracking suggested that movement rates and net displacement was similar between sea urchin barrens and more complex kelp bed habitats offering greater overall shelter. Food availability also appears non-limiting on sea urchin barrens given that dietary breadth is known to increase with increasing lobster size (e.g. Pederson & Johnson 2006; Langlois et al. 2006), and can include emergent *C. rodgersii* when lobsters reach a carapace length of 140 mm (Ling et al. 2009a). Furthermore, the acoustic tracking results show clearly that large predatory capable lobsters not only reside on barrens but show elevated nocturnal movement in summer consistent with their peak in foraging activity (Ziegler et al. 2004) which overlaps with that time when the nocturnally grazing *C. rodgersii* is emergent from crevices and vulnerable to attack (Ling et al. 2009a; Ling & Johnson 2012; see Fig. 23).

Translocation of large lobsters had the effect of immediately enhancing the abundance of large lobsters within the research reserves. However, an initial 'flight' response immediately post translocation (as previously described by Green & Gardner 2009) was evident, and within ~ 2 years the translocated population was overtaken by residents growing to large size within both research reserves through being afforded protection from fishing (Fig. 24B&C). Based on densities of large lobsters known to impact urchin populations at low densities in kelp beds (Ling & Johnson 2012), i.e. ~ 1 large lobster per 200 m^2 (~ 50 individuals & ~ 67.8 kg per hectare), from the observed increase in net biomass per hectare, we project (assuming a simple linearly relationship and several years of average lobster recruitment) that ~ 3.6 years of reef closure would be sufficient to reach this density of large lobsters within kelp beds at NBRR from the initial reef closure. To achieve the same overall density of large lobsters at ERRR, ~ 5.2 years is required. But while our previous experiments (Ling & Johnson 2009a, 2012) indicate that this density is likely to have meaningful impact on *C. rodgersii* within kelp beds in the North Bay Research Reserve, whether it will be sufficient to have meaningful ecological impact and reduce *C. rodgersii* populations to the point where seaweed regrowth can occur within the Elephant Rock Research reserve is much less certain. Nonetheless, taking the average time required to achieve such an increase in large lobsters across both eastern Tasmanian sites, an approximate time of 4.4 yrs ($\pm 0.77\text{SE}$) of reef protection is required. But importantly, expectations of any predator-driven recovery of kelp habitat on widespread urchin barrens grounds are likely to be in the order of five times longer at closer to ~ 25 years, i.e. an additional 20 years from the time at which a minimum level of predatory function has been restored - as has been empirically observed in temperate settings of north eastern New Zealand (reviewed by Babcock et al. 2010).

Conclusions

Collectively, these results suggest that protection of rocky reefs from intensive fishing can allow populations of large predatory-capable lobsters to not only rebuild within kelp beds and thus increase resilience against overgrazing by sea urchins in the first instance (Fig. 26a), but also that predatory lobster populations can be rebuilt on heavily overgrazed reef, reducing the resilience of the barrens state (Fig. 26b). (This assumes that the importance of large lobsters as predators of *C. rodgersii* demonstrated at small scales (Ling et al. 2009a) extrapolates to larger scales, and is the topic of the next section). Clear evidence that extensive *C. rodgersii* barrens can support dense populations of large lobsters but not small ones, which are instead clearly associated with the seaweed beds (Fig. 25; this study), is a new finding that provides for a more optimistic view of the future of the rock lobster fishery than was possible from data collected solely from fished areas (Fig. 25) which largely reflects the abundances of small sub-legal and 'just legal' animals.

The results also suggest that ongoing heavy fishing of lobsters on sea urchin barrens will have the effect of increasing the resilience of the barrens state by driving down predator size and abundance and reducing the likelihood of kelp bed recovery (Fig. 26c). Given the degraded status of many ecosystems, this research highlights that management for local-scale resilience of natural systems must recognise possible alternative community configurations and seek to understand not only the mechanisms that act to both increase desirable and diminish undesirable resilience, but also to identify the likely time scales involved for transitions between them.

If it is demonstrated that elevated populations of large rock lobsters can significantly impact sea urchin populations on incipient and/or extensive barrens at large scales (see next section), then the challenge for management will be to first rebuild densities of large rock lobsters on the east coast of Tasmania, and then to manage the potentially conflicting requirements of maintaining populations of large lobsters sufficient to effect elevated resilience of seaweed beds and reduced resilience of extensive *C. rodgersii* barrens while at the same time ensuring a viable commercial and recreational rock lobster fishery.

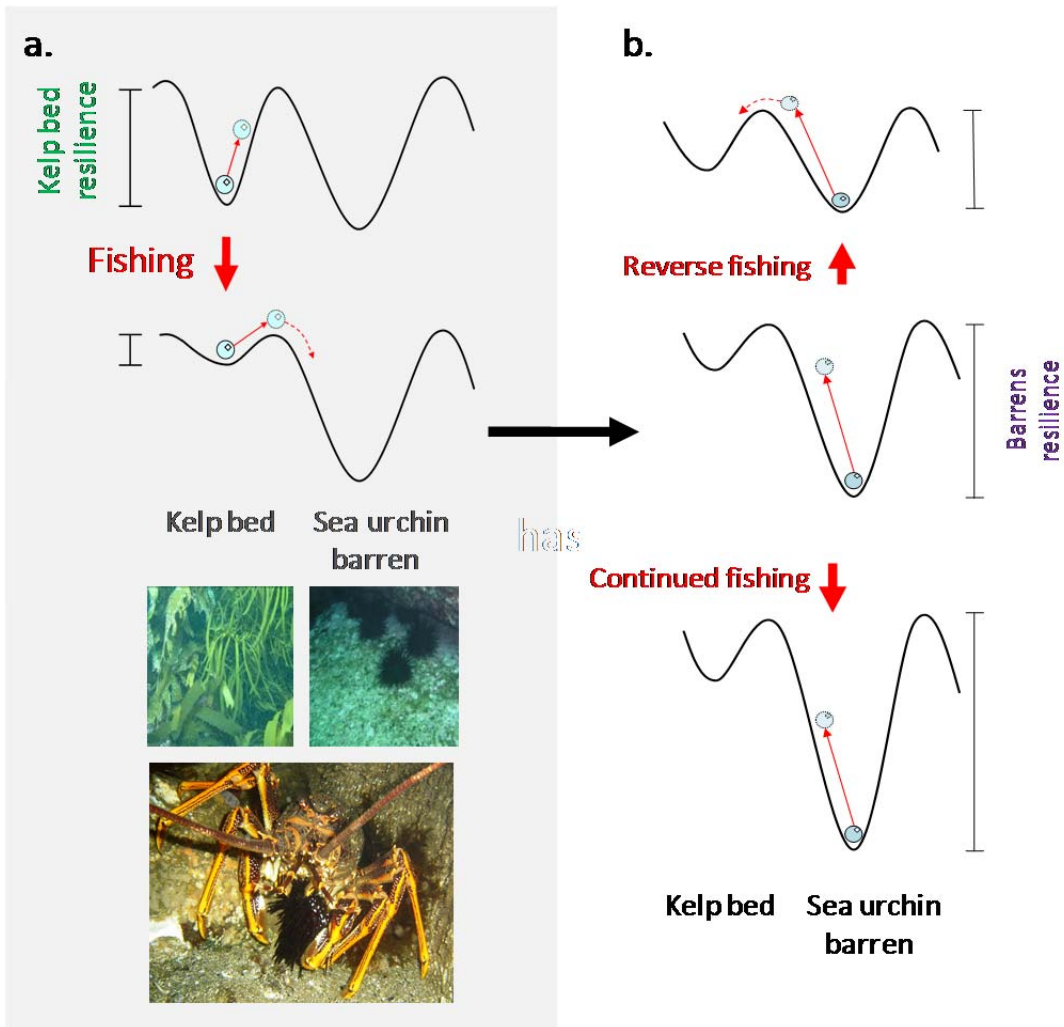


Figure 26. (a.) Conceptualization of loss of kelp bed resilience as a result of fishing down large predatory lobsters and risk of barrens formation (after Ling et al. 2009) and (b.) representation of resilience of the alternative and stable urchin barrens state; our experimental evidence shows that reversing fishing by protecting reef and enhancing large predatory lobsters has the effect of increasing likelihood of a 'reverse' phase-shift back to kelp beds (middle plot moving upwards); conversely, continuation of lobster fishing on urchin barrens has the effect of increasing the resilience of the barrens state making it more difficult for recovery of kelp beds (i.e. the 'reverse' phase-shift) to occur.

Impact of populations of large lobsters on sea urchins and benthic community structure

Overall, while sea urchin populations declined in the reserve site at Elephant Rock in the north east (ERRR), this change was not significant relative to controls. Not surprisingly then, there were no overall changes in benthic community structure detected at any of the sites in the north east, although at the control site at Sloop Rock measurements at small scales showed expansion of the extensive barren into the kelp bed (by ~1.25 m) over the ~2.5 y of the study.

In the south east within the incipient barrens sites, densities of both species of sea urchins and abalone declined significantly within the reserve site with elevated numbers of large lobsters relative to control sites. Flow on effects of reduced densities of *C. rodgersii* within the reserve were evident as a significant reduction in the size of incipient barrens patches (as a result of regrowth of seaweeds) relative to equivalent patches at control sites that either remained a similar size or increased in size. Further details of these results are presented below.

Lobster enhancement effect

It is worth briefly reiterating results from the previous section, which demonstrated that at both reserve sites there was a clear effect of lobster enhancement following lobster translocations and as a result of protecting lobsters from fishing within the reserve sites. As indicated by trapping data for the experiment at the north east reserve, catch of large lobsters was on average more than 5 times greater at 0.44 large lobsters per trap lift compared to 0.07 and 0.10 individuals per trap lift at the two control sites. In the south east, total large lobsters observed *in situ* following the initial translocation of lobsters was almost 10 times greater than at control sites, with 52 large lobsters observed with NBRR while only 9 and 2 large lobsters were observed at C1 and C2 respectively.

Response of sea urchin populations

For the north east experiment, even though both sea urchin species (*C. rodgersii* and *H. erythrogramma*) declined over the course of the experiment in both kelp beds and on extensive urchin barrens within ERRR (Fig. 27a), the decline was not statistically significant relative to controls sites (Table 15a). ANCOVA did not reveal any significant declines or differences among sites in trends for *C. rodgersii*, *H. erythrogramma* or abalone, either in kelp bed or extensive barrens habitat (Table 15a). Similarly, neither in kelp beds or on extensive barrens habitat in the NE was there any change in the extent of barrens cover (Fig. 27a; Table 15a), and there were no trends observed in understory macroalgae (Fig. 27a).

In the south east, there was a general decline of sea urchins and abalone (a known prey of large lobsters) over the two years of the experiment (Fig. 27b), consistent with the lobster enhancement treatment at NBRR (Table 15b). Importantly, *C. rodgersii* was observed to undergo significant decline within NBRR while trends for this species at control sites were generally stable and not different from each other, enabling pooling of control sites and testing for an overall effect of the lobster enhancement treatment which was significant (*Treatment * Days* effect, $P=0.018$; Table 15b). For *H. erythrogramma*, there was also an overall decline within NBRR, however trends at control sites were dissimilar, so an overall test of the lobster enhancement was not possible (i.e. variability between control sites meant that control sites could not be pooled, Table 15b.). However, lobster enhancement had a significant negative effect on the abundance of abalone (Table 15b.), with a significantly greater decline in abalone observed within NBRR than at control sites (Fig. 27b). The habitat level response estimated using benthic transects revealed a decline in cover of incipient urchin barrens at NBRR, while an increase in barrens cover was observed at Fortescue Bay but not at control site 1 (Cape Paul Lemanon) (Fig. 27b). There were no differences among SE sites in trends in cover of both canopy and understory macroalgae (Fig. 27b).

The overall stable patterns revealed among univariate responses for the NE experiment were generally reflected in the community level analysis where there was also no evidence that lobster enhancement in the reserve had any effect on benthic community structure, either in kelp beds or on extensive urchin barrens (Fig. 28a), i.e. the 'Period * Site' interactions for NE algal and invertebrate communities were not

significant (Table 16). Conversely, in the SE, while an overall community level effect was not evident for benthic macroalgae, there was a clear and significant effect of the lobster enhancement treatment on the principal herbivorous benthic invertebrates, i.e. sea urchins and abalone (Fig. 28b.; Table 16). The significant 'Period * Treatment' effect for the invertebrate community in the SE reflects a clear difference in the NBRR invertebrate community between the initial (prior to lobster translocation) and final survey period (PERMANOVA, $t=3.75$, $P(\text{perm}) < 0.005$, unique permutations = 462), while changes in the invertebrate communities at both SE control sites over the same period were not significant (Table 16).

Fine-scale patterns at the kelp/barrens interface

Results from video belt transects surveyed perpendicular to the kelp/barrens interface at sites in the north-east, indicated a small scale recovery (averaging less than 1 m) in canopy cover at ERRR and St. Helens Island (control site 2 – albeit temporarily at this site) between 2008 and 2011, but ongoing decline in macroalgal cover at Sloop Rock (Fig. 29a) where there was an average ingression of ~1.25 m of barrens displacing the seaweed bed at this site. At coarser spatial resolution, these fine-scale changes in canopy macroalgae were not observable as changes in cover within either 0 to 5 m, or 5 to 10 m either side of the kelp/ barrens interface (Fig. 29b; Table 17a). There was also no detectable increase in the formation of incipient barrens within the kelp habitat occurring on the shallow margins of the widespread barrens between 2008 and 2011 (Fig. 29b). For the barrens side of the habitat interface, where *C. rodgersii* was reliably assessable from video transects, there was also no evidence of change in the sea urchins density within this zone through time (Fig. 29c; Table 17b).

Dynamics of incipient patch barrens

An overall pattern of stability in both the mean density and size of incipient *C. rodgersii* patch barrens was evident across all sites in the SE (Fig. 30a, b respectively). There were differences between sites in the mean size of barrens patches (incipient barrens patches were smaller at Cape Paul Lemanon than at the other 'control' site at Fortescue Bay and at the site with added lobsters at NBRR). However, there was no 'Site by Time' effect when patches were sampled randomly through time to indicate an overall effect of the lobster enhancement treatment. However, this result is not straightforward to interpret since changes in patch size through time are likely to be swamped by large variability in patch size within each site (Table 18a). Similarly, the mean density of incipient patches was similar through time, and across the translocation and control sites (Table 18b). However, individually marked barrens patches monitored through time showed a significant decrease in size within NBRR relative to control sites (Table 18c, Fig. 30c), reflecting regrowth of algae within these patches within the reserve site. Individually marked barrens patches at the control sites showed the opposite pattern, and increased in size over the ~2 years of the study (Fig. 30d). Unsurprisingly, proportional change in patch size in either direction (increase or decrease) was greatest for smallest patches (Fig. 31), suggesting that management intervention to influence urchin density will have greater impact on dynamics of smaller patches than on large patches. Changes in the size of individually marked patches reveal a distinct effect of the treatment with added lobsters relative to controls without lobsters (Fig. 30d; Table 18c), but patch size trends based on randomly selected patches at each assessment time do not (Fig. 30b; Table 18a); this is because marked patches show changes in size independent of the distribution of patch sizes within sites, while when patches are selected randomly at each time of observation the variability in patch size within sites is confounded with – and swamps – the changes in patch size.

The most important point to emerge from these findings is that building populations of predatory-capable lobsters can have significant and relatively immediate effects in mitigating trends in barrens formation in incipient barrens, even within the short ~2 year time frame of this study, while similar rebuilding of large lobsters at the site of extensive barrens had no detectable impact despite that many thousands of sea urchins were consumed within the ~2.5 y time course of the experiment (see next section). In the context of resilience, rebuilding lobsters in the incipient barrens clearly increased the resilience of the seaweed dominated state of the system but had little effect in reducing the resilience of the state of extensive barrens towards a point where macroalgal recovery is likely. This result exemplifies the inherent hysteresis in the *C. rodgersii* – seaweed dynamic (Ling et al. 2009a) such that sea urchin densities have to be reduced to much lower densities than are required to create extensive barrens in the first place. Experimental

studies in NSW have shown that removing 66% of urchins is insufficient to initiate seaweed regrowth (Andrew & Underwood 1993). Indeed seaweed recovery has been observed only when attempts are made to remove all urchins from barrens sites (Andrew 1991; Andrew & Underwood 1993; Hill et al 2003; Ling 2008; Strain & Johnson 2013). Later in this report we outline modelling work suggesting that *C. rodgersii* densities will need to be reduced to $\sim 0.25 \text{ m}^{-2}$ before meaningful regrowth of seaweeds on extensive barrens is likely, although this needs to be corroborated empirically.

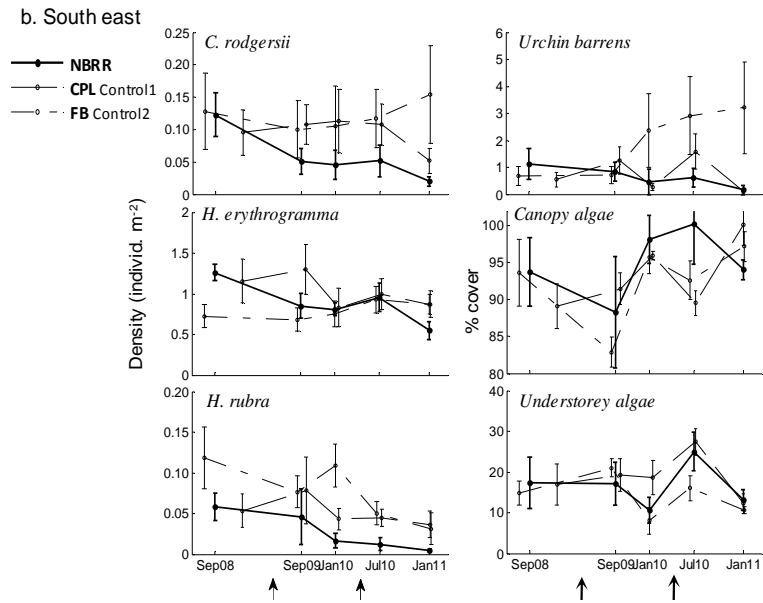
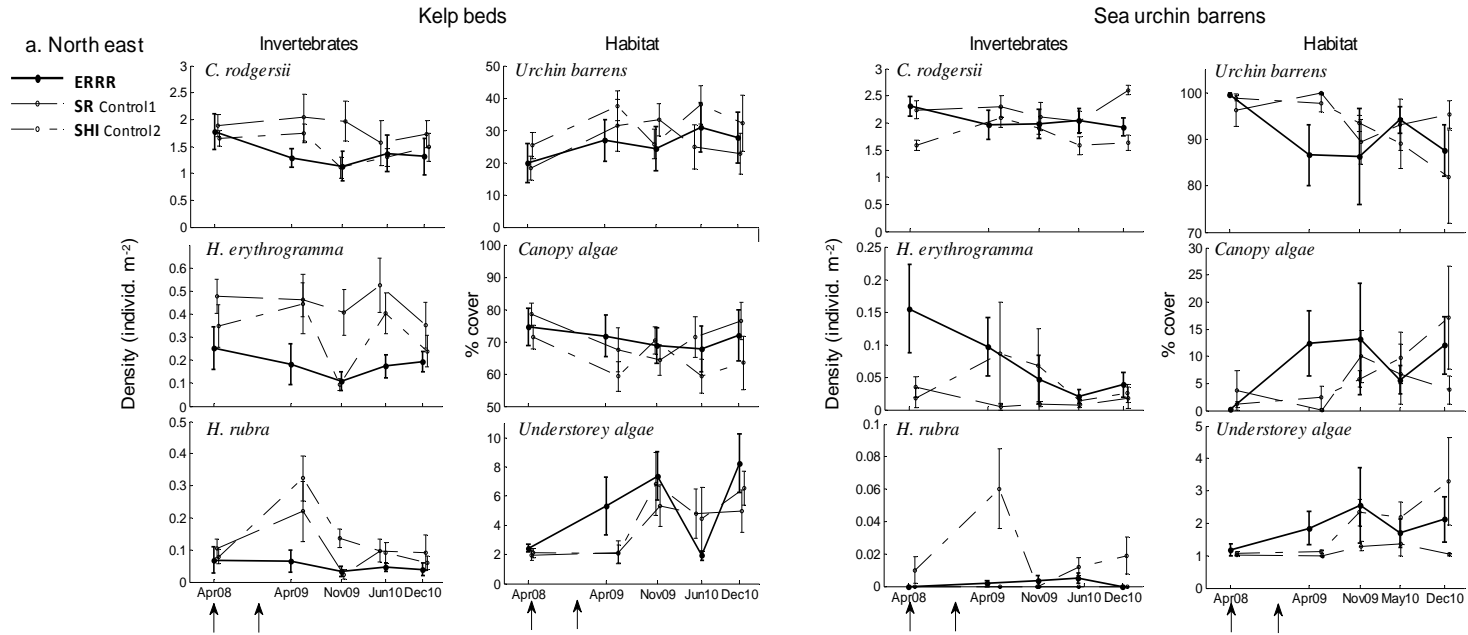


Figure 27. Each group of six plots show patterns of invertebrate abundance (left-hand graphs) and benthic cover (right-hand graphs) at experimental and control sites in (a) north east (top panels) and (b) south east (bottom panels) regions of eastern Tasmania. For the north east, data are presented for kelp beds (top left graphs) and extensive barrens habitat (top right graphs) separately. ERRR = Elephant Rock Research Reserve (solid line) with associated control sites at SHI (St. Helens Island, dot-dashed line and open circles) and SR (Sloop Rock, dashed line and open circles) not protected from fishing and without added lobsters. For the south east, NBRR = North Bay Research Reserve with associated control sites at CPL (Cape Paul Lemanon, dot-dashed line and open circles) and FB (Fortescue Bay, dashed line and open circles). Arrows on x-axis indicate dates of translocation of large rock lobsters. Points represent averages from six replicate transects \pm SE.

Table 15. Summary of ANCOVA on the response in sea urchin and abalone densities and cover of sea urchin barrens through time for experimental sites in (a.) north east (NE), and (b.) south east (SE) Tasmania. Effects in bold indicate significance at $\alpha = 0.05$ (other than for slope intercepts). The overall effect of ‘treatment’ (i.e. translocation site vs. controls) was examined only if significant differences were detectable at the level of ‘site’ (i.e. if the ‘Sites * Days’ interaction was significant; where ‘Days’ = time from initial translocation), and if differences between controls sites (C1 & C2) within each region were not different ($P > 0.25$).

Habitat: Kelp beds								Habitat: barrens								
Region	Response	Analysis	Effect	Sum Sq	Df	F	Pr(>F)	Response	Effect	Sum Sq	DF	F value	Pr(>F)			
a.NE	<i>Centrostephanus rodgersii</i> [transformation= Log(<i>C. rodgersii</i>)]	Sites (ERRR vs C1 vs C2)	(Intercept)	0.674	1	26.17	<0.001	***	(Intercept)	0.85	1	65.40	2.0E-05	***		
			Site	0.049	2	0.96	0.420		[trans.= Log(<i>C. rodgersii</i>)]	Site	0.03	2	1.15	0.36		
			Days	0.015	1	0.59	0.462		Days	0.002	1	0.16	0.70			
			Site*Days	0.005	2	0.09	0.916		Site*Days	0.02	2	0.58	0.58			
			Residuals	0.232	9				Residuals	0.12	9					
	<i>Heliocidaris erythrogramma</i> [no trans. Required]			(Intercept)	0.334	1	24.24	<0.001	***	(Intercept)	23.94	1	29.68	0.00	***	
				Site	0.054	2	1.94	0.199		[trans.= Log(<i>H. erythrogramma</i>)]	Site	4.07	2	2.52	0.14	
				Days	0.004	1	0.26	0.624		Days	0.27	1	0.33	0.58		
				Site*Days	0.015	2	0.56	0.590		Site*Days	3.22	2	2.00	0.19		
				Residuals	0.124	9				Residuals	7.26	9				
	<i>Haliotis rubra</i> [trans.= log(<i>H. rubra</i>)]			(Intercept)	6.74	1	10.44	0.010	*	(Intercept)	0.00	1	0.00	1.00		
				Site	0.79	2	0.61	0.563		[trans.= = log(<i>H. rubra</i> +1)]	Site	0.00	2	0.37	0.70	
				Days	0.14	1	0.22	0.648		Days	0.00	1	0.00	1.00		
				Site*Days	0.30	2	0.24	0.795		Site*Days	0.00	2	0.22	0.81		
				Residuals	5.84	9				Residuals	0.003	9				
	<i>Centrostephanus rodgersii</i> urchin barrens [trans.= barrens ⁻¹]			(Intercept)	0.003	1	40.46	<0.000	***	(Intercept)	0.003	1	40.46	0.00	***	
Site				3.39E-05	2	0.24	0.790		[trans.= barrens ⁻¹]	Site	3.39E-05	2	0.24	0.79		
Days				4.52E-05	1	0.65	0.442		Days	4.52E-05	1	0.65	0.44			
Site*Days				5.09E-05	2	0.36	0.705		Site*Days	5.09E-05	2	0.36	0.71			
Residuals				0.001	9				Residuals	0.001	9					

Table 15. Continued ...

Habitat: Kelp beds								
Region	Response	Analysis	Source	Sum Sq	Df	F value	Pr(>F)	
b. SE	<i>Centrostephanus rodgersii</i> [trans.= $C. rodgersii^{0.4}$]	Sites (NBRR vs C1 vs C2)	(Intercept)	0.247407	1	172.6348	3.54E-07	***
			Site	0.000094	2	0.0327	0.96796	
			Days	0.002281	1	1.5913	0.23885	
			Site*Days	0.01473	2	5.1391	0.03246	*
			Residuals	0.012898	9			
	<i>Centrostephanus rodgersii</i> [trans.= $C. rodgersii^{0.25}$]	Treatment (NBRR vs Controls)	(Intercept)	0.93184	1	637.3665	4.34E-11	***
			Treat	0	1	0.0008	0.9773	
			Days	0.0003	1	0.2073	0.65775	
			Treat*Days	0.01118	1	7.6468	0.01838	*
			Residuals	0.01608	11			
	<i>Heliocidaris erythrogramma</i> [trans.= $\text{Log}(H. \text{erythrogramma})$]	Sites (NBRR vs C1 vs C2)	(Intercept)	0.050358	1	2.1645	0.17531	
			Site	0.315208	2	6.7742	0.01603	*
			Days	0.058766	1	2.5259	0.14645	
			Site*Days	0.256516	2	5.5129	0.02735	*
			Residuals	0.209387	9			
	<i>Haliotis rubra</i> [trans.= $\log(H. rubra)$]	Sites (NBRR vs C1 vs C2)	(Intercept)	10.5346	1	103.2932	3.13E-06	***
			Site	0.4551	2	2.2313	0.16331	
			Days	0.1236	1	1.2122	0.29947	
			Site*Days	1.2227	2	5.9942	0.02214	*
			Residuals	0.9179	9			
Treatment (NBRR vs Controls)		(Intercept)	15.594	1	124.682	2.43E-07	***	
		Treat	0.044	1	0.352	0.565		
		Days	0.861	1	6.884	0.024	*	
		Treat*Days	1.0372	1	8.293	0.015	*	
		Residuals	1.3758	11				
<i>C. rodgersii</i> urchin barrens [trans.= $\sqrt{\text{barrens}}$]	Sites (NBRR vs C1 vs C2)	(Intercept)	1.1424	1	12.9852	0.006	**	
		Site	0.09088	2	0.5165	0.613		
		Days	0.02355	1	0.2677	0.617		
		Site*Days	0.92016	2	5.2295	0.031	*	
		Residuals	0.79179	9				
<i>C. rodgersii</i> urchin barrens [trans.= $\sqrt{\text{barrens}}$]	Treatment (NBRR vs Controls)	(Intercept)	1.87084	1	10.0886	0.009	**	
		Treat	0.07021	1	0.3786	0.551		
		Days	0.23965	1	1.2923	0.280		
		Treat*Days	0.42091	1	2.2697	0.160		
		Residuals	2.03986	11				

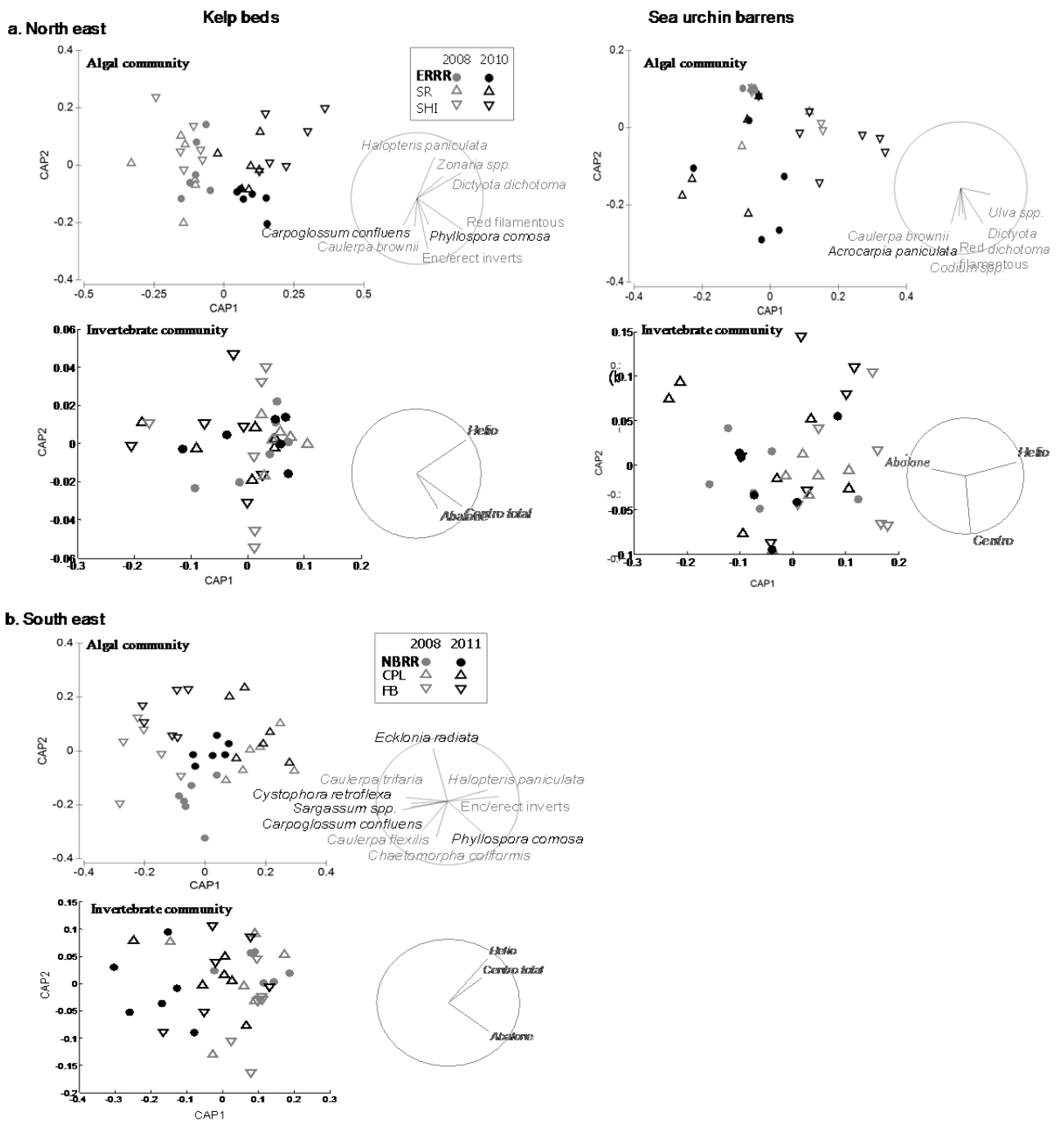


Figure 28. Two-way CAP ordinations of algal and invertebrate community composition (top and bottom respectively within each panel) for transects in kelp habitat (LHS) and urchin barrens (RHS) for the ERRR lobster translocation site (solid circles) and two control sites (SHI = St. Helens Island, SR = Sloop Rock, open triangles) for the north eastern Tasmanian experiment (a.); and (b.) community composition for transects in kelp habitat at the translocation site at North Bay (NB, filled circles), and two control sites (CPL = Cape Paul Lemanon, FB = Fortescue Bay, open triangles) in south-eastern Tasmania. Only transects from the first (2008) and last (2010) sampling periods are included, and the ordination is constrained by the factor Period * Site. Pearson correlations between variables and ordination axes are represented to the right of ordination plots (only correlations > 0.4 are shown in (a)). In (a), canopy species are shown in black text, while understory species are shown in grey text. For the south east lobster enhancement site, transects in the final sampling period are generally characterized by lower densities of invertebrate groups.

Table 16. Summary of results from PERMANOVA and PERMDISP based on transect data from the first and last survey periods. Bold font indicates significant effects at $\alpha = 0.05$. Post-hoc pair-wise comparison revealed that the significant *Period by Site* interaction term for the SE invertebrate community (declines in both sea urchin species and abalone) was a treatment level effect driven by change in the NBRR invertebrate community from *Before* lobster enhancement to the final survey period $t = 3.75$, $P(\text{perm}) < 0.005$ (unique permutations = 462), while no change occurred for the invertebrate communities at either control site.

Analysis	Location	Effect	df	PERMANOVA		PERMDISP		
				Pseudo-F	P(perm)	df	F	P(perm)
Algal community	NE (Kelp)	Period	1	6.821	0.0008**	1	1.649	0.220
		Site	2	1.720	0.127			
		Period*Site	2	0.535	0.771			
	NE (Barrens)	Period	1	6.474	0.0064**	1	19.845	0.0005*
		Site	2	1.411	0.225			
		Period*Site	2	1.422	0.225			
	SE	Period	1	2.132	0.093			
		Site	2	6.308	0.0002**	2	2.795	0.153
		Period*Site	2	0.641	0.690			
Invert community	NE (Kelp)	Period	1	1.753	0.170			
		Site	2	1.267	0.284			
		Period*Site	2	0.169	0.963			
	NE (Barrens)	Period	1	0.695	0.520			
		Site	2	10.151	0.0001**	2	1.49	0.294
		Period*Site	2	2.151	0.097			
	SE	Period	1	5.872	0.002*	1	0.512	0.492
		Site	2	1.049	0.407			
		Period*Site	2	2.609	0.032*	2	2.043	0.151

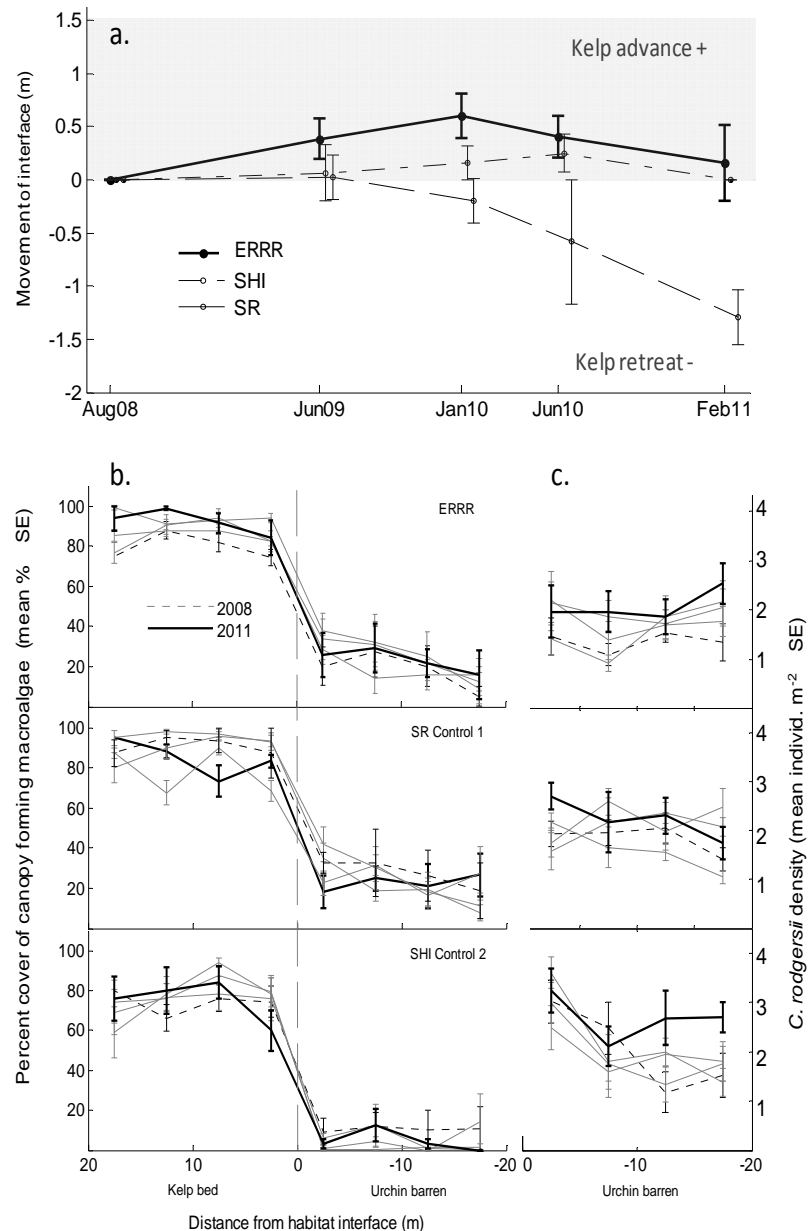


Figure 29. (a.) Movement of the kelp/barrens habitat boundary over five sampling periods from transects at Elephant Rock (ER), St. Helens Island (SHI) and Sloop Rock (SR) in north-eastern Tasmania. Negative movement indicates an advance of barrens habitat into the kelp, while positive movement indicates recovery of kelp cover into barrens habitat. Points represent means from six replicate transects (\pm SE). There is a significant difference between positions in the final sampling period ($F_{2,13}=8.15$, $P=0.005$), with pairwise comparisons (Tukey's HSD) indicating that movement at SR is significantly different from ER and SHI at $\alpha = 0.05$, reflecting retreat of the barrens/kelp interface at SR into the kelp bed because of an expanding barren. (b.) Mean canopy cover, and (c.) *C. rodgersii* density at fixed distances from markers set at the kelp/barrens interface at sites in north-eastern Tasmania in 2008. Negative distances represent the direction into barrens habitat, while positive distances represent the direction into kelp habitat. *C. rodgersii* densities are presented for the barrens habitat only since estimates of sea urchin density from video transects in kelp habitat are unreliable. Points represent means from 6 video transects (\pm SE), where data at $1\text{ m} \times 1\text{ m}$ resolution has been aggregated into 5 m blocks. Each line represents a different sampling period, with 2008 shown as dashed line, 2011 shown in solid black, and intervening sampling periods shown in solid grey. There is slight recovery of canopy cover at Elephant Rock and St. Helens Island between 2008 and 2011, but not at Sloop Rock. *C. rodgersii* density was stable across all sites.

Table 17. Summary of results from 1-way ANOVAs of high resolution mapping of fixed transect across the kelp/barrens interface in the north-east, cover at final sampling minus cover at start of sampling. (a.) Response in cover of canopy macroalgae at start of sampling (2008) minus canopy macroalgae at final sampling (2011) at 0-5 m and 5-10 m from permanent fixture towards centre of widespread barrens ground (Barrens 0-5 m & Barrens 5-10 m respectively); and 0-5 & 5-10 m from the fixture into adjacent kelp beds (Kelp 0-5 m & Kelp 5-10 m respectively). (b.) Comparison of change in *Centrostephanus rodgersii* density on barrens adjacent to the habitat interface between 2008 (first sampling) and 2011 (final sampling). Note that due to obscuring of the benthos by canopy algae, *C. rodgersii* abundance was not assessable within kelp beds using videographic methods.

Analysis	Zone	Source	Df	Sum Sq	Mean Sq	F value	Pr(>F)
a. Canopy cover	Barrens 0 – 5 m	Site	2	1603.7	801.8	1.79	0.205
		Residuals	13	5814.6	447.3		
	Barrens 5-10 m	Site	2	172.1	86.1	0.11	0.895
		Residuals	13	10003.3	769.5		
	Kelp 0 – 5 m	Site	2	1769.2	884.6	1.90	0.189
		Residuals	13	6043.9	464.9		
	Kelp 5-10 m	Site	2	10.9	5.5	0.03	0.975
		Residuals	13	2777.8	213.7		
b. <i>C. rodgersii</i>	Barrens 0 – 5 m	Site	2	0.416	0.208	0.12	0.889
		Residuals	13	22.828	1.756		
	Barrens 5-10 m	Site	2	4.6927	2.3464	1.40	0.282
		Residuals	13	21.8417	1.6801		

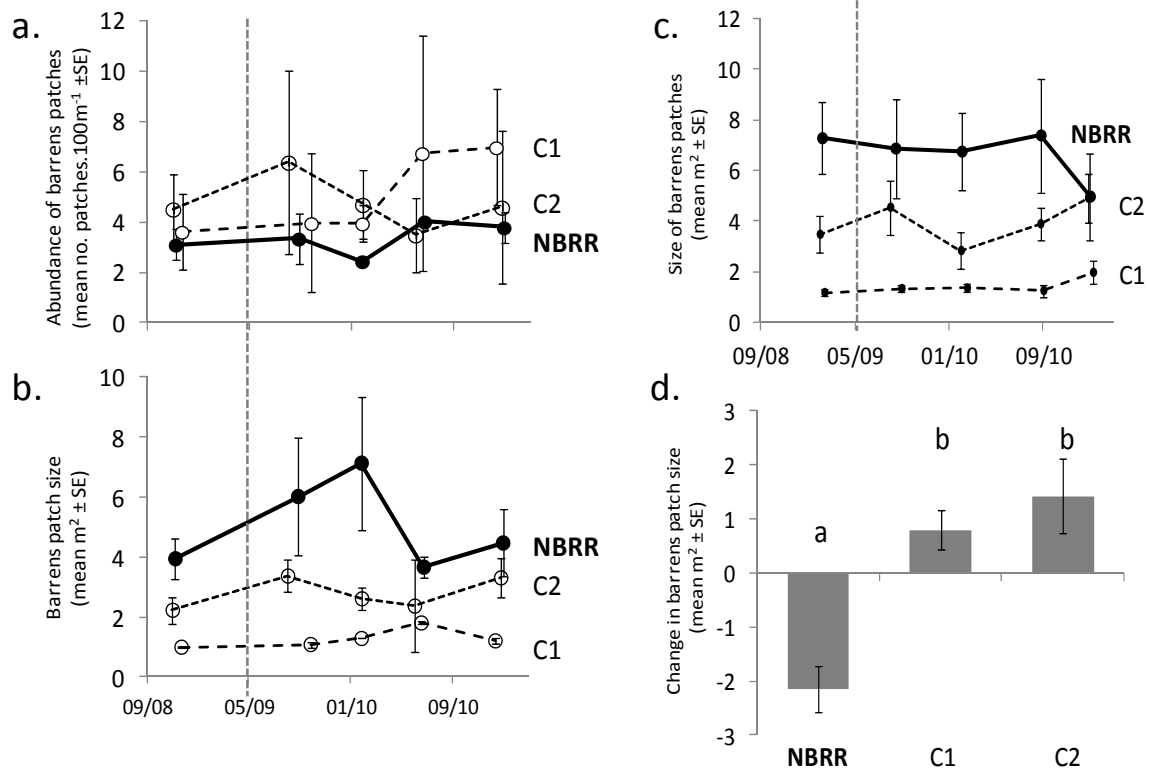


Figure 30. Dynamics of incipient *C. rodgersii* barrens in south east Tasmania at lobster translocation (North Bay Research Reserve, NBRR) and control sites. (a) Mean density of barrens patches, and (b) mean size of barrens patches encountered during timed swims parallel to the shore within the NBRR and control sites. (c) Mean size of individually marked barrens patches through time, expressed as (d) change in patch size from before lobster enhancement to final sampling at NBRR and control sites. Vertical dashed lines indicate the timing of initial translocation of large lobsters.

Table 18. Summary of ANOVA models on (a.) patch size (randomly chosen incipient barrens patches), and (b.) counts of *Centrostephanus rodgersii* incipient barrens patches during timed swims for 'Before versus After' (= initial versus final time periods, dependent variable = patches encountered per 10 minutes swim time); and (c.) change in area of marked (i.e. fixed) *Centrostephanus rodgersii* incipient barrens patches (i.e. area of barrens at initial sampling minus area at final sampling) inside and outside the North Bay Research Reserve (NBRR). 'Control' sites outside the NBRR are at Fortescue Bay (C1) and Cape Paul Lemanon (C2). Transformations are expressed in terms of the untransformed variate Y . Asymmetric ANOVA comparing the 'treatment' site with added lobsters to both 'control' sites is indicated by the contrast NBRR vs. (C1,C2). Levels of 'Time' are initial and final sampling periods. Bold font indicates significant effects at $\alpha = 0.05$. For (a.) patterns of significance reflect significant differences in mean patch size between C1 and C2, and between NBRR and C1, but not between NBRR and C2, and show no indication of a change in patch size over time. This result reflects confounding the effects of variability in patch size within sites, and changes in patch size during the experiment. The true nature of changes in patch size (independent of effects in patch size distribution within sites) is reflected in (c.) showing significant differences in the change in patch size between the 'treatment' site with added lobsters and 'control' sites without added lobsters. Over the experimental period patches declined in size at NBRR but increased in size at control sites (see also Fig. 30d).

Analysis	Source	Sum Sq	DF	F-value	Pr(>F)	
a. Patch size transform = $\log(Y)$	Site	51.09	2	30.75	<0.0001	***
	C1 vs. C2	25.78	1	31.03	<0.0001	***
	NBRR vs. (C1,C2)	25.31	1	30.46	<0.0001	***
	Time	0.06	1	0.07	0.785	
	Site*Time	0.37	2	0.22	0.800	
	C1 vs. C2	0.03	1	0.03	0.862	
	NBRR vs. (C1,C2)	0.35	1	0.42	0.519	
	Residuals	158.69	191			
b. Patch count (per 10 min) transform = $\log(Y)$	Site	0.06	2	0.09	0.914	
	C1 vs. C2	0.04	1	0.12	0.746	
	NBRR vs. (C1,C2)	0.02	1	0.07	0.805	
	Time	0.00	1	0.01	0.931	
	Site*Time	0.05	2	0.08	0.928	
	C1 vs. C2	0.05	1	0.15	0.711	
	NBRR vs. (C1,C2)	0.00	1	0.00	0.998	
	Residuals	1.99	6			
c. Change in patch area 'Before – After' of marked fixed patches (no transformation required)	Site	96.21	2	16.23	<0.0001	***
	C1 vs. C2	6.77	1	2.29	0.14	
	NBRR vs. (C1,C2)	89.43	1	30.18	<0.0001	***
	Residuals	94.84	32			

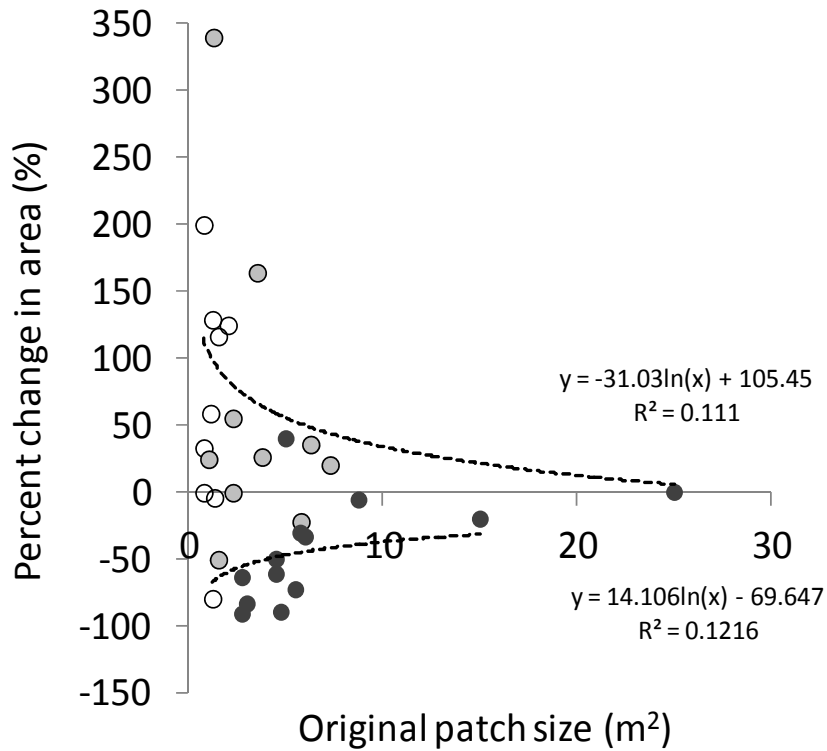


Figure 31. Percentage change in size of incipient barrens patches over ~2 y at the North Bay Research Reserve (NBRR) and control sites in south east Tasmania as a function of initial patch size at the beginning of the research project. Larger patches show greater stability relative to absolute size. Fitted lines (logarithmic) are to data on each side of zero on the ordinate. Black circles are patches within NBRR (most of which decreased in size), white are patches at control site 1 (CPL) and grey are patches at control site 2 (FB).

Predation rates of lobsters on sea urchins

The potential for molecular detection of predation

The ecological dynamics between *Centrostephanus rodgersii* and rock lobsters and their broader effects on ecosystem dynamics, continues to present challenges to management authorities and the rock lobster and abalone fisheries in Tasmania. Manipulative experiments have clearly identified the singular importance of rock lobsters as the principle predator of both *Heliocidaris erythrogramma* (Pederson & Johnson 2006) and *C. rodgersii* in this region (Ling et al. 2009a), and the catastrophic impact of overgrazing seaweed beds by the sea urchin is all too apparent (Johnson et al. 2005, 2011; Ling 2008), but there remain challenges to provide an unambiguous answer to the question of the absolute magnitude of predation on emergent sea urchins across large spatial scales in the field. Only by obtaining these estimates can appropriate 'target' densities of large lobsters be identified so that a sustainable balance between a viable rock lobster fishery and conservation of desired kelp bed habitat be achieved. The application of molecular prey detection – 'forensic ecology' – can potentially inform this important question.

Use of molecular prey detection in marine trophic interactions is well documented for some mammals and other large 'top' marine predators (Deagle *et al.* 2005; Deagle *et al.* 2009; Jarman & Wilson 2004) that are of interest as keystone species targeting particular pelagic prey and influencing pelagic ecosystem structure. The present study investigated the possibility of using the presence of prey DNA in lobster faecal material to estimate predation rates on ecologically important sea urchins, in part because direct observation of predation is extremely difficult to observe and aquatic invertebrate predators present greater challenges to determine diet from gut contents (Blankenship & Yayanos 2005) than do many other organisms (Agusti *et al.* 2003; Casper *et al.* 2007b). Aquatic invertebrate predators often consume prey with no hard parts (bones, otoliths, scales, etc.) and have extremely efficient digestive systems (Braley, *et al.* 2010; Harper *et al.* 2005), rendering traditional gut content analysis unreliable or unfeasible, and unlikely to yield quantitative dietary information (Passmore *et al.* 2006; Read *et al.* 2006). It is not surprising therefore that despite clear evidence of the importance of rock lobsters as predators of sea urchins (e.g. Tegner & Levin 1983; Shears & Babcock 2002; Pederson & Johnson 2006; Ling *et al.* 2009a; Mayfield *et al.* 2001; Blamey *et al.* 2010; Blamey & Branch 2012), studies based on analysis of lobster gut contents usually fail to identify sea urchins as prey (Hickman 1945; Mayfield *et al.* 2000a; Mayfield *et al.* 2001). This is possibly due to heavy maceration of urchin hard parts in the gastric mill and/or lobsters only consuming soft tissues such as gonad and connective ligaments through the urchin's peristomial opening while the remainder of the test remains intact and is not consumed (S. D. Ling, pers.obs.).

A further complication is the necessity to sample the population frequently enough to account for the highly seasonal nature of foraging activity (e.g. Ziegler *et al.* 2002, 2003, 2004) and diet structure (Ennis 1973; Mayfield *et al.* 2000b) in temperate lobsters. Lobsters in Tasmania present an additional problem because they are the target of a valuable live fishery with a discerning market (Mayfield *et al.* 2000a), so to obtain meaningful sample sizes, it is essential that animals are sampled live and returned to the reef at sea or to commercial holding tanks for live trade in perfect condition. The non-lethal faecal collection technique we employed allows for rapid, efficient and repeated sampling with replacement. Thus, for animals such as rock lobsters, DNA approaches emerge as a promising tool to assess predation on specific prey across a variety of spatial and temporal scales (Chow *et al.* 2006; Mayfield *et al.* 2000b; Redd *et al.* 2008).

Detection of sea urchin DNA in lobsters at reserve sites

Detection rates of sea urchin DNA in lobster faeces at ERRR and NBRR indicated ingestion of both *Centrostephanus rodgersii* and *Heliocidaris erythrogramma* tissue across all lobster size-classes examined (Fig. 32C). Within the ERRR, which supported extensive *C. rodgersii* barrens, the overall detection rates for *C. rodgersii* and *H. erythrogramma* DNA across all lobster size-classes was similar, at 0.38 and 0.36 respectively. In contrast, within NBRR, the overall rate of detection for *C. rodgersii* DNA in lobster faeces

was lower at 0.25, while the detection rate for *H. erythrogramma* was 0.32. These patterns broadly reflected the rank abundance of the two sea urchin species at these sites, i.e. higher *C. rodgersii* and lower *H. erythrogramma* at ERRR, and lower *C. rodgersii* and higher *H. erythrogramma* at NBRR (Table 19). At a finer temporal resolution, detection rates varied significantly across years for *C. rodgersii* and *H. erythrogramma* at both sites variously depending on lobster size and season (Fig. 32C; Tables 20,21), and across seasons depending on the year and/or lobster size (Tables 20, 21a) for all but *H. erythrogramma* at NBRR (Table 21b).

In general, the proportion of positive assays to sea urchin DNA increased with increasing lobster size (Fig. 32C; and Table 23). Notably, the proportion of smaller lobsters (<140 mm CL) testing positive for sea urchin DNA was higher than expected based on results of *in situ* field experiments showing that only large lobsters could directly predate sea urchins (Fig. 32 and Table 23). For ERRR, the GLM revealed an effect of lobster size on the proportion of positive assays for *Centrostephanus rodgersii* but this was dependent on year and season; lobster size also interacted significantly with season and habitat (Table 20A). For *Heliocidaris erythrogramma* at ERRR, the effect of size was both dependent on habitat and season (Table 20B). At NBRR, lobster size yielded significant effects in combination with year and season for *C. rodgersii*, but lobster size had no effect on *H. erythrogramma* detections at this site where both season and year had significant effects on detection rates for *H. erythrogramma* as main effects (Table 21).

‘Extraneous’ sources and passive ingestion of sea urchin DNA

The assays showed that *Centrostephanus rodgersii* and *Heliocidaris erythrogramma* DNA was present in the unconsolidated sediments accumulated between boulders on the reefs at both sites, and at different depths and habitats (Table 22Ai.). There were also a small number of positive detections of sea urchin DNA in the faeces of lobsters that were fed gelatine ‘food parcels’ containing sediments collected from the benthos at both sites, although on most occasions (10 of 14 tests) no urchin DNA was detected in faeces of lobsters fed sediment, presumably because the digestion process further degraded urchin DNA contained in the sediment (Table 22Aii.).

There were also positive detections of sea urchin DNA in the faeces of both *C. rodgersii* and *H. erythrogramma* (obtained from animals collected from incipient barrens patches at NBRR where the species co-occur, Table 22Bi.), and low but non-zero rates of detection of urchin DNA (of both species) in lobster faeces from individuals fed food parcels containing *C. rodgersii* sea urchin faecal pellets (Table 22Bii.). There were no detections of urchin DNA in the faeces of lobsters fed *H. erythrogramma* faeces (Table 22Bii.). We draw particular attention to the result that DNA from one urchin species was sometimes detected in the faecal pellets of the other urchin (suggesting that each species may ingest faecal material of the other in the incipient barrens patches from which the urchins were collected), and that faecal pellets obtained from each species don’t universally contain detectable DNA from that species.

Table 19. Habitat distribution and mean abundance of (i) sea urchins, and (ii) lobsters retained on reefs inside (A.) Elephant Rock Research Reserve (ERRR) and (B.) North Bay Research Reserve (NBRR). The ERRR experiment commenced with declaration of the protected area on 21/04/2008, while the NBRR experiment started on 30/09/2008. Based on reef area and observed patterns in sea urchin abundance within the ERRR, the population of *Centrostephanus rodgersii* (*C.r.*) on widespread barrens declined from a density of 2.31 to 1.93 individuals m⁻² and in kelp bed habitat (*Ecklonia radiata*) from 1.77 to 1.32 m⁻², while *Heliocidaris erythrogramma* (*H.e.*) declined from 1.77 to 1.32 m⁻² and from 0.25 to 0.20 m⁻² on barrens and kelp habitat respectively over the 955 day study period. Within NBRR, the *C. r.* population declined from 0.12 to 0.02 m⁻² and *H.e.* from 1.26 to 0.55 m⁻² over the 840 day study period. Note that the remaining 17% of reef at ERRR was classified as deep invertebrate community / sediment matrix occurring along the sand edge of the reef at ~35-45 m depth for which we had no diver-based information on sea urchin densities at either the start or end of monitoring. For (ii), population estimates for are based on mark-recapture ratios of large lobsters CL≥140 mm and total legal lobsters CL ≥110 mm and are averaged over the duration of the study period.

				Abundance							
				Sea urchin						Lobster	
Site	Habitat	Area (m ²)	% reef	Start		End		loss		Time Integrated pop.	
				<i>C.r.</i>	<i>H.e.</i>	<i>C.r.</i>	<i>H.e.</i>	<i>C.r.</i>	<i>H.e.</i>	Large	Total Legal
ERRR	Seaweed bed	183,318	40	324,473	45,830	241,980	36,664	82,493	9,166	340	832
	Widespread Barrens	197,867	43	457,073	31,659	381,883	15,829	75,190	15,830	367	898
B. NBRR	Seaweed bed with incipient barrens	175,523	100	21,589	221,159	3,558	96,538	18,031	124,621	661	1,713

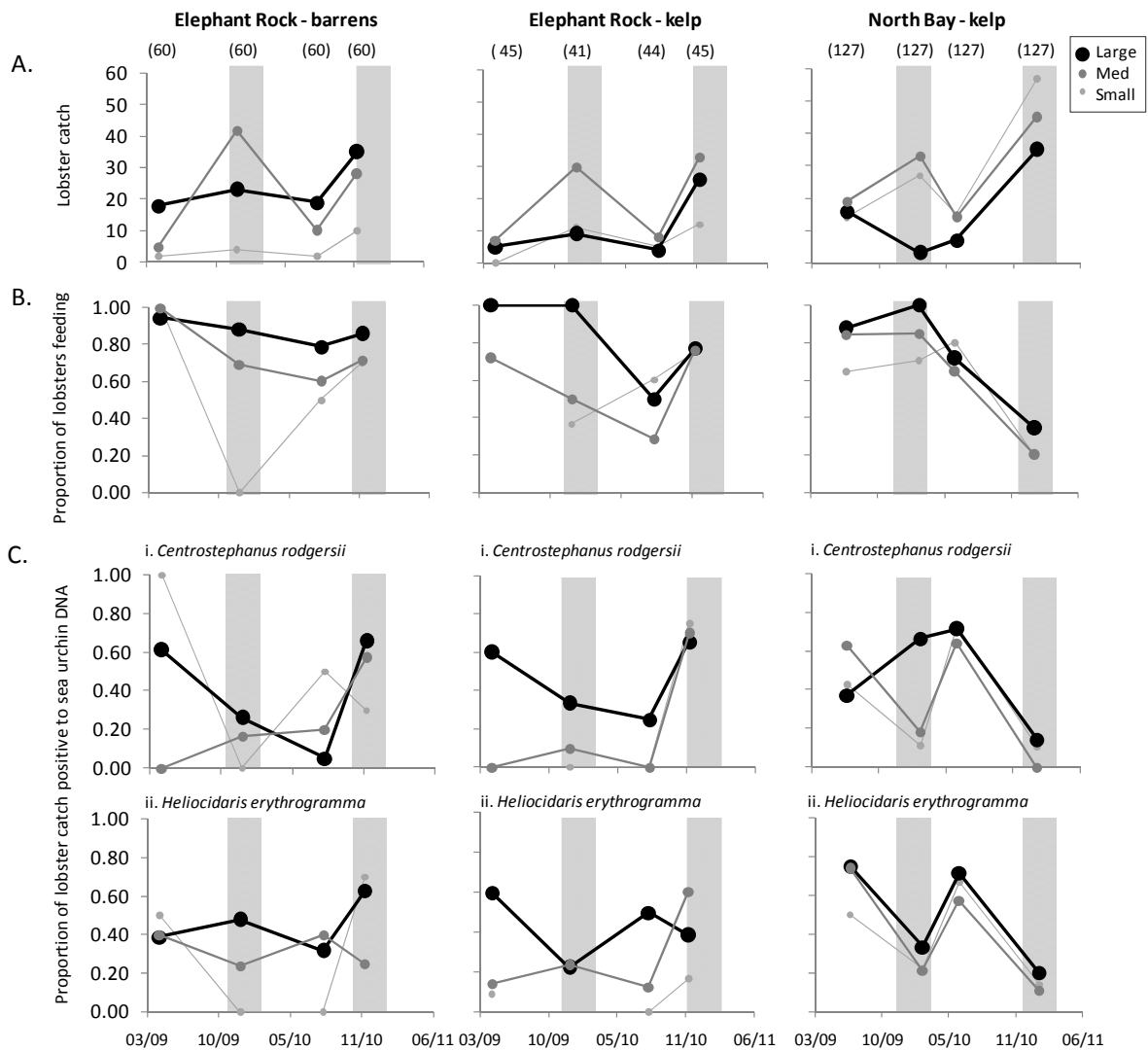


Figure 32. (A.) Catch of lobsters by size-class (see legend); number of trap lifts to attain catch is shown in parentheses above each sampling occasion. (B.) Proportion of trap-caught lobsters by size-class deemed to be feeding; i.e. those for which a faecal sample was obtainable. (C.) Proportion of trap-caught lobsters by size-class testing positive to DNA assay for sea urchins (i) *Centrostephanus rodgersii* and (ii) *Heliocidaris erythrogramma* in lobster faecal material sourced from research reserves at Elephant Rock (barrens & seaweed habitats; LHS & middle columns respectively) and North Bay (seaweed / incipient barrens only; RHS column) during winter and summer sampling 2009-2011. Note that lobster size classes are: Large, ≥ 140 mm carapace length (CL); medium, ≥ 110 mm & < 140 mm CL; small, < 110 mm CL. Filled grey regions represent summer periods where feeding rates of lobsters and catch-ability reach an annual high (see Ziegler et al. 2002, 2003, 2004).

Table 20. Analysis of deviance for binomial GLM model fitted to presence/ absence of detections of sea urchin DNA in lobster faecal material for (A.) *Centrostephanus rodgersii*; and (B.) *Heliocidaris erythrogramma* at Elephant Rock Research Reserve 2009-2010. Signif. codes: '***' <0.001; '**' <0.01; '*' <0.05.

A. Source	df	Deviance	Resid. df	Resid. Dev	P(> Chi)	
NULL			347	460.96		
Year	1	28.69	346	432.27	8.5E-08	***
Season	1	9.58	345	422.69	0.002	**
Size	2	9.07	343	413.62	0.011	*
Habitat	1	0.24	342	413.39	0.628	
Year*Season	1	42.41	341	370.98	7.4E-11	***
Year*Size	2	6.36	339	364.62	0.042	*
Season*Size	2	6.84	337	357.78	0.033	*
Year*Habitat	1	1.57	336	356.2	0.210	
Season*Habitat	1	1.57	335	354.64	0.210	
Size*Habitat	2	0.77	333	353.87	0.682	
Year*Season*Size	2	10.23	331	343.64	0.006	**
Year*Season*Habitat	1	1.21	330	342.42	0.271	
Year*Size*Habitat	2	0.69	328	341.73	0.708	
Season*Size*Habitat	2	7.63	326	334.1	0.022	*
Year*Season*Size*Habitat	1	0.00	325	334.1	1.000	

B. Source	df	Deviance	Resid. df	Resid. Dev	P(> Chi)	
NULL			347	455.6		
Year	1	6.70	346	448.9	0.010	**
Season	1	1.07	345	447.83	0.301	
Size	2	9.95	343	437.88	0.007	**
Habitat	1	0.84	342	437.04	0.359	
Year*Season	1	5.69	341	431.36	0.017	*
Year*Size	2	1.14	339	430.21	0.565	
Season*Size	2	0.30	337	429.91	0.861	
Year*Habitat	1	0.05	336	429.86	0.820	
Season*Habitat	1	0.05	335	429.82	0.828	
Size*Habitat	2	9.26	333	420.55	0.010	**
Year*Season*Size	2	3.09	331	417.47	0.214	
Year*Season*Habitat	1	0.87	330	416.6	0.352	
Year*Size*Habitat	2	5.38	328	411.22	0.068	
Season*Size*Habitat	2	9.80	326	401.42	0.007	**
Year*Season*Size*Habitat	1	0.28	325	401.14	0.598	

Table 21. Analysis of deviance for binomial GLM model fitted to presence/ absence data of positive DNA tests of lobster faecal material for (A.) *Centrostephanus rodgersii*; and (B.) *Heliocidaris erythrogramma* at North Bay Research Reserve 2009-2010. Signif. codes: '***' <0.001; '**' <0.01; '*' <0.05.

A.	Source	df	Deviance	Resid. df	Resid. Dev	P(> Chi)	
	NULL			284	319.98		
	Year	1	3.91	283	316.07	0.048	*
	Season	1	61.63	282	254.44	4.1E-15	***
	Size	2	0.06	280	254.39	0.973	
	Year*Season	1	7.87	279	246.52	0.005	**
	Year*Size	2	6.45	277	240.07	0.040	*
	Season*Size	2	6.53	275	233.55	0.038	*
	Year*Season*Size	2	3.21	273	230.34	0.201	

B.	Source	df	Deviance	Resid. df	Resid. Dev	P(> Chi)	
	NULL			284	355.48		
	Year	1	9.11	283	346.38	0.003	**
	Season	1	56.38	282	289.99	6.0E-14	***
	Size	2	1.69	280	288.31	0.431	
	Year*Season	1	0.78	279	287.53	0.376	
	Year*Size	2	1.15	277	286.38	0.563	
	Season*Size	2	0.50	275	285.88	0.779	
	Year*Season*Size	2	0.79	273	285.09	0.673	

Table 22. (A.) Detections of sea urchin DNA in (i.) benthic sediment and (ii.) faecal samples taken lobsters fed in the laboratory with ‘food parcels’ containing sediments from both research reserves. (B.) detections of sea urchin DNA in (i.) sea urchin faecal material and (ii.) in lobster faecal material for lobsters fed with ‘food parcels’ containing urchin faecal material. Numbers in parentheses indicate the number of independent replicate samples. Note that due to mixed success in obtaining faecal material from lobsters fed artificial ‘food parcels’ under laboratory conditions, replicate faecal samples from these lobsters were variable and generally low.

				<i>Samples detecting positive for the presence of sea urchin DNA</i>			
				i). Sediment		ii). Lobsters fed sediment	
A.	Site	Habitat	Depth	<i>C.r</i>	<i>H.e</i>	<i>C.r</i>	<i>H.e</i>
	ERRR	Kelp	10 m	80% (5)	20% (5)	0% (2)	0% (2)
		Barrens	15 m	100% (5)	60% (5)	50% (2)	50% (2)
		Barrens	20 m	100% (5)	80% (5)	<i>no data</i>	<i>no data</i>
		Barrens	25 m	100% (5)	60% (5)	<i>no data</i>	<i>no data</i>
	NBRR	Kelp	10 m	100% (5)	60% (5)	0% (2)	0% (2)
		Incip. barrens	10 m	100% (5)	40% (5)	0% (1)	0% (1)

				i). Sea urchin faeces		ii). Lobsters fed sea urchin faeces	
B.	Sea urchin faecal material source			<i>C.r</i>	<i>H.e</i>	<i>C.r</i>	<i>H.e</i>
	<i>Centrostephanus rodgersii</i>			75% (4)	50% (4)	27% (11)	55% (11)
	<i>Heliocidaris erythrogramma</i>			75% (4)	50% (4)	0% (1)	0% (1)

DNA based estimates of predation vs. observed sea urchin declines

Comparing the proportion of lobsters testing positive to sea urchin DNA (averaged across all sampling periods of the study; Table 23i) with estimates determined independently to account for the observed decline in sea urchin abundance at each site (Table 23ii; both proportions represent equivalent instantaneous 3-day ingestion rates averaged over the ~2.5 year study period), revealed broad agreement between methods based on mean values and overlap of 95% confidence intervals. However, for the sizes of lobsters known to prey directly on emergent size-classes of sea urchins, DNA assays consistently showed higher proportions of lobsters testing positive than that required to account for the observed decline in abundance of both sea urchin species at both ERRR and NBRR. Similarly, given prior observations over an extensive range of sizes of both lobsters and urchins showing that only large lobsters are capable of directly preying on emergent sea urchin size-classes for *Centrostephanus rodgersii*, and only medium and large lobsters for the sea urchin *Heliocidaris erythrogramma*, the proportions of positive DNA detections in faecal pellets of smaller size-classes of lobsters were notably high (Table 23, cf. i. & ii.), suggesting ingestion of urchin DNA other than through direct predation.

Table 23. Proportions of trap-caught lobsters whose faecal pellets tested positive to DNA from (A.) *Centrostephanus rodgersii* (*C.r.*) and (B.) *Heliocidaris erythrogramma* (*H.e.*) for two eastern Tasmanian research reserves (Elephant Rock, ERRR, & North Bay, NBRR, Research Reserves). Lobster catch indicates the total catch of lobsters by size class; S=small lobsters CL<110 mm (below legal size); M=medium lobsters CL≥110 mm & <140 mm; L=Large lobsters CL≥140 mm. (i) Proportion of lobsters testing positive to urchin DNA (averaged across 4 periods; winter & summer seasons in years 2009 & 2010). (ii.) independent estimates of the mean number of sea urchins consumed per lobster per 72 hour period averaged across seasons and years derived from data on the decline in abundance of sea urchins at the reserve sites (see footnotes) plus estimates of mean densities of predation-capable lobsters over the study period (from Table 1ii). Given that the DNA signal from a single feeding event is detectable for ~60 hours i.e. 3-days (Redd, Jarman et al. 2008) the two measures are directly comparable. Note that in (i.) the asterisks shows the predatory capable size-class(es) of lobsters capable of preying on emergent size-class of *C. r* (after Ling et al. 2009a) and *H.e.* (after Pederson & Johnson 2006). Ranges given in parentheses for both (i.) & (ii.) are 95% confidence intervals of estimates obtained by bootstrapping data 10,000 times.

Site	Lobster catch			<i>Centrostephanus rodgersii</i>			ii. Prop. positive based on obs. <i>C.r.</i> decline	<i>B. Heliocidaris erythrogramma</i>				
	S	M	L	i. Mean prop. of catch positive to <i>C.r.</i> DNA assay across years & seasons				i. Mean prop. of catch positive to <i>H.e.</i> DNA assay across years & seasons				
				Lobster size				Lobster size				
				S	M	L*		S	M*	L*	M*+L*	
ERRR	46	163	139	0.42 (0.35-0.51)	0.22 (0.17-0.28)	0.41 (0.33-0.49)	0.31† (0.12 – 0.54)	0.25 (0.08-0.41)	0.30 (0.22-0.39)	0.43 (0.31-0.54)	0.37 (0.30-0.43)	0.03‡ (0.00 – 0.07)
NBRR	113	111	61	0.35 (0.25-0.44)	0.36 (0.27-0.45)	0.47 (0.29-0.63)	0.10* (0.05 – 0.16)	0.38 (0.28-0.48)	0.41 (0.31-0.50)	0.50 (0.34-0.68)	0.43 (0.36-0.51)	0.25** (0.17 – 0.35)

† At ERRR there was a 21% decline in mean *C. rodgersii* density over the study as assessed from changes in mean density on n=12 fixed belt transects (pooled habitats) between the start of the experiment immediately before lobster translocation, and conclusion of the study (paired t-test, 1-tailed $P=0.0139$, adjusted $\alpha = 0.017$). The decline was from a mean density of 2.04 to 1.62 m⁻², equating to a decline in population size of 129,868 individuals within the reserve. Significant declines in *C. rodgersii* abundance were not observed at adjacent control sites (in 1-tailed paired t-tests $P=0.293$ & $P=0.289$); *C. rodgersii* abundance increased by 5% at Control Site 1 but declined by 4% at Control Site 2. Mean change in density at experimental and control sites differed significantly (1-way ANOVA, $F_{1,34} = 5.313$, $P = 0.027$).

‡ At ERRR there was a 43% decline in mean *H. erythrogramma* density over the study as assessed from changes in mean density on n=12 fixed belt transects (pooled habitats) between the start of the experiment immediately before lobster translocation, and conclusion of the study (this decline was non-significant, paired t-test, 1-tailed $P=0.0496$, adjusted $\alpha = 0.017$). The decline was from a mean density of 0.20 to 0.12 m⁻², equating to a decline in population size of 27,829 individuals within the reserve. A smaller and non-significant decline of 28% in mean *H. erythrogramma* density was observed across both control sites; paired t-tests yielded $P=0.077$ & $P=0.197$ for the two control sites. Mean change in density at experimental and control sites did not differ significantly (1-way ANOVA, $F_{1,34} = 0.181$, $P = 0.673$).

*At NBRR there was an 85% decline in mean *C. rodgersii* density over the study as assessed from changes in mean density on n=6 belt transects between the start of the experiment immediately prior to lobster translocation, and at the conclusion of the study (paired t-test, 1-tailed $P=0.007$, adjusted $\alpha = 0.017$). The decline in mean density was from 0.12 to 0.02 m⁻², equating to a decline in population size of 17,961 individuals inside the reserve. A decline of 45% and an increase of 21% in *C. rodgersii* density at Control Site 1 ($P=0.186$) and Control Site 2 ($P=0.283$) respectively were not significant. Mean change in density at experimental and control sites did not differ significantly (1-way ANOVA, $F_{1,16} = 3.652$, $P = 0.074$), but the test is likely to be unreliable given notable variance contamination (in an unbalanced design) that could not be rectified with transformation.

**At NBRR there was a 57% decline in *H. erythrogramma* density over the study as assessed from changes in mean density on n=6 belt transects between the start of the experiment immediately prior to lobster translocation, and at the conclusion of the study (paired t-test, 1-tailed $P=0.0002$, adjusted $\alpha = 0.017$). The decline in mean density was from 1.26 to 0.55 m⁻², equating to a decline in population size of 125,299 individuals within the reserve. A non-significant decline of 25% and an increase of 21% were observed at Control Site 1 ($P=0.096$) & Control Site 2 ($P=0.046$) respectively. Mean change in density at experimental and control sites differed significantly (1-way ANOVA, $F_{2,15} = 13.255$, $P = 0.00048$), with significant differences between the two control sites (Tukey's HSD, $P = 0.026$) and between C2 and the experimental site (Tukey's HSD, $P = 0.00034$), but not between C1 and the experimental site (Tukey's HSD, $P = 0.105$).

Interpreting molecular detection of prey

Despite the high potential of the technique for the purpose, interpreting molecular detection of prey is far from straightforward, and our results suggests that it may be particularly problematic for benthic foraging species. Where estimates of minimum absolute predation rate are required, it is necessary to consider both the degradation of DNA during digestion in a predator's gut, and the power of PCR to amplify a prey-specific region of DNA from semi-digested material (Deagle et al. 2005; Jarman et al. 2002; Nejtgaard et al. 2003; Parsons et al. 2005; Soininen et al. 2009). The longevity of the molecular signal in the lobster *Jasus edwardsii* (from 7-60 hours post consumption, Redd et al. 2008) indicates that individuals obtained from traps during routine commercial fishing or research operations can possess prey DNA in their faeces from material consumed prior to the lobster entering the trap. In the commercial lobster fishery in Tasmania, traps are typically set for a maximum of 24 hours, so that prey consumed by a lobster within ~30 hours of entering a trap would be detectable using this approach. To be conservative, we assumed that 3 days (72 h) was the maximum time after ingestion that prey could be detected.

It is unlikely that top predators in pelagic environments inadvertently ingest DNA of their usual prey. In contrast, many benthic predators will forage among the detritus and sedimentary material of the benthos, where they may consume 'extraneous' sources of their prey DNA. Sea urchin DNA is most likely to occur in sediments as a result of release of their faecal material. We found that both sets of sea urchin species-specific PCR primers revealed the presence of sea urchin DNA in most (but not all) samples of total environmental DNA extracted from sediment accumulated between boulders in both incipient and extensive barrens habitat (Table 22). This is not unexpected because marine sediments are well known as repositories for both prokaryotic and eukaryotic DNA (Bowman & McCuaig 2003). If lobsters do consume sea urchin DNA by feeding on sedimentary material, then clearly this has the potential to bias estimates of direct predation based on detection of prey DNA in faecal material. The magnitude of the bias will depend on how frequently and how much sediment-associated DNA is consumed, rates of denaturation of prey DNA in the sediment, and the extent of further denaturation of the DNA once it is ingested and passes through the lobster digestive system. It has been previously suggested that rock lobsters may consume marine sediment (Cox et al. 1997; Steyna & Schleyera 2011), and lobsters (*Jasus edwardsii*) have been reported foraging in sediment-based habitats away from rocky reefs (Langlois et al. 2006). However, the extent to which lobsters ingest sediments and associated detritus is uncertain, in part because direct feeding on sediment is difficult to determine without sacrificing the animal to examine gut contents. We have observed large males active during the day appearing to 'taste' the sediment with their maxillipeds, and while it was not possible to discern from *in situ* observation whether this sediment or associated detritus is ultimately consumed (S.D. Ling, pers. obs.), it is possible that sedimentary material can be ingested if bound with other food material. While further experimentation is needed to quantify the extent of ingestion of sediment-associated organic material, our initial experiments suggest that prey DNA ingested in this way can lead to positive detection of urchin DNA in lobster faecal material, although detection rates are low suggesting that in most cases ingested DNA is degraded. Even when starved lobsters ingested fresh sea urchin faecal pellets embedded in 'food parcels', in relatively few cases did the lobster faeces subsequently recovered test positive for sea urchin DNA (Table 22). Our tentative conclusion is that inflation of estimates of direction predation as a result of lobsters ingesting sea urchin DNA from sediments is likely to be low, but nonetheless partially explains the higher than expected rates of DNA detection (particularly for small lobsters) relative to lobster predation rates required to explain observed declines in sea urchin abundance within the research reserves.

Interpreting results of molecular analysis can also be complicated by detection of prey DNA as a result of secondary predation, which is often speculated and occasionally substantiated in controlled feeding experiments (Juen & Traugott 2005; King et al. 2008; Sheppard et al. 2005; Deagle et al. 2009). There is considerable evidence to suggest that direct predation on adult emergent-sized sea urchins in Tasmania is unlikely other than by large lobsters (Pederson & Johnson 2006; Ling et al. 2009a), and there is no case to suggest that lobsters of any size consume other animals that have fed on sea urchins. However, from extensive deployment of remote infra-red video *in situ*, we have commonly observed smaller lobsters to

scavenge the remains of sea urchins killed by large ones. From 19 'primary kills' of tethered sea urchins by large lobsters at night (that were consumed within the field-of-view), on average we observed an additional 1.47 (SE = 0.22) smaller scavenging lobsters to forage on the fresh sea urchin carcass (i.e. only 40% of all lobsters observed consuming urchins were responsible for the primary kill). Clearly, this is likely to lead to over-estimating direct predation based on detection of DNA in lobster faeces. This rate of scavenging is, on its own, sufficient to account for all positive DNA detections in small and medium sized lobsters at the ERRR site, although falls short of accounting for all positive detections in small and medium sized lobsters in the incipient barrens at the NBRR (from data in Table 22).

Another possibility to consider is that smaller lobsters incapable of tackling and killing a large emergent sea urchin are able to find and directly predate the smaller sea urchins that live within the interstices of the reef matrix [and that were not readily available for the predation trials conducted by Ling et al. (2009a)]. This possibility needs to be adequately researched, but we think it is highly unlikely because we have never observed any kill that did not proceed by the lobster standing over the urchin to prise it from the substratum, and then rolling the sea urchin through 180° before penetrating and consuming the soft parts through the soft peristomial region of the urchin's oral surface. In the confines of crevices, using their long spines (which are disproportionately long in juveniles) the urchins wedge themselves into the crevice and it is not possible for lobsters to prise them from the surface to commence the rolling manoeuvre.

It is also possible that estimating predation rates based on DNA analysis of faecal pellets from trap-caught lobsters would underestimate actual predation rates. This would arise if sampling was undertaken during periods when lobsters were not motivated to forage (Ziegler et al. 2002, 2003, 2004), or if the motivation to enter traps baited with fish is lower for lobsters that habitually feed on the urchins (S. D. Ling pers. obs.).

Limitations of qPCR for determining absolute rates of predation for benthic predators

Quantifying dietary intake is something of a 'holy grail' of study of predator-prey interactions. Recent advances in molecular biology have shown that prey DNA can be used to not only identify the prey being consumed (Symondson 2002) but also to quantify its intake (Deagle & Tollit 2006), at least in relative terms. The latter authors showed that ratios of prey DNA in faecal material of marine mammals closely matched the amounts of fish species fed during captive trials (Deagle & Tollit 2006). However, whether qPCR can be used to quantify either relative or absolute ingestion of prey from field samples is much less certain (Nejstgaard et al. 2008; Troedsson et al. 2007; Weber & Lundgren 2009). Because the time of ingestion is unknown for material obtained from wild populations, it is well acknowledged that it is unlikely to be possible to discern among (i) low levels of ingestion, (ii) high levels of very recent ingestion, or (iii) high levels of ingestion in the relatively distant past, as reasons for observation of relatively low levels of prey DNA in predator faeces.

In addition, our results clearly demonstrate there are arguably even more fundamental considerations in applying and interpreting qPCR to the detection of prey in predator faeces as a means of estimating absolute rates of predation, even when the signal is interpreted at a binary level (i.e. to indicate 'presence' or 'absence' of ingested prey material). This is because there are two elements in the approach that usually require a level of subjectiveness in interpretation, and which can have a bearing on absolute estimates of predation rates. The first is the fluorescence threshold, and the other is the C_t values below or above which amplification curves are deemed not to reflect the presence of target DNA (very low C_t values are usually interpreted as machine error, e.g. commonly ascribed to optics in the qPCR machine, while high values are typically interpreted to indicate primer dimerisation). In the present work, there was an unambiguous discontinuity in the asymptotic value of amplification curves which suggested that identifying the fluorescence 'threshold' and related artefacts in samples was robust. However, decisions on cut-offs for C_t values were not so readily identified. While the few samples with very low C_t scores were well separated from the remaining samples, again suggesting a clear or 'natural' lower limit to identify this kind of erroneous result (see Appendix 7; samples requiring <8 cycles were not interpreted as positive detections), we took the upper limit of C_t values (at 40 cycles for *C. rodgersii* and 45 cycles for *H. erythrogramma*) as the

mode of the distribution of *Ct* scores. While this approach is common, and is defensible at some level, it nonetheless has a subjective component, and it needs to be acknowledged that the problem of primer dimerisation as an artefact may begin to arise at *Ct* values less than or greater than the mode of the distribution of values. Clearly, this decision has a direct effect on results and on estimates of absolute predation rates.

Conclusions

It is critical to understand the limitations of qPCR detection of prey items in faeces in addressing trophic interactions and complex ecological questions in general and for rocky reefs in particular. The quest to obtain an unambiguous estimate of absolute predation rates by lobsters on emergent sea urchins in the field using qPCR is complicated by the lobsters ingesting sea urchin DNA from sources other than by direct predation, subjective decisions in interpreting qPCR output, and temporal variability in the DNA signal. The latter is likely to reflect real temporal (and spatial) variability, and can be addressed by sampling over several years and seasons to obtain a time-averaged result, as we have done here. The other two issues are not so readily resolved. Thus, while we are encouraged that the two methods used here, at a broad level, give similar results in indicating high rates of predation by lobsters on sea urchins when the prey species occurs at high abundance, sufficient challenges in interpretation remain such that estimates of direct predation based on qPCR cannot be interpreted unambiguously, and are best corroborated by independent approaches.

Given this, and significant declines in sea urchin densities at the experimental sites with translocated lobsters, but inconsistent and non-significant changes at control sites, we take the change in urchin density at experimental sites over the ~2.5 years of the study, related to average abundances of large (>140 mm CL) lobsters at these sites over this period, as a robust estimate of absolute predation. Over the ~2.5 year study period, at the site characterized by incipient barrens, a mean density of lobsters on the reef in the reserve of 37.66 per hectare inflicted an annual mortality rate on *C. rodgersii* of 0.492, while on extensive barrens 18.55 large lobster per hectare inflicted an overall mortality rate on *C. rodgersii* of 0.039 y^{-1} .

Large scale – Are there acceptable options to manage the rock lobster fishery to build the biomass of large lobsters sufficiently to control *C. rodgersii* numbers coast-wide?

In keeping with the development of the Methods section, here we organize results and discussion of the modelling components of the project in three sections dealing with (1) calibration, validation and sensitivity analysis of the TRITON ecosystem model, (2) application of the TRITON model to assess the likely outcome of alternative management strategies that might be applied to the *Centrostephanus rodgersii* problem in eastern Tasmania, and (3) an evaluation of strategies directed at management of the rock lobster fishery assessed by application of a single species population model for *C. rodgersii* and the current rock lobster stock assessment model (more detailed and technical presentations of these topics are given Appendices 8,9 and 10 respectively). Finally, the outcomes of the separate approaches are synthesized and integrated.

Sensitivity analysis and pattern-oriented validation of a model with alternative community states: an ecosystem model of temperate rocky reefs in eastern Tasmania

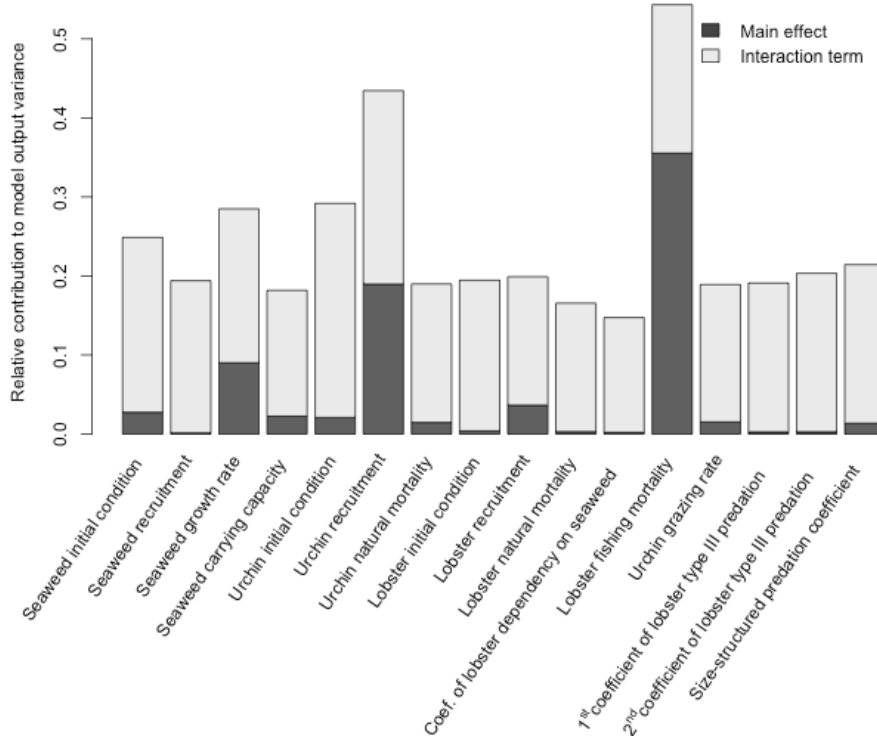
We first consider sensitivity of model behaviour to the various parameters before considering the calibration and validation of the model.

Identifying the parameters that most influence model behaviour

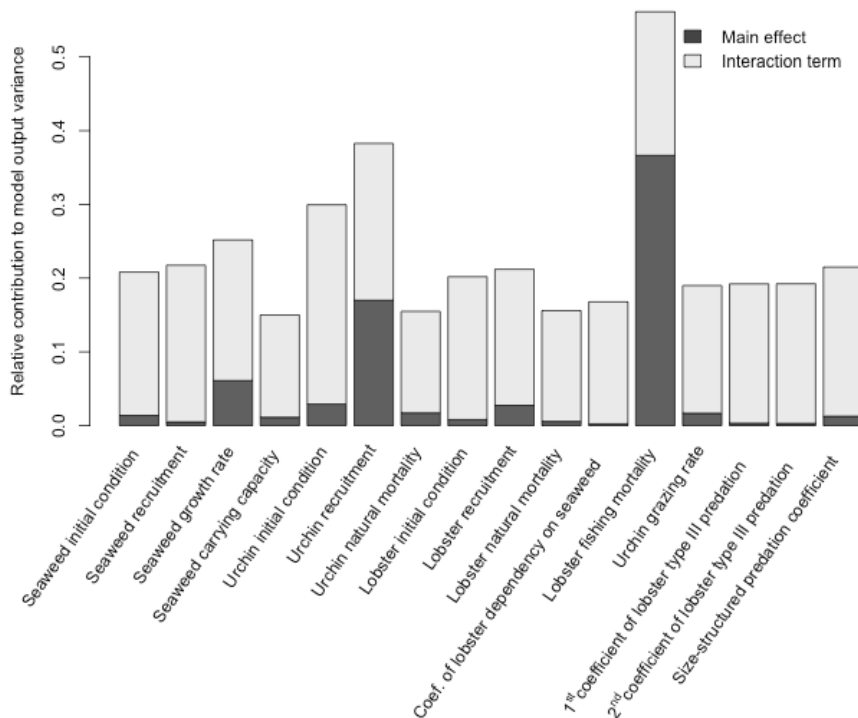
The first set of sensitivity tests investigated the effects of alternative formulations of lobster predation on sea urchins, i.e. of implementing Holling's Type I, II or III functional responses (note that this assessment can also be viewed as an essential component of model validation). FAST sensitivity indices were computed for all parameters in TRITON under each formulation of the functional response (Fig. 33). For each of the three response types, the two parameters defining the shape of the response had no more influence on model behaviour than most of the other 14 input factors. Indeed, the influence of these two parameters was unimportant compared to parameters with greatest influence on model behaviour (i.e. lobster fishing mortality, sea urchin recruitment, initial sea urchin population density, seaweed growth rate), and was also smaller than the influence of the coefficient defining the allometry of rock lobster size-structured predation on sea urchins. In addition, projection of simulation outcomes on the first two principal components (PCs) describing community structure (which captured 87.4% of the total variability) shows that the pattern of scores is very similar for the three types of functional response (Fig. 34), also indicating that the nature of the functional response has little influence on model behaviour. Given that overall model behaviour was not sensitive to either the choice of functional response or to its parameterisation, we adopted the Type III functional response which is consistent with most models of predation behaviour in decapods based on field observations (e.g. Breen 1974; Evans & Mann 1977; Eggleston 1990; Eggleston et al. 1992; Hagen & Mann 1992; Wong & Barbeau 2006; Griffen & Delaney 2007; Wong et al. 2010).

In the global sensitivity analysis, the sensitivity to input parameters of final abundances (after 50 years of community development) of seaweed, sea urchins and lobsters, and of overall community structure, was examined across 8000 Monte-Carlo simulations with unconstrained initial conditions (Figs. 33c, 35). Total extended FAST sensitivity indices quantify input parameters' relative contribution to model output variance for a given sensitivity test (but note that their absolute values are not comparable across different tests). Overall, the most influential variables were similar for each component of community structure we examined, namely fishing mortality of lobsters, sea urchin recruitment rate, sea urchin initial abundance and seaweed growth rate (although some other variables were moderately influential for some components). However, the rank order of influence differed depending on whether it was seaweed, sea urchins or lobsters that were examined. Final biomass density of seaweed is predominantly determined by, in order of importance: the initial density of sea urchins; urchin recruitment rates; seaweed growth rate; size-structured lobster predation on sea urchin; lobster fishing mortality and initial biomass (cover) of

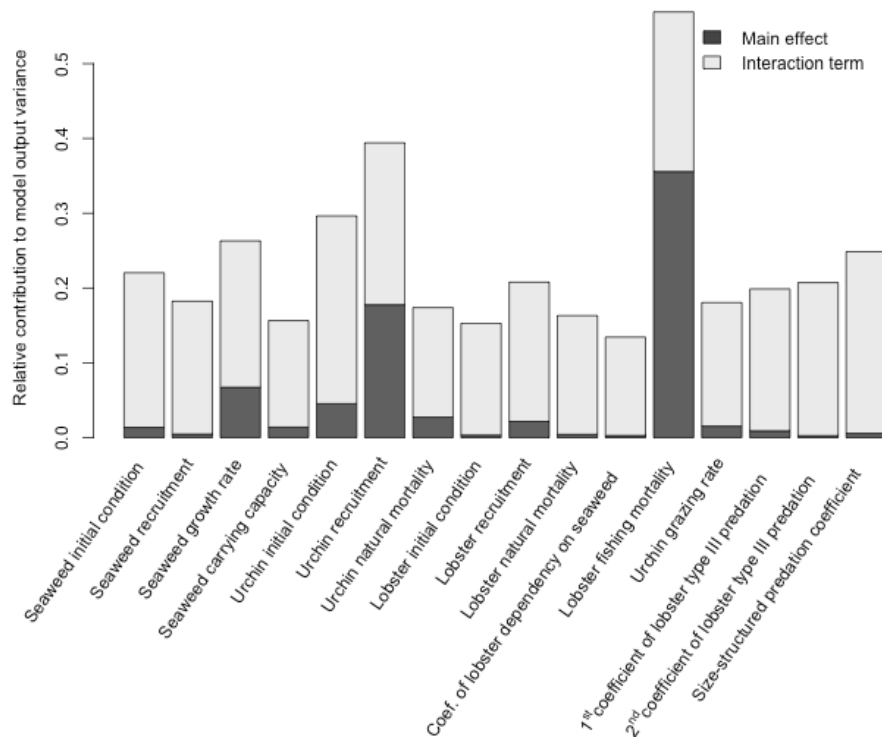
seaweed (Fig. 35a). The two most influential parameters on final sea urchin biomass densities are sea urchin recruitment rate and lobster fishing mortality (Fig. 35b). Not surprisingly, the final biomass density of lobsters is mostly determined by lobster fishing mortality and, to a lesser extent, lobster recruitment rate (Fig. 35c). In comparison, other input parameters defining lobster population dynamics (e.g. initial biomass, natural mortality, the extent of dependency on the state of the seaweed bed) have a marginal influence.



(a) Sensitivity analysis of TRITON model using Holling's Type I functional response



(b) Sensitivity analysis of TRITON model using Holling's Type II functional response



(c) Sensitivity analysis of TRITON model using Holling's Type III functional response

Figure 33. Extended FAST indices quantifying the contribution of input parameter values to model output variance, using the first principal component from the PCA (accounting for 73% of the total variance) on mean-centred normalised biomass density outputs, under alternative formulations of the functional response of lobster predation on sea urchin, assuming either (a) Holling Type I, (b) II, or (c) III relationships. Fig. 34 provides a graphical summary of final model state across the three model groups.

Given these results, it is not surprising that overall community structure described by the first principal component of the mean-centred normalised biomasses (accounting for 73% of the total variance) is most influenced by, in order of importance: lobster fishing mortality; sea urchin recruitment rate; initial sea urchin abundance; seaweed growth rate; and the three parameters defining lobster predation on sea urchins (Fig. 33c). Across all four outputs considered in this sensitivity analysis, the remaining parameters – including carrying capacity and recruitment rate of the seaweed assemblage; sea urchin natural mortality and their grazing rate; initial abundance and natural mortality of lobsters; and the coefficient of lobster dependency on the state of the seaweed bed – had relatively marginal influence on the end point community structure in the simulations.

The final two sets of sensitivity tests quantify the contribution of input parameters to two specific and important features of model behaviour, respectively, the 'forward' shift from the seaweed assemblage to sea urchin barren habitat (Fig. 36), and the 'reverse' shift from extensive sea urchin barrens to recovery of dense seaweed cover (Fig. 37). We conducted these analyses on the scores of the first principal component of the mean-centred normalised simulated biomasses of the three model groups, as a one-dimensional summary of final community state (which explained 73% of the total variance in final community composition). Sea urchin recruitment rate, lobster fishing mortality, seaweed growth rate and the three parameters defining lobster predation rate most influenced the tendency to shift from dense seaweed assemblage to sea urchin barrens (Fig. 36a). TRITON's ability to shift from an established sea urchin barren state back to dense seaweed cover was essentially driven by the values of lobster fishing mortality and recruitment rate (Fig. 37a).

Breaking down the sensitivity analysis into a series of tests screening for different model outputs and different aspects of model behaviour (i.e. 'forward' and 'backward' shifts) is a means to robustly identify input parameters that have a consistently small or large influence on simulation outcome (Klepper 1997). Overall, our results show that the identity of variables most influential in accounting for variance in

simulation outcomes is similar across the different types of sensitivity tests we conducted (unconstrained initial conditions, or a constrained focus on the ‘forward’ or ‘backward’ shift), and whether we considered final abundances of individual groups (seaweed, sea urchins and lobsters) or of the community as a whole. These analyses identified lobster fishing mortality, lobster and urchin recruitment rates, size-structured predation of lobsters on urchins, as well as initial urchin densities as the key drivers of model dynamics.

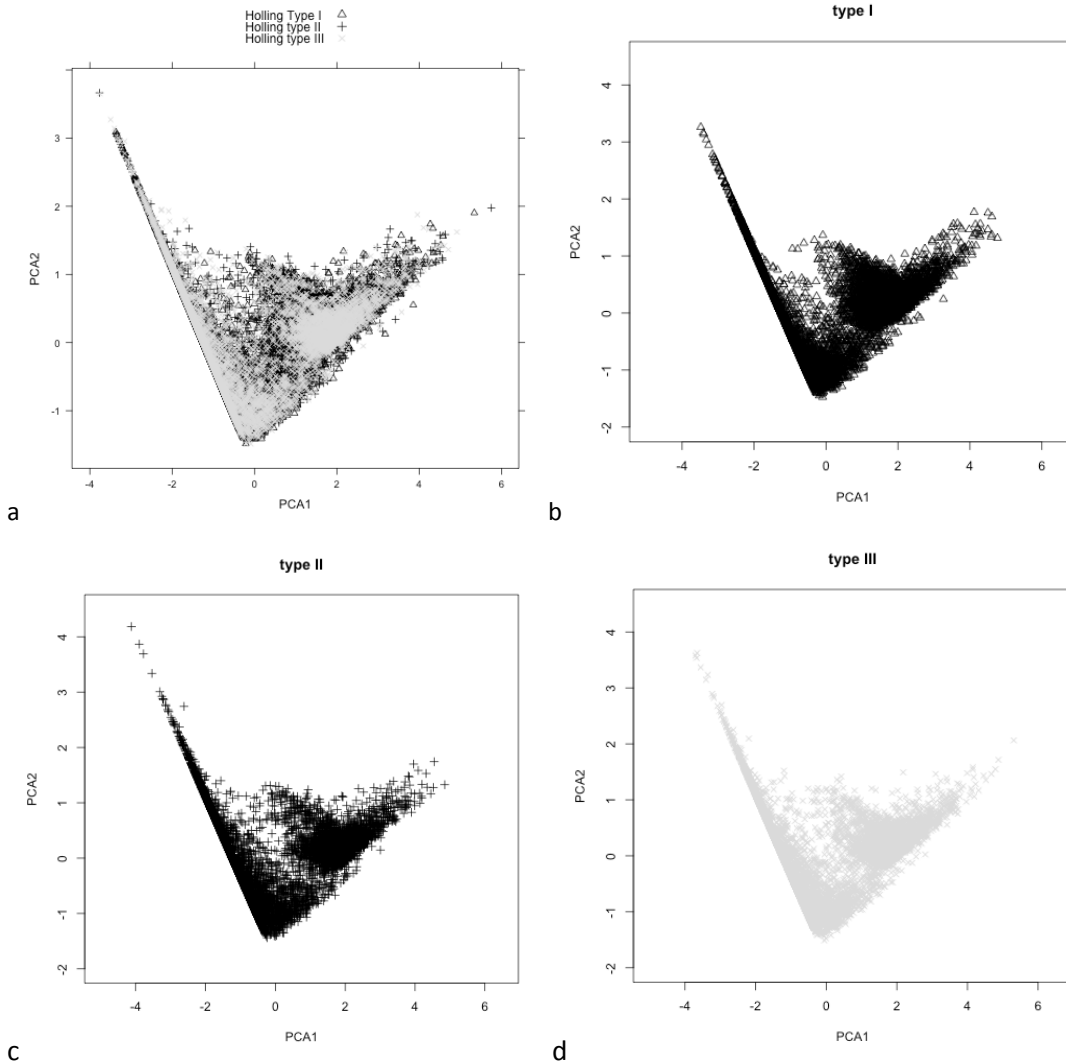
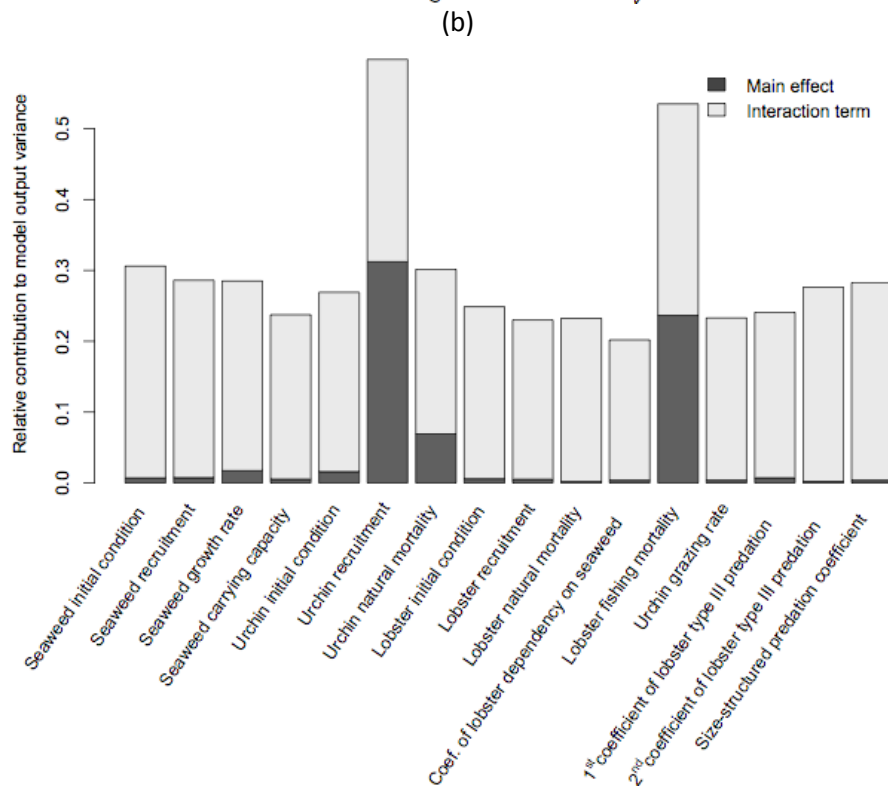
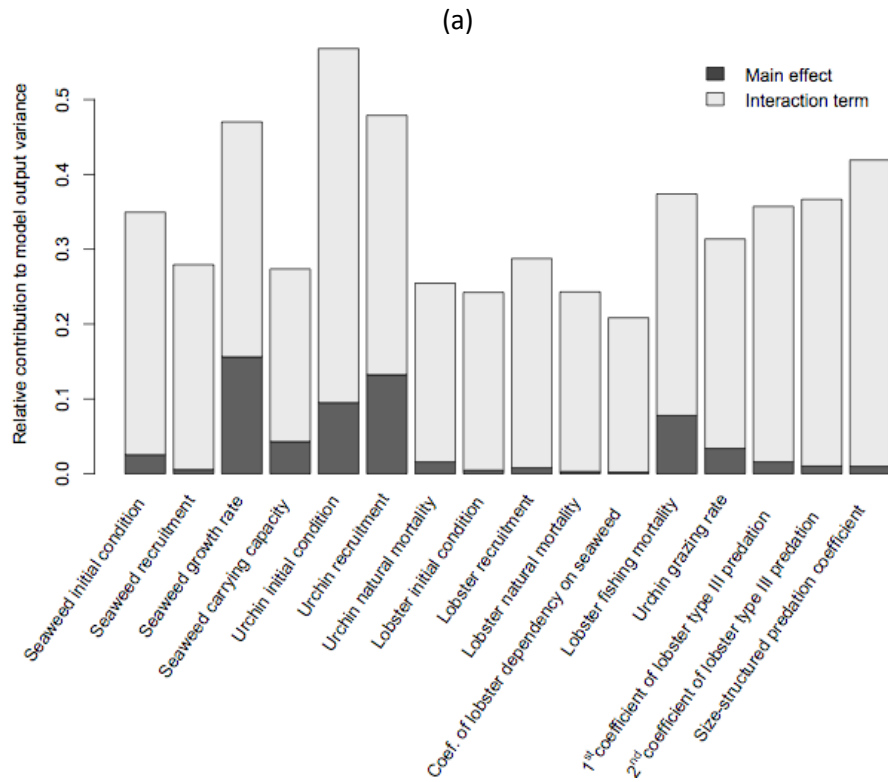


Figure 34. Effect of different formulation of lobster predation rate on the final community composition captured as scores on the first two axes of the PCA, which capture 87.4% of the total variance. Scores are plotted for (a) all functional responses together, then respectively for (b) Holling Type I, (c) II and (d) III functional responses respectively. It is clear that simulation outcomes as described by community structure across seaweeds, *C. rodgersii* and rock lobsters are little affected by the nature of the functional response of lobsters to the sea urchins.

At a more detailed level, the independent sensitivity tests were useful to identify differences in the key variables influencing the different individual components of community structure, and in comparing the influence of each input variable on particular groups (seaweed, sea urchins or lobsters) with the influence on overall community structure (described by the first principal component from the PCA). While input parameters that most influence model dynamics are broadly similar for each component of the community, the detailed differences between the four different tests (Fig. 35) are informative. They show that:



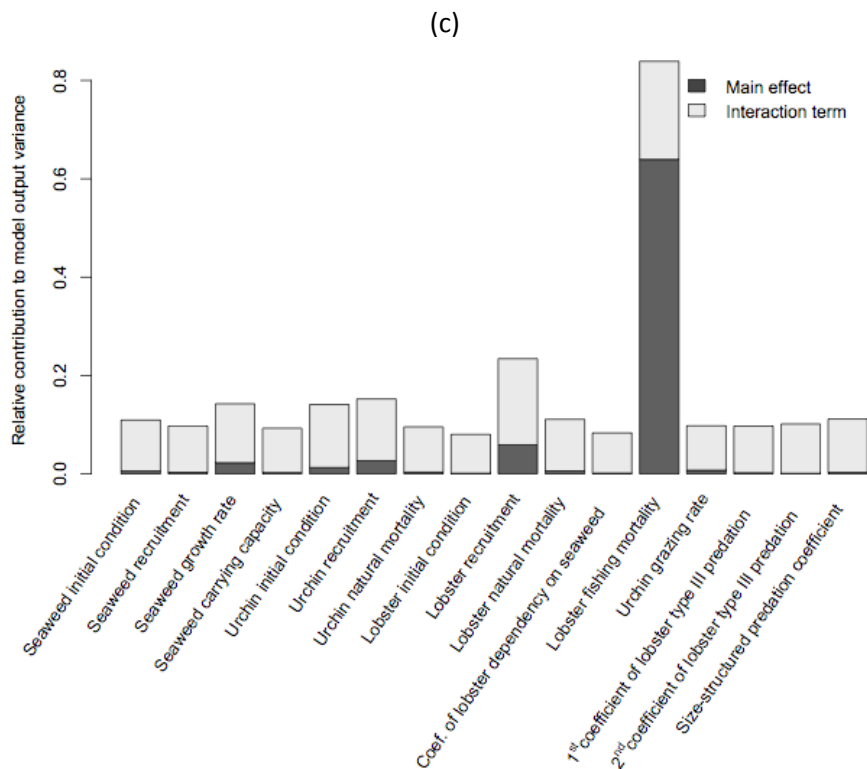


Figure 35. Sensitivity analysis based on extended FAST indices quantifying the contribution of all model input parameter values to model output variance. Results are for outputs of final biomass densities of (a) seaweeds, (b) sea urchins and (c) rock lobster at the end of 50-year simulations with unconstrained initial conditions.

- (i) Seaweed biomass density is the only component for which dynamics is driven primarily by the initial state of the sea urchin population rather than lobster fishing mortality. This occurs as a result of the hysteresis in model dynamics, with initial sea urchin biomass density sitting either higher or lower than the threshold above which the seaweed bed gets depleted by grazing (cf. Fig. 39a). Note that seaweed growth rate also exerts relatively high influence on seaweed dynamics, suggesting that rocky reefs where seaweed productivity is low (due to shading, unsuitable substratum or nutrient-poor conditions) will be more prone to sea urchin barren formation for the same level of grazing pressure from sea urchins. Declining nitrate levels as a result of a changing ocean climate increasingly influenced by nitrate-poor waters of the East Australian Current (Johnson et al. 2011) may play a key role in this context.
- (ii) Sea urchin dynamics is essentially affected by input factors related to lobster predation pressure (i.e. the recruitment rate of lobsters, fishing mortality and the coefficients of the Type III functional response), as well as recruitment rates of the sea urchins themselves. This implies that, at the scale of an individual rocky reef, exposure to large-scale oceanographic features transporting urchin larvae (Banks et al. 2007), the suitability of the reef substratum (e.g. appropriate settlement cues, complexity of crevice structure; Andrew 1993) for metamorphosis and settlement of urchin larvae, or exposure to predation can locally limit the potential for the *C. rodgersii* population to develop. Of all of these variables, lobster fishing mortality is clearly the single variable most amenable to ready management intervention.
- (iii) Rock lobster biomass is influenced largely by fishing and the mean recruitment rate to the population in the model.
- (iv) Not surprisingly, sensitivity indices focused on effects on the variance in overall community structure (as described by the first principal component; Fig. 33c) identify all the parameters important to each of the three components of community structure when they are examined separately (Figs. 35a-c).

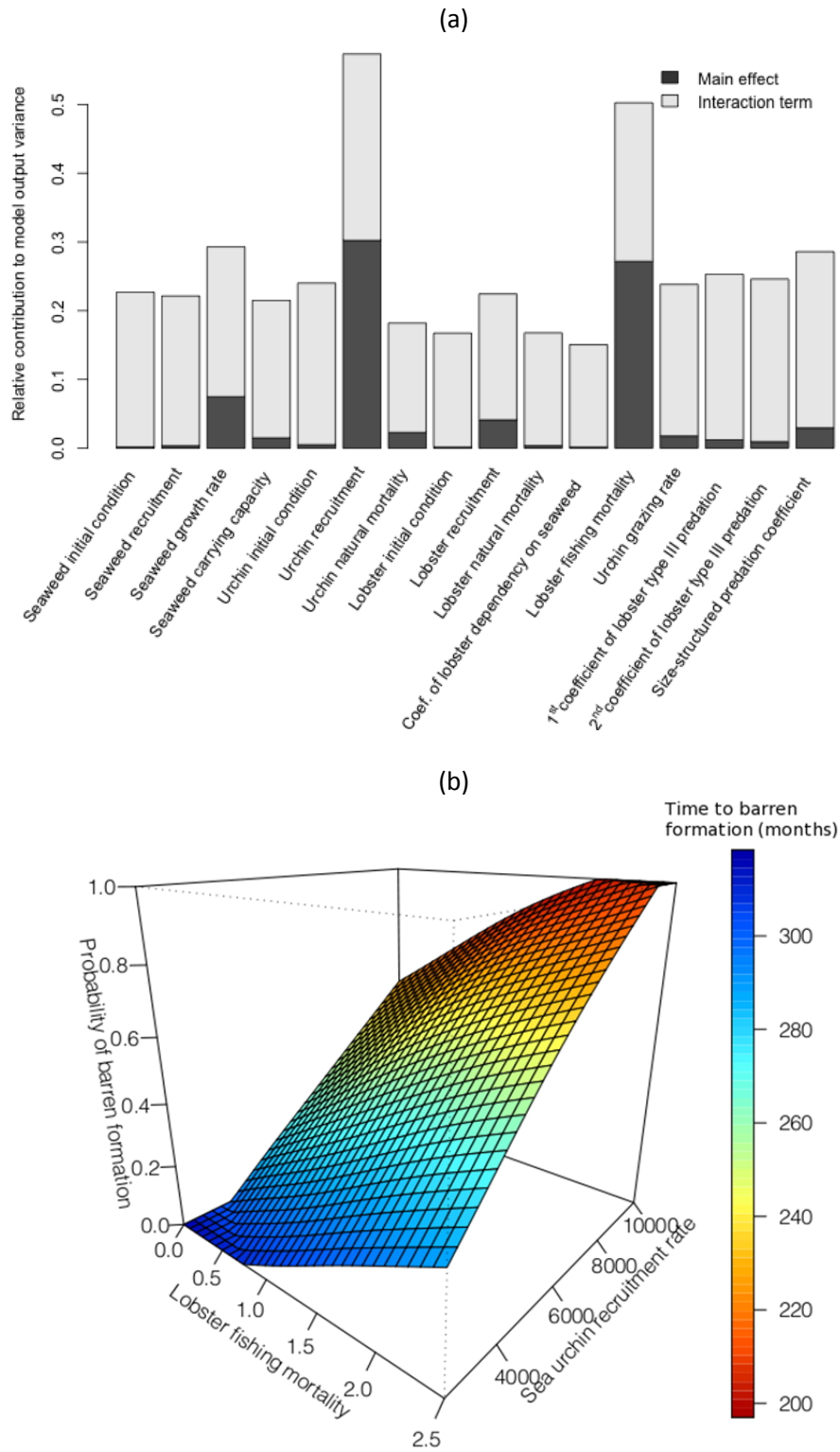


Figure 36. Sensitivity of the ‘forward’ shift (from high seaweed biomass to sea urchin barrens habitat) to model input parameters (i.e. analysis based on simulations in which ‘forward’ shift occurred). Initial conditions correspond to the seaweed bed state with seaweed cover at >50% of carrying capacity, low initial sea urchin density (< 40000 g. 200 m⁻²) and random rock lobster biomass density. (a) Extended FAST indices quantifying the contribution of input parameters to model output variance in overall community structure (described as the first PC from PCA on mean-centred normalised biomass density of all groups) for 50-year simulations. (b) 3D plot representing both the probability of (z axis) and the time for (colour scaling) barrens establishment (in months) as a function of the two parameters most influential in affecting the likelihood of the transition to barrens, *viz.* sea urchin recruitment rate (in g. 200 m⁻². year⁻¹) and lobster fishing mortality (in year⁻¹).

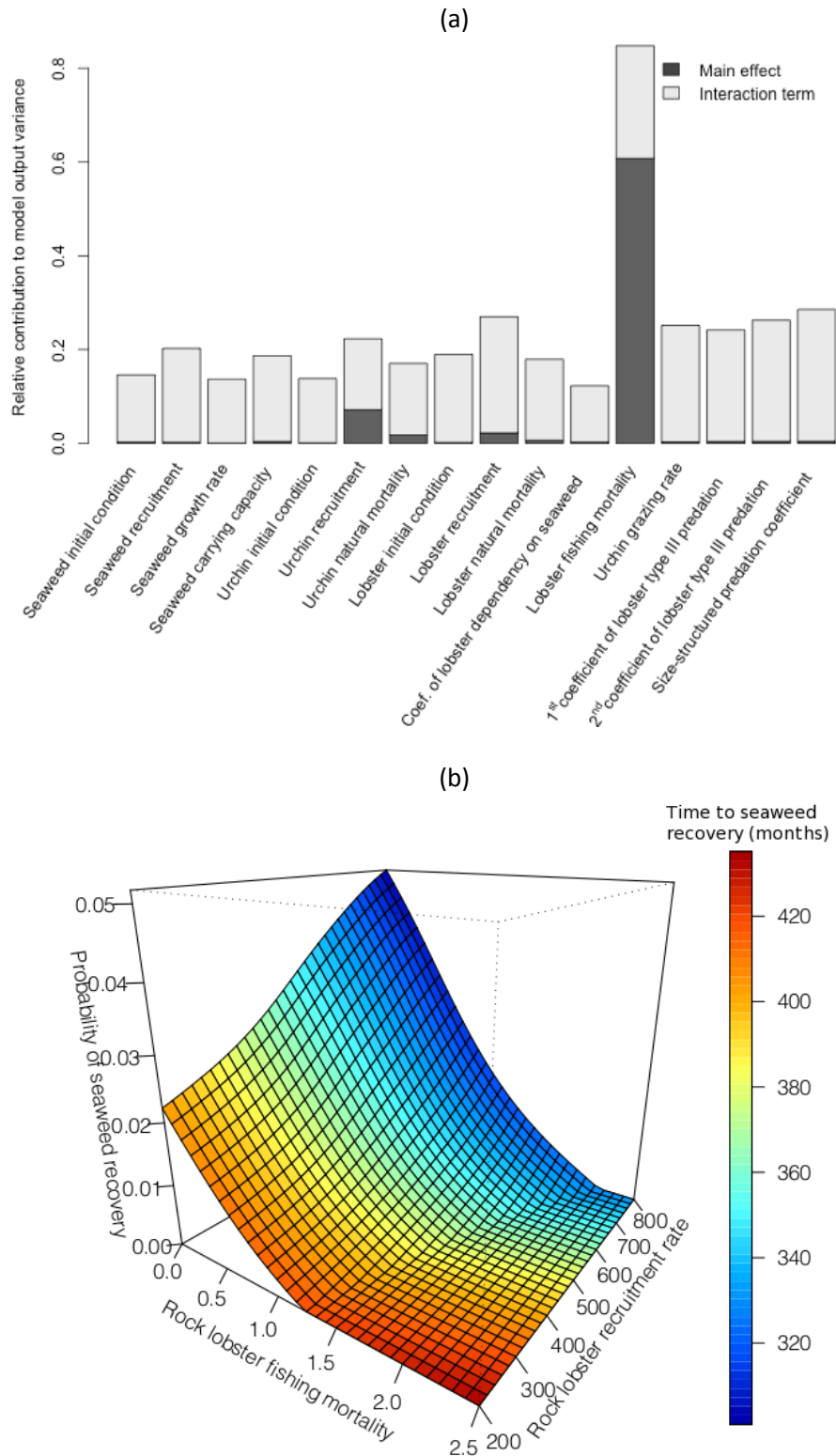


Figure 37. Sensitivity of the ‘backward’ shift (from sea urchin barrens to recovery of dense seaweeds) to model input parameters (i.e. analysis based on simulations in which the ‘backward’ shift occurred). Initial conditions correspond to sea urchin barrens habitat, with seaweed cover <10% of carrying capacity, initial urchin density > 70000 g. 200 m⁻² and random rock lobster biomass density. (a) Extended FAST indices quantifying the contribution of input parameters to model output variance in overall community structure (described as the first PC from PCA on mean-centred normalised biomass density of all groups) for 50-year simulations. (b) 3D plot representing both the probability of (z axis) and the time to (colour scaling) seaweed bed recovery from sea urchin barrens (in months) as a function of the two parameters most influential in affecting the likelihood of seaweed recovery, viz. lobster recruitment rate (g. 200 m⁻². year⁻¹) and lobster fishing mortality (year⁻¹).

In considering only the subset of simulations that either shifted ‘forward’ (Fig. 36b) or ‘backward’ (Fig. 37b), we investigated the effects of the most influential parameters (i.e. lobster fishing mortality and the mean recruitment rates of sea urchins (Fig. 36a) and rock lobsters (Fig. 37b) on the time to transition from one state to the other. Formation of extensive sea urchin barrens becomes more likely and the time to destructive grazing of seaweed beds becomes shorter in an essentially linear manner with increasing lobster fishing mortality and increasing sea urchin recruitment (Fig. 36b). Conversely, as fishing mortality on lobsters decreases and their recruitment rate increases, the time to recovery of a dense seaweed cover from the barren state decreases, also in an approximately linear fashion (Fig. 37b). Note, however, that the likelihood of seaweed bed recovery from extensive sea urchin ‘barrens’ is small (less than 10%), even as fishing mortality of lobsters is reduced and their recruitment increased.

Conducting independent sensitivity tests in this way, i.e. dissecting model sensitivity in the ‘forward’ and ‘backward’ shifts separately, proved useful. This approach overcomes concerns about sensitivity analyses of models with multiple equilibria (van Nes & Scheffer 2003). It identified that shifts from high seaweed cover to sea urchin barren habitat, and the reverse shift realising recovery of seaweeds, are both driven predominantly by lobster fishing mortality, lobster and sea urchin recruitment rates, and lobster predation rates. Note that, surprisingly, the reverse shift is not so sensitive to the coefficient that scales lobster recruitment to the level of canopy cover. A strong dependency of lobster recruitment on the seaweed canopy reinforces the positive feedback between seaweeds, urchins and lobsters once the macroalgal canopy is lost and contributes to the high resilience of the urchin barren state (Marzloff et al. 2011). This result, along with the relatively poor likelihood of seaweed recovery from a fully established barren state (Fig. 37b), suggests that, in TRITON, the barren state is highly resilient irrespective of the strength of the dependency of lobster recruitment on the state of the seaweed cover. The high stability of the ‘deteriorated’ community state, i.e. of sea urchin barrens, is a common feature of the dynamics of ecosystems with alternative community states where one state is characterized by low productivity and diversity (e.g. deforestation of tropical dry forest; Lawrence et al. 2007).

Transition times in shifting from one state to the other are also important characteristics of the dynamics of systems with alternative states and hence, are a key element in exploring model sensitivity (Figs. 36, 37b). For models with hysteresis, simulation outcomes are essentially binary, which can prove problematic when conducting sensitivity analyses, in particular in undertaking partial sensitivity tests to one input parameter at a time (van Nes and Scheffer 2003, 2004). In the case of TRITON, the simulated community ultimately moves either towards the barren or the seaweed-dominated state (Fig. 39), and so quantifying the influence of parameters on the time for the model to shift ‘forward’ from seaweed bed to sea urchin barrens, or ‘backward’ to effect seaweed recovery, provided valuable insight into the detailed dynamics. Notably, the ‘forward’ shift (22.1 years +/- 0.19 standard error) occurs on average about ten years more quickly than the ‘backward’ shift (31.8 +/- 0.92 standard error). These mean transition times, which provide another illustration of hysteresis in model dynamics in the sense that ‘forward’ and ‘backward’ shifts are independent dynamics with different transition times, have strong implications for management of rocky reef communities in Tasmania. Preventing the further spread of extensive sea urchin barrens appears as the most cost-efficient management option, and is more likely to succeed than rehabilitation of extensive barrens. If solely relying on predation by rock lobsters to deplete sea urchin populations, the time frame for restoration of established barrens habitat to the seaweed dominated state from *C. rodgersii* barrens is of the order of three decades, and even then the predicted probability of seaweed recovery is low, even under the most drastic measures for the lobster fishery. We note that the predicted timeframe for seaweed recovery exceeds by far the time span of current management plans for the Tasmanian lobster fishery.

A final important point to emerge for all sensitivity analyses (Figs. 33, 35, 36 & 37) is that interaction terms contribute consistently more – and in most cases very much more – to the variance of model outputs than first order ‘main’ effects due to single input parameters acting directly on their own (interactions terms refer to synergistic ‘higher degree’ effects of the parameter of interest with other parameters in all possible combinations; Saltelli et al. 1999). This result highlights the importance of ecosystem modelling and of including all key interactions among species or functional groups. The dominant influence on model

behaviour of interactions among input parameters is common in models of complex dynamics (Saltelli et al. 1999, 2009). In the context of the dynamics of Tasmanian rocky reef, strong interactions between input parameters highlight the value of ecological models to inform natural resource managers about non-trivial effects of management interventions and environmental change on ecosystem state. While qualitative modelling can track the broad influence of indirect effects and the contribution of high level feedback to community dynamics (Marzloff et al. 2011), simulation-based sensitivity analysis of TRITON (as a quantitative model) captures non-trivial interactions between modelled processes, and can provide valuable insights about indirect responses of the reef community to perturbations or management intervention, that the qualitative approach cannot provide.

Calibration and pattern-oriented validation of TRITON

To calibrate model behaviour to empirical observations, attention was paid to parameters influencing the 'forward' shift (i.e. lobster fishing mortality, sea urchin recruitment, seaweed growth rate, allometry of lobster size-structured predation on sea urchin; *cf.* Fig. 36). Lobster size-structured predation was based on extensive field observations of interactions between a wide range of sizes of lobsters and sea urchins indicating that only large lobsters (>140 mm carapace length) can prey on emergent sea urchins (Ling et al. 2009a). There are no observations to assess the possibility of smaller lobsters preying smaller non-emergent *C. rodgersii* individuals that, until they grow larger, remain confined to the matrix of the reef. However, we believe this is highly unlikely given that lobsters must grasp and roll over urchins to access the soft peristomial region on their oral surface to be able to penetrate, kill and eat them, and that urchins within the confines of a crevice use their spines to wedge their body and prevent this manoeuvre from occurring. It is also worth noting that spines on smaller urchins are disproportionately long relative to emergent animals. Our inability to quantify predation of smaller urchins within the reef matrix is likely to be more than offset by our conservative assumption that any lobster >140 mm CL can predate any emergent lobster it encounters. The effects of other influential parameters (i.e. seaweed growth rate and sea urchin recruitment rate), on the risk of barren formation is non-linear (Fig. 38a), with the likelihood of barrens forming increasing dramatically, and becoming almost certain, when sea urchin recruitment rates exceed a threshold of about 7000 g. 200m⁻². year⁻¹, and based on a range of lobster fishing mortality corresponding to historical levels in eastern Tasmania.

Sea urchin recruitment rate (to the emergent size class) emerged as an important parameter in TRITON, but there are no direct empirical estimates, so the model was used to calibrate an upper range of urchin recruitment. The proportion of simulations shifting to sea urchin barrens increases non-linearly from about 15% up to 80% as the maximum value of the range of sea urchin mean recruitment rate is increased from 2,000 to 10,000 g. 200m⁻². year⁻¹ (Fig. 38b). The two grey dashed horizontal lines in Fig. 8b delimit the observed range in extent of sea urchin barrens habitat (~50% of total reef area) in NSW (Andrew & O'Neill 2000) and northeastern Tasmania (Johnson et al. 2005, 2011) where *C. rodgersii* populations are long established. Consequently, in calibrating the model, maximum sea urchin recruitment rate was set to 6000 g. 200 m⁻². year⁻¹ to ensure that the probability of the TRITON model shifting to barrens is in line with large-scale observations of the extent of sea urchin barrens in reef areas where *C. rodgersii* has been long established.

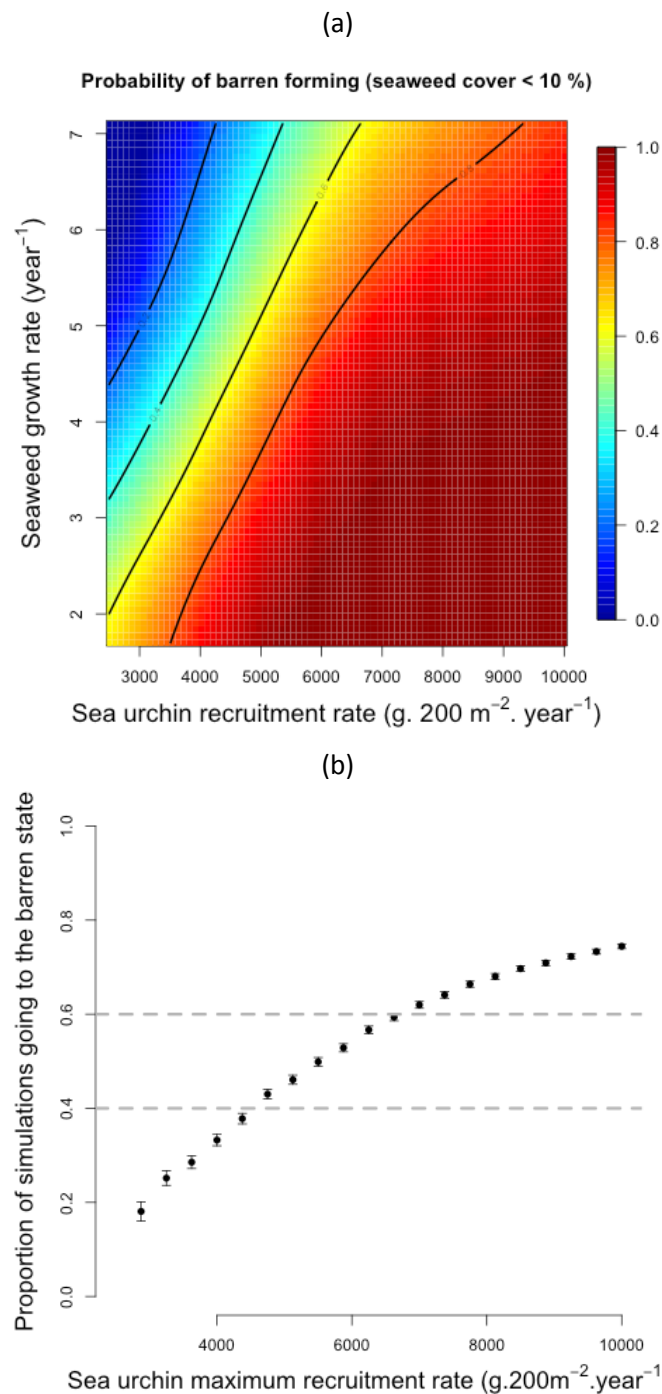


Figure 38. Results from 50-year-long Monte-Carlo simulations used to calibrate ranges in sea urchin recruitment from the model's propensity to shift to sea urchin barrens under historical rock lobster fishing conditions. (a) Probability of barren formation as a function of the two most influential input parameters, sea urchin recruitment rate and seaweed growth rate; (b) Probability of the shift from seaweed bed to sea urchin barren as a function of sea urchin maximum recruitment rate. The dashed horizontal lines mark the observed range of sea urchin barren cover across rocky reefs in New South Wales (Andrew and O'Neill, 2000) and Tasmania (Johnson et al. 2005, 2011; this study) where *C. rodgersii* is long established and where populations of reef predators have been depleted by fishing.

In the context of model validation, mean community state, which is commonly used as a benchmark to calibrate and validate complex ecosystem models (e.g. Marzloff et al. 2009), is neither a reliable or meaningful criterion to assess the realism of a model for a system characterised by alternative community states. Further, given that the set of difference equations comprising the TRITON model are not analytically tractable (as has been possible with other similar but simpler models; see Fung et al. 2011), calibration and

validation of TRITON relies on its capacity to reproduce several large-scale features of the dynamics of rocky reef communities supporting established *C. rodgersii* populations. The first and most obvious is the capacity to shift between the persistent states of the seaweed- and urchin-dominated configurations. Second, regions of inshore reef in which *C. rodgersii* has been long established and where key urchin predators are ostensibly at low abundances support about 50% coverage of extensive barrens habitat (Andrew & O'Neill 2000; Johnson et al. 2005, 2011). Third, intensive surveys of seaweed cover and barren habitats along the east and southeastern coasts of Tasmania, including quantifying densities of sea urchins and other reef species, provide a benchmark of the range and frequency of community states observed on the east coast of Tasmania (Johnson et al. 2005, 2011; this study) which we would expect TRITON to reproduce. The ability of TRITON to reproduce these large-scale patterns, showing the two main community states of high seaweed bed with low sea urchin abundance or sea urchin barren habitat with virtually no macroalgal cover (Fig. 39), provides a useful validation of the model. The primary difference in the observed (Fig. 39b) and predicted (Fig. 39a) states is the 'hole' of 'low frequency' of observations of the system at very low urchin abundance and seaweed cover at $\sim 10^5$ g.200 m⁻² (bottom left, Fig. 39b). This part of the surface represents the trajectory of recovery of seaweed cover on extensive urchin barrens (see vectors, Fig. 39a), but this is yet to be observed at sites where extensive barrens have been monitored in eastern Tasmania.

The capacity of the model to demonstrate shifts (in either direction) between seaweed and sea urchin dominated reefs represents a validation of the observed dynamics. Further, when we compare patterns emerging from simulations using TRITON with patterns observed in large-scale surveys (Johnson et al. 2005, 2011; this study) of Tasmanian temperate reef communities (Fig. 39), both the modelled and observed reef communities identify two persistent and dominant states representing the seaweed bed state (with a high cover of seaweed and a low density of sea urchins) and the sea urchin 'barrens' state (with virtually no algal cover and a high density of sea urchins). This indicates broad agreement of the behaviour of the model with observations of the occurrence of the two states in the field. Note that the volume of output from the TRITON model enables a much more continuous picture of the range of community states encountered on Tasmanian reefs than can be obtained by direct diver-based measurements. Moreover, the model can provide insight on aspects of reef dynamics that have not been able to be documented from field observations, in particular the point at which recovery from extensive sea urchin barrens commences as urchin density falls (bottom left, Fig. 39a).

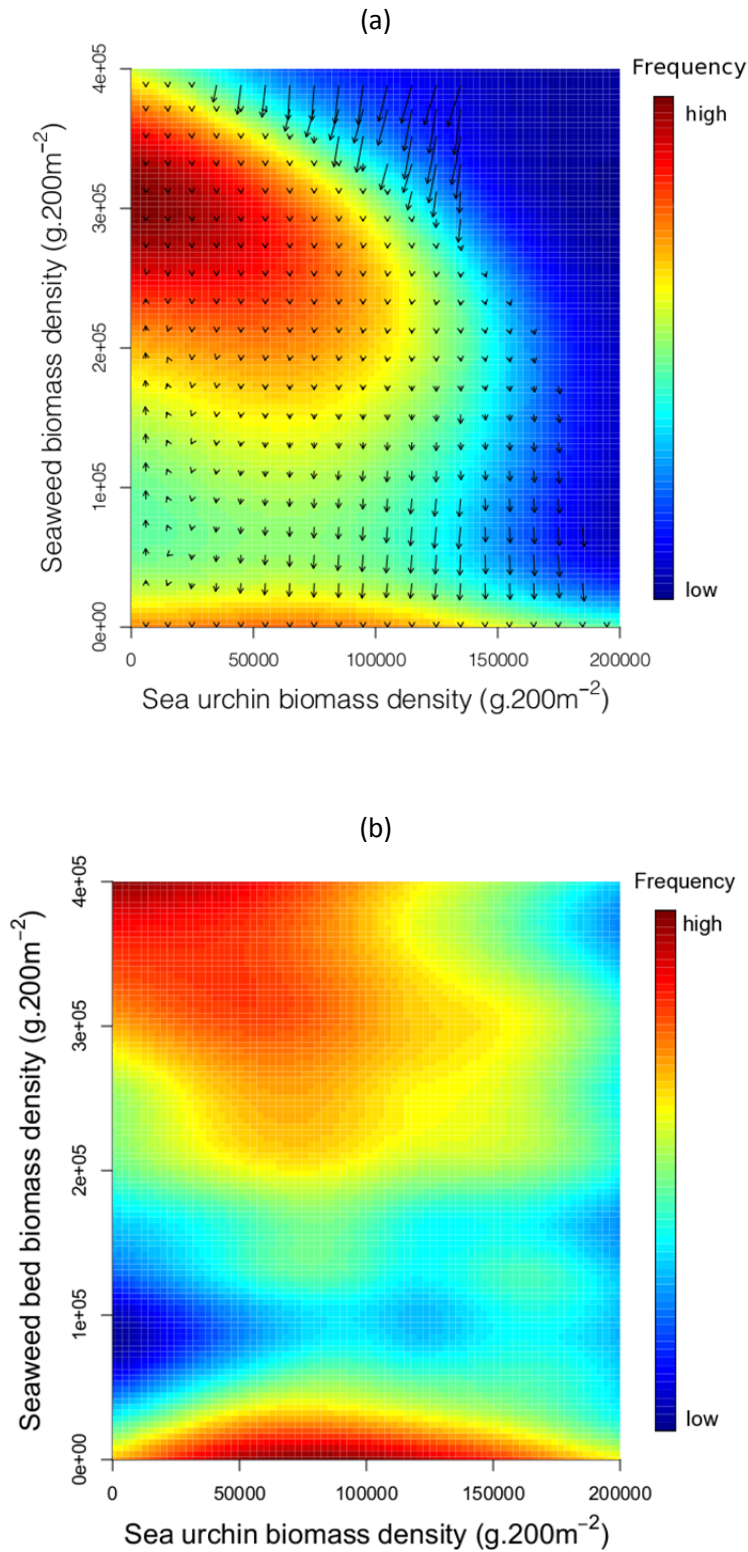


Figure 39. Frequency (logarithmic scale) of community states as a function of sea urchin versus seaweed bed biomass densities from (a) the 8000 Monte-Carlo simulations with TRITON and from (b) large-scale surveys on the east coast of Tasmania (Johnson et al. 2005, 2011; this study). Arrows in (a) represent the mean simulation trajectory in terms of fortnightly change in sea urchin and seaweed bed biomass densities.

Conclusion

Communities with the potential for multiple stable states and ecological hysteresis offer particular challenges and higher stakes for managers because one of the alternative states is usually poorly productive and less desirable (Johnson & Mann 1988; van de Koppel et al. 1997; Lawrence et al. 2007; Melbourne-Thomas et al. 2011; Strain & Johnson 2012). Thus it is often of critical importance to avoid transition to the less desirable state, in particular when management intervention to facilitate the return shift may be impractical. In this context, and particularly because it is not usually possible to identify tipping points from field observation (Hastings & Wysham 2010; Osman et al. 2010, but see Carpenter et al. 2011 for a unique 'whole-ecosystem' experiment), models of ecological communities with alternative states are essential to inform key thresholds in system dynamics and test the effects of alternative management strategies (Mumby et al. 2007; Fung et al. 2011; McClanahan et al. 2011; Melbourne Thomas et al. 2011a,b,c). However, validating this kind of model remains challenging, not the least reason for which is that transitions between states are rarely, if ever, observed with any precision. Our comprehensive simulation-based exploration of the TRITON model captures the potential for Tasmanian seaweed-sea urchin-lobster community dynamics to shift between two alternative states, dense seaweed bed or sea urchin barrens habitat. The series of Monte-Carlo simulations depicts the model's overall behaviour, and pattern-oriented-modelling, i.e. comparison of patterns emerging from simulations to large-scale patterns observed in the field, provided an efficient way to calibrate the broad dynamics of TRITON prior to its application. The extended FAST routine (Saltelli et al., 1999) provides a computationally efficient framework to identify parameters that most influence both overall model dynamics, and the separate 'forward' and 'backward' shifts between the alternative states. This enabled assessment of whether management intervention in this system is practicable, and to identify the nature of the intervention that is likely to have most effect in influencing community dynamics. Of the relatively small suite of parameters to which the model is most sensitive, fishing mortality of lobsters emerges as the single factor to which the model is particularly sensitive and on which human behaviour has a large and direct effect.

Our overall conclusion is that the behaviour of TRITON is well validated as a complex system simulating the dynamics among seaweeds, *C. rodgersii* and rock lobsters on the east coast of Tasmania. Given this, and that the model indicates that transitions between seaweed beds and urchin barrens is largely determined by lobster fishing mortality, lobster and sea urchin recruitment rates, and lobster predation rates, then the model is likely to be useful to examine management strategies in response to the threat of *C. rodgersii* in eastern Tasmania. This is addressed in the next section.

Application of the TRITON ecosystem model: Identifying thresholds in community dynamics and assessing management intervention to limit destructive grazing of sea urchins

We consider results from simulations with TRITON along three main avenues: (1) estimates of tipping points in reef community dynamics and identification of critical reference points for management; (2) comparison of the effectiveness of different management options to limit the effects of sea urchin destructive grazing of Tasmanian seaweed beds; and (3) performance of the lobster fishery under different management scenarios, comparing assessment approaches with and without consideration of the ecosystem effects of fishing.

Tipping points in reef dynamics and defining reference points for management

Figs. 40 and 41 respectively focus on the forward shift, from dense seaweed cover to extensive sea urchin barrens ($\geq 90\%$ of barren cover), and the backward shift, from extensive barrens habitat to recovered seaweed bed. Monitoring Monte-Carlo simulations of monthly seaweed cover and biomass densities of sea urchin and predatory lobsters (carapace length ≥ 140 mm) provides some insight on tipping points in community dynamics (Figs. 40b, 40d, 41b, 41 d). Additionally, we assess reference management points (biomass densities of large predatory lobsters and sea urchins) related to 5% probability of long-term barren formation (e.g. Fig. 40a) or 75% probability of long-term restoration of the seaweed bed (e.g., Fig. 41a) across Monte-Carlo simulations. Red sigmoid curves in Figs. 40 and 41 represent binomial logistic models fitted against the biomass densities of (a, b) sea urchins; and (c, d) large predatory lobsters (carapace length ≥ 140 mm). Green vertical lines represent estimates of tipping points in modelled community dynamics (Fig. 40b) or critical reference points for management (Figs. 40a, 40c). The 95% confidence intervals around these estimates are delimited by green dotted lines.

Threshold estimates reveal the presence of a hysteresis in model dynamics, i.e. different tipping points are associated with the forward (Fig. 40) and the backward (Fig. 41) shifts. Mean model behaviour suggests that extensive barrens form once sea urchin population density builds up beyond $\sim 55,000$ g. 200m^2 (Fig. 40b) while seaweed recovery from a state of extensive barrens requires virtually zero urchin biomass density (Fig. 41b). The binomial logistic GLM in Fig. 40b closely relates the decline in seaweed to sea urchin biomass density ($\sim 43\%$ of total variance explained), while TRITON's ability to return to a state of dense seaweed poorly relates to the biomass density of the different model groups (Figs. 41b, 41d). The GLM relating seaweed decline to predatory rock lobster biomass density (Fig. 40d) does not provide a good fit for two reasons: (1) seaweed bed cover only starts to decline when the density of predatory lobsters drops below 800 g. 200m^2 so the actual decline in seaweed is poorly described over the range of simulated large rock lobster densities; and (2) seaweed cover plateaus at $\sim 80\%$ when lobster predation pressure is high (predatory lobster density ≥ 800 g. 200m^2) because, while extensive barrens do not establish, low densities of sea urchins still impact cover of macroalgae through their grazing.

The probability of barrens formation is closely related to the final simulated densities of sea urchin and exceeds 5% when urchin density exceeds $\sim 16,000$ g. 200m^2 (Fig. 40a). Conversely, the recovery of the seaweed bed from extensive sea urchin barrens virtually requires no sea urchins present (Fig. 40a). This is because a low density of sea urchins and new individuals recruiting to the emergent size class (test diameter ≥ 70 mm) on barrens can maintain extensive barrens in TRITON. Large predatory lobsters (carapace length ≥ 140 mm) can maintain the risk of extensive sea urchin barrens forming below 5% when biomass density is higher than $700\text{--}900$ g. 200m^2 (Fig. 40c). However, the critical biomass density of large lobsters required to achieve a 75% likelihood of seaweed bed recovery is much higher at $\sim 10,000$ g. 200m^2 (Fig. 41c; based on projections outside of the range of model simulated densities using the fitted GLM). Note that the probability of seaweed recovery increases unevenly with an increase in biomass density of predatory lobsters (Fig. 41c). This occurs because of the fickleness of seaweed recovery from extensive sea urchin barrens, and in only 14% of the simulations did large rock lobster population reach a final biomass density higher than $3,000$ g. 200m^2 (note the rapid increase in standard errors because of very low sample size).

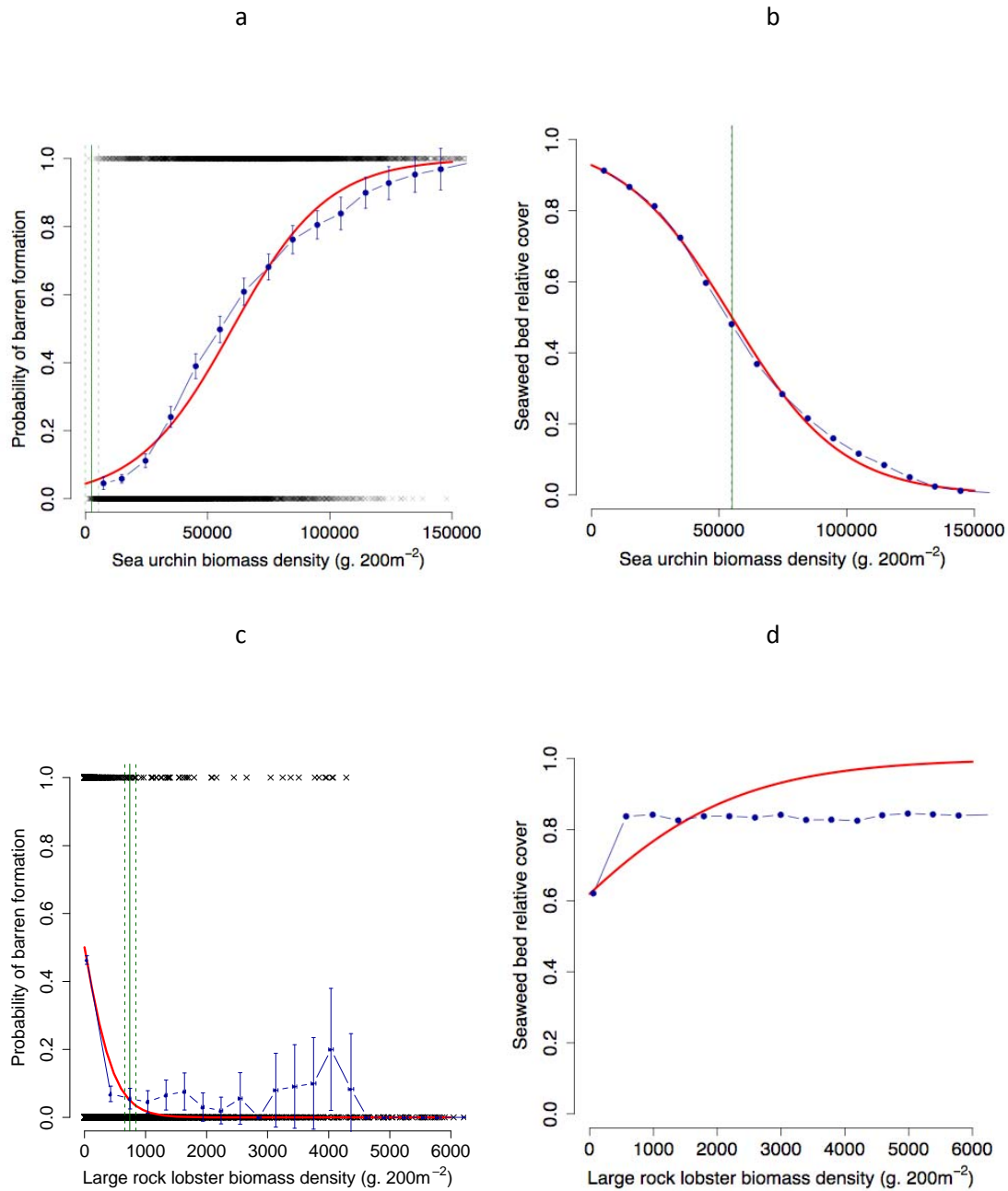


Figure 40. Probability of extensive sea urchin barrens forming (a, c) and proportional seaweed bed cover (b, d) through 7500 Monte-Carlo simulations initialised with high seaweed cover and corresponding to current rock lobster fishery practice (i.e. minimum legal size). Black crosses (a, c) show the final state for each simulation. The blue line with dots and error bars (standard error) corresponds to all data points binned into 15 even intervals of biomass density (between 0 and the maximum value). Red sigmoid curves represent binomial logistic models fitted against the biomass densities of the different species modelled, i.e. (a, b) sea urchins; and (c, d) large predatory lobsters (carapace length ≥ 140 mm). Both, reference management points (a, c), and thresholds or tipping points beyond which the TRITON model shift from the seaweed bed state to extensive sea urchin barren state (b) are marked by green solid lines with 95% confidence intervals given as dashed lines.

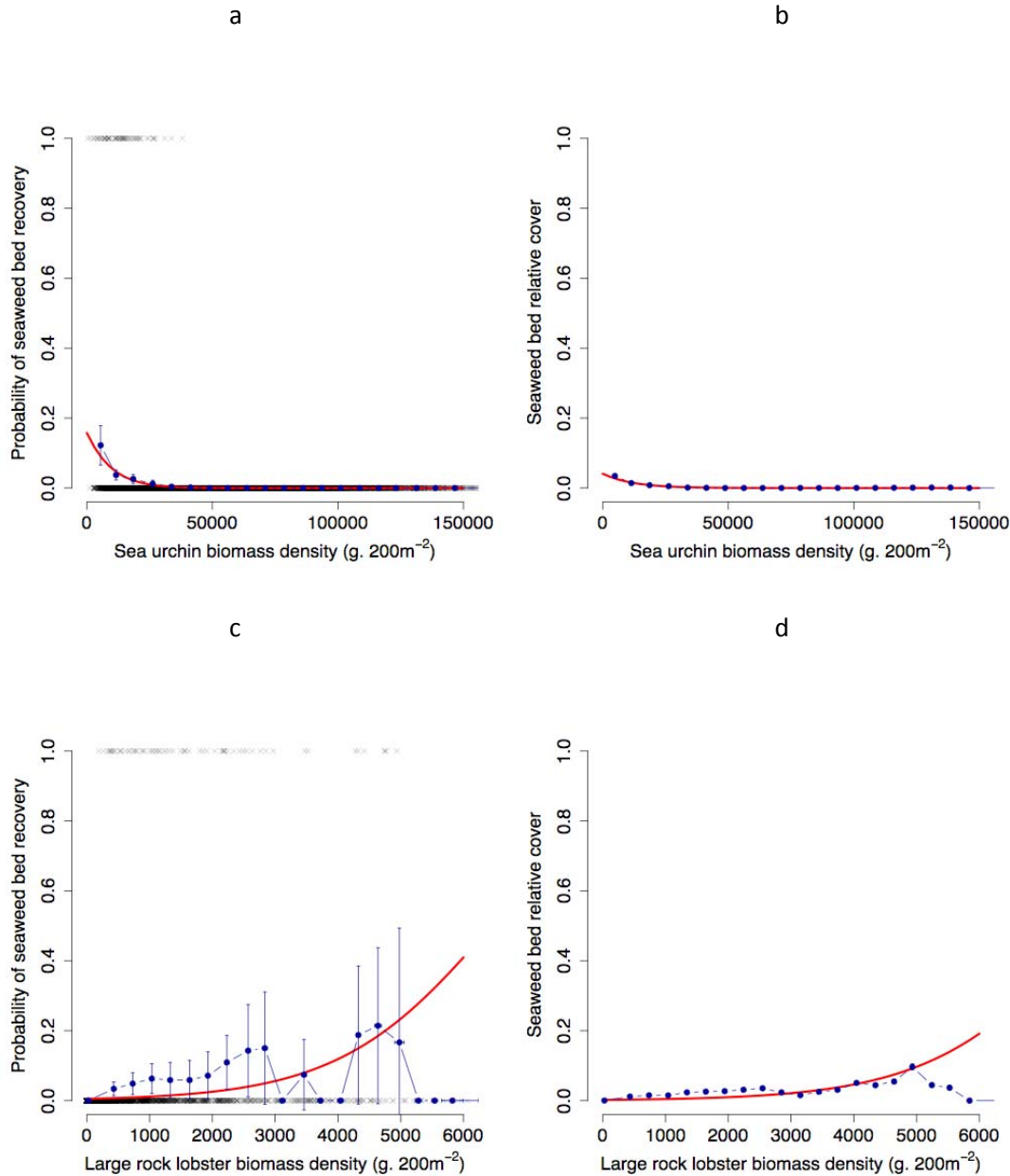


Figure 41. Probability of seaweed bed recovery (a, c) and proportional seaweed bed cover (b, d) through 7500 Monte-Carlo simulations initialised as sea urchin barrens and corresponding to current rock lobster fishery practice (i.e. minimum legal size). Black crosses (a, c) show the final state for each simulation. The blue line with dots and standard error bars corresponds to data binned into 20 even intervals of biomass density (between 0 and the maximum value). Red sigmoid curves represent binomial logistic models fitted against the biomass densities of the different species modelled: (a, b) sea urchins; and (c, d) large predatory lobster individuals (carapace length ≥ 140 mm). Note that, both, target reference points (to achieve a 73% likelihood of seaweed recovery), and the tipping points beyond which model community shift from extensive sea urchin barrens back to dense seaweed habitat, fall outside of the plot areas.

Management of marine ecosystems and the scientific underpinning of management is becoming increasingly sophisticated as it increasingly moves towards diminishing the risk of phase shifts to some less desirable alternative community state (Mumby *et al.* 2007; Suding & Hobbs 2009; Briske *et al.* 2010; Osman *et al.* 2010; Fung *et al.* 2011; McClanahan *et al.* 2011; Melbourne-Thomas *et al.* 2011). System-specific ecosystem models provide unique tools to explore these thresholds in community dynamics (Scheffer & Carpenter 2003; de Young *et al.* 2008). Among other marine examples, several applications have successfully described thresholds in coral reef dynamics (Mumby *et al.* 2007; Fung *et al.* 2011; McClanahan *et al.* 2011). Here, results of the TRITON model informs tipping points in community dynamics (from high seaweed cover to sea urchin barrens [Fig. 40], and to realise seaweed recovery on extensive barrens habitat [Fig. 41]) and helps to estimate critical reference points for management. The differences in threshold biomass densities, i.e. tipping points associated with a 50% seaweed cover, of sea urchins and large rock lobsters (≥ 140 mm CL) between the forward shift (from seaweed bed to sea urchin barrens habitat; Figs. 40b and 40d) and the backward shift (recovery of seaweed cover; Figs. 41b and 41d) strongly reflects the presence of a hysteresis in community dynamics, as suggested by field observations (e.g. Ling *et al.* 2009a).

While the initial stage of sea urchin destructive grazing of seaweed beds through formation of small 'incipient' barrens patches in otherwise intact seaweed beds has been thoroughly studied (Flukes *et al.* 2012), mean TRITON behaviour provides new insight on the tipping point beyond which extensive (i.e. 10^2 - 10^5 m²) barrens form. Across all simulations, the shift to extensive barrens is likely when sea urchin density builds beyond 55,000 g. 200 m⁻² (i.e. ~ 0.8 individuals m⁻²), while surveys of 'incipient' barrens patches in eastern Tasmania reveal a remarkably constant density of ~ 1.6 m⁻² (Flukes *et al.* 2012), and extensive barrens support urchins at ~ 1.9 - 2.3 m⁻² (Johnson *et al.* 2005, 2011; this study).

Because seaweed recovery from extensive barrens has not been observed empirically, our simulations provide unique information about the 'backward' shift. The extensive barren state is highly stable through simulations with TRITON and seaweed recovery can only be effective when sea urchin population gets depleted to close to zero. Thus, seaweed recovery is very fickle in TRITON as relatively few sea urchins recruiting to barren grounds can maintain the barren state (Figs. 41a,b) even in the presence of high densities of large lobster ($\geq 3,000$ g. 200 m⁻²; Figs. 41c,d)

Our estimates of management reference points, associated either with a 5% risk of extensive barren formation or 75% chance of seaweed recovery, are more conservative than the actual tipping points in the dynamics (e.g. Fig. 40b), where small changes in standing biomass densities can induce large shifts in community structure (van Nes & Scheffer 2004). Importantly, model dynamics indicate that minimising the risk of extensive sea urchin barrens establishing is achievable under sound management (Fig. 40c; critical density of large rock lobster of 700-900 g. 200 m⁻²). However, restoration of seaweed beds once sea urchin barrens have formed constitutes a major challenge (Ling *et al.* 2009a) that requires depletion of the sea urchin population to very low levels and with very high densities of predatory lobsters ($\sim 10,000$ g. 200 m⁻²; Fig. 41). Additionally, because small lobsters occur in low numbers on extensive barrens, despite that large lobsters can live on extensive barrens, rebuilding critical biomass densities of lobsters is likely to be more challenging on extensive sea urchin barrens than in dense seaweed beds (Johnson *et al.* 2005; Johnson *et al.* 2011; Figs. 40,41), and this challenge will escalate with the spatial extent of the barrens.

On a more technical level, logistic binomial models provide a convenient and objective approach to both identify tipping points and define limits or target reference points (e.g. critical densities predatory lobster) depending on the level of risk averseness that management wishes to adopt. However, changing these risk levels within reasonable bounds is unlikely to have any effect on the qualitative results and associated conclusions presented here. Finally, the binomial models relate the probability of community shifts to the biomass density of the different model groups, and hence goodness-of-fit criteria (% of variance explained) can identify groups of interest for ecosystem monitoring as most closely associated with changes in community state.

Assessing the effectiveness of alternative management strategies to minimise barrens formation

Here we focus on the effects of alternative management strategies to influence the likelihood of shifting from either high seaweed cover to sea urchin barrens, or backward to realise recovery of seaweed cover from sea urchin barrens. In addition to recruitment rates of lobsters being important in the overall dynamic, lobster fishing and direct sea urchin removal (by culling or harvesting) emerge as the main drivers of these shifts (Figs. 42a, 43a), as we observed in our comprehensive sensitivity analysis of the model (Marzloff *et al.* 2013). Conversely, the initial state of the lobster population (where high initial densities of lobster can represent translocations of lobsters from deeper waters) and the lobster maximum legal catch size exert only a marginal influence on the model's ability to shift.

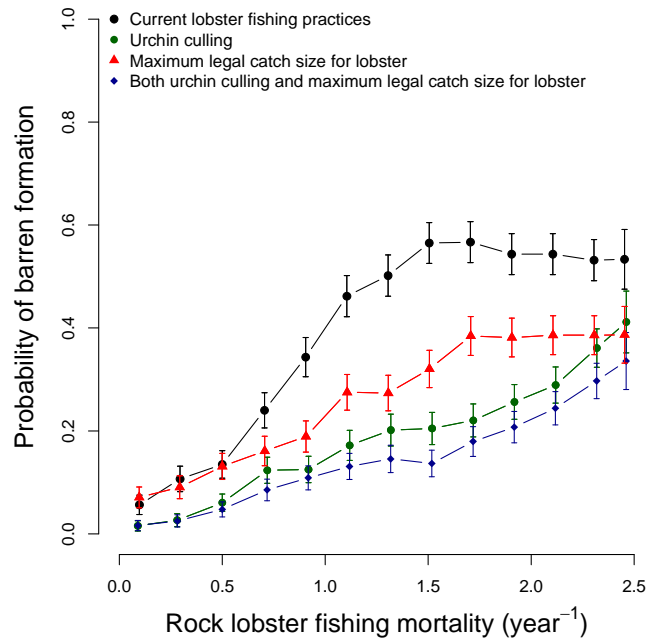
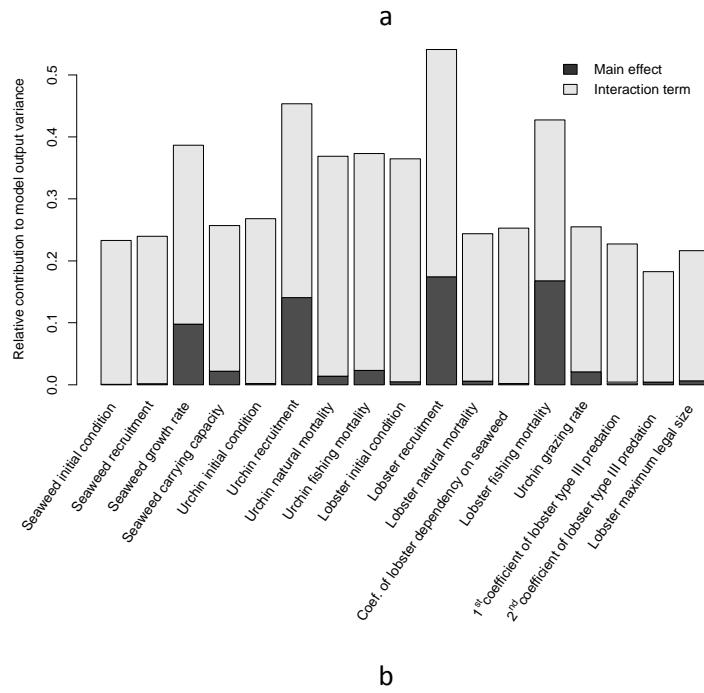
Under a range of lobster fishing mortality, we assessed different management interventions in terms of the probability of the model shifting forwards (Fig. 42b-e) or backwards (Fig. 43b). The risk of sea urchin barrens forming increases markedly with lobster fishing mortality, from ~15% with no fishing to ~ 50-60% under intense harvesting ($F_{RL} \geq 2 \text{ year}^{-1}$; Figs. 42 b-e). Considering current fishing practice (black line; $F_{RL} \sim 1-1.5 \text{ year}^{-1}$ and with only a minimal legal size but no maximum size limit), direct removal of sea urchins (culling for harvesting) considerably mitigates the ecological effects of sea urchin destructive grazing in terms of preventing barren formation (Fig. 42b). Indeed, even low intensity harvesting of urchins ($F_{CR} < 0.5 \text{ year}^{-1}$) reduces the overall risk of barren formation by 15-20% and brings it to zero at low lobster fishing mortality (Fig. 42c).

Conversely, implementing a maximum legal size significantly reduces the risk of seaweed destruction by 10-15% only when it is also associated with low-moderate fishing pressure ($0.5 < F_{RL} < 0.8 \text{ year}^{-1}$; Fig. 42d). Additionally, the absolute value of an upper size limit (between 135 – 165 mm CL), which would likely have considerable effect on the economics of the fishery, has relatively little effect on the extent to which the effects of sea urchin destructive grazing are mitigated (Fig. 42d). A maximum legal size $\geq 155 \text{ mm CL}$ provides only marginal benefits at moderate to high lobster fishing pressure. In combination with sea urchin culling, the implementation of a maximum legal size for lobster fishing still has only marginal effect in mitigating the effects of destructive grazing (Figs. 42b, 42e, 43b). Only when an upper legal size is imposed together with significantly reduced lobster harvesting, is risk of extensive barrens habitat formation reduced notably. Within a time frame of 50 years, the likelihood of restoring dense seaweed beds on extensive sea urchin barrens remains marginal under all management interventions we considered (Fig. 43b).

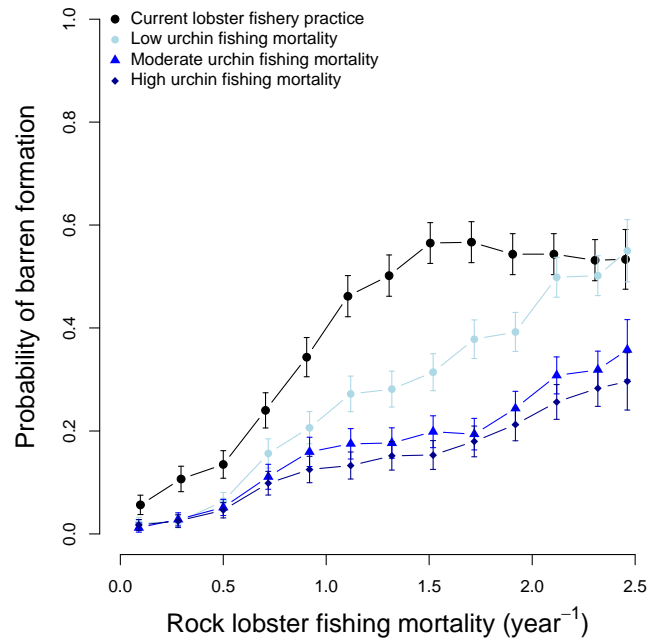
The caveat for all scenarios is that future uncertainty in lobster recruitment in eastern Tasmania (Pecl *et al.* 2009; Johnson *et al.* 2011) can significantly limit the effectiveness of any management interventions (Fig. 44). Thus, even when adopting the most efficient measures (i.e. combining sea urchin culling, a maximum legal size for lobster with reduced fishing of lobster) destructive grazing of seaweed beds by *C. rodgersii* may continue apace if there is failure of lobster recruitment. Fig. 44 illustrates how variability in lobster recruitment can alter the effects of management scenarios on the long-term probability of 'forward' (Figs. 44 a-d) and 'backward' (Figs. 44 e-h) shifts in reef dynamics. Note, that across all scenarios considered (Figs. 44a-h), lobster fishing has a greater influence on the probability of shifts than lobster recruitment rate. Again, these simulations indicate that chances of seaweed bed recovery from extensive barrens are marginal (~ 10% chance of seaweed recovery under an optimal scenario of low lobster fishing, moderate urchin culling and imposition of a maximum legal size for lobster; Figure 44h).

For a given level of lobster recruitment and fishing (e.g. $0.5 < F_{RL} < 1.5 \text{ year}^{-1}$), while protecting predatory lobsters with a maximum legal size (Fig. 44b) reduces the likelihood of barrens formation by ~10% relative to current practice (Fig. 44a), sea urchin culling appears as the single most effective intervention to both prevent barren formation (Fig. 44c) and restore seaweed beds (Fig. 44f). In particular under high lobster recruitment scenarios, moderate sea urchin culling ($0.5 < F_{CR} < 1.5 \text{ year}^{-1}$) reduces the chance of barrens forming to below ~20% even under current levels of lobster fishing ($F_{RL} \sim 1.2-1.4 \text{ year}^{-1}$). Moderate sea urchin culling constitutes a necessary condition for seaweed recovery from extensive barrens in TRITON

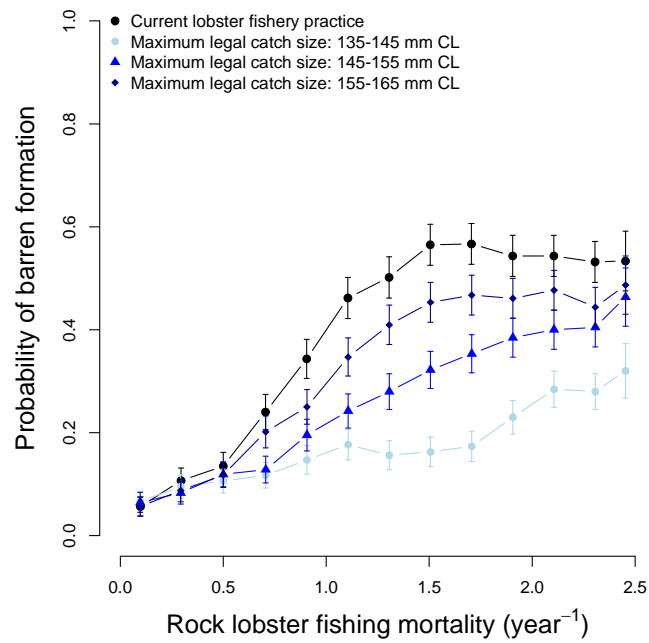
(~10% chance of recovery under high lobster recruitment; Figs. 44 g, h). Finally, protecting large predatory lobsters with a maximum legal size can slightly buffer the effects of low lobster recruitment scenarios but, relative to sea urchin culling, it has a marginal influence on chances of community shift in TRITON (Figs. 44d, 44h).



c



d



e

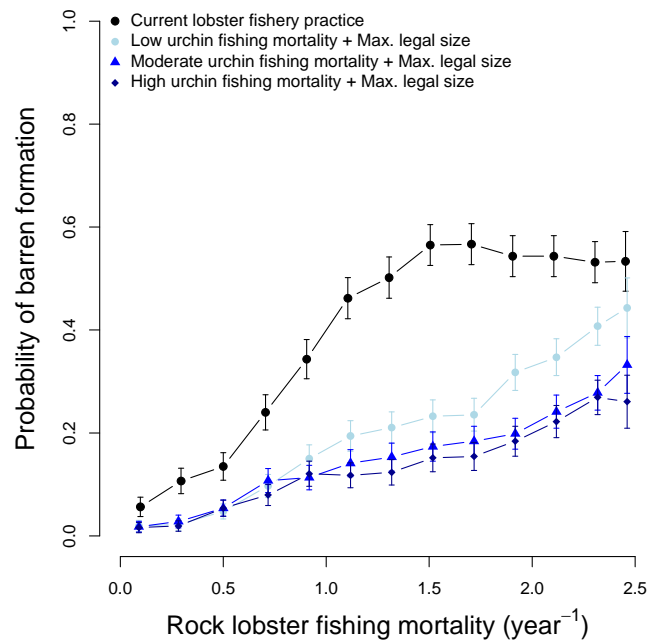


Figure 42. Effects of alternative management measures on the long-term risk of barrens formation in the model: (a) Extended FAST sensitivity indices showing the relative influence of all inputs on model behaviour (based on the first axis of the PCA conducted on normalised mean biomass densities for the last 10 years of simulations). Risk of barren formation against lobster fishing mortality (b) under different management interventions (direct removal of sea urchin or imposing a maximum legal size [carapace length = 145-155 mm] for lobsters, or both), (c) with different levels of sea urchin culling, (d) with different maximum legal sizes for lobster, (e) with a combination of maximum legal size [carapace length = 145-155 mm] for lobster and different sea urchin culling mortalities. All Monte-Carlo simulations are initiated in the seaweed bed state. 'Current lobster fishery practice' refers to a minimum legal size. The fishery is also managed by a catch quota that, in recent years, equates with a rock lobster fishery mortality of 1.2-1.5 y^{-1} .

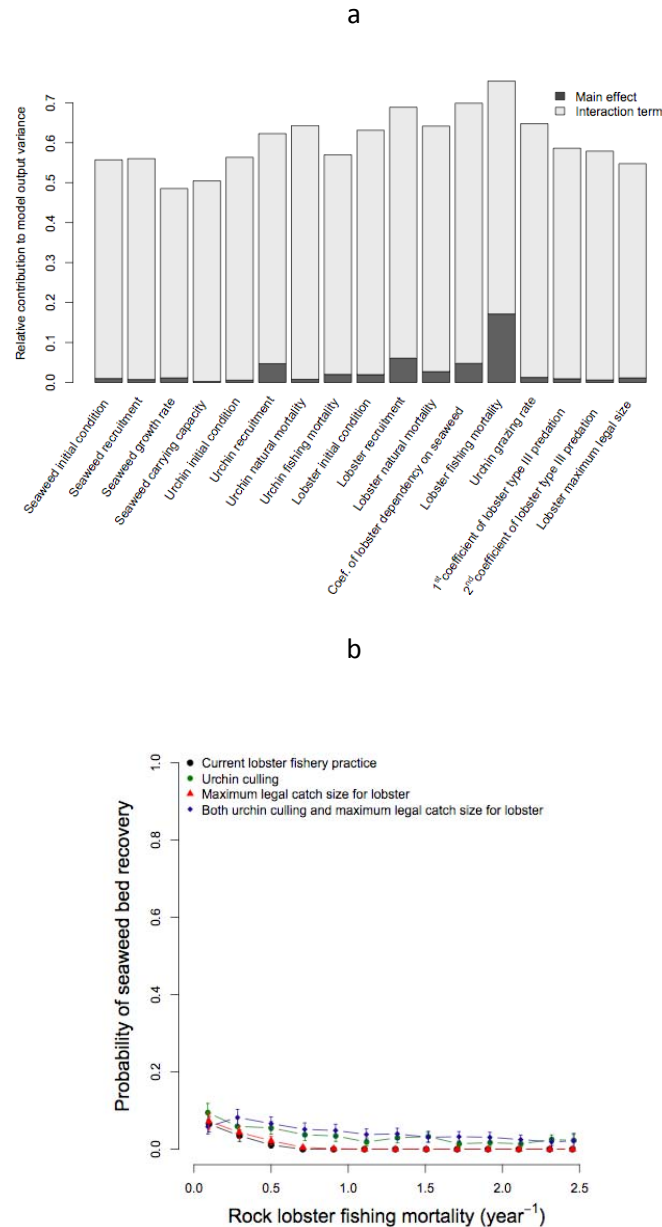
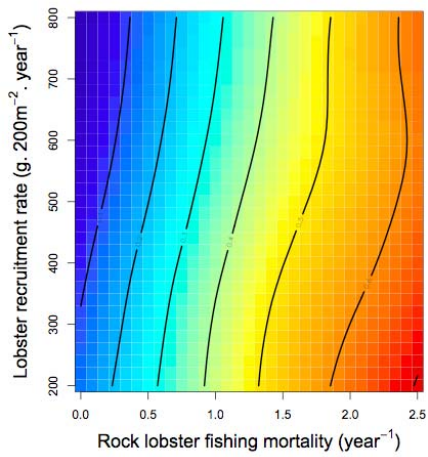
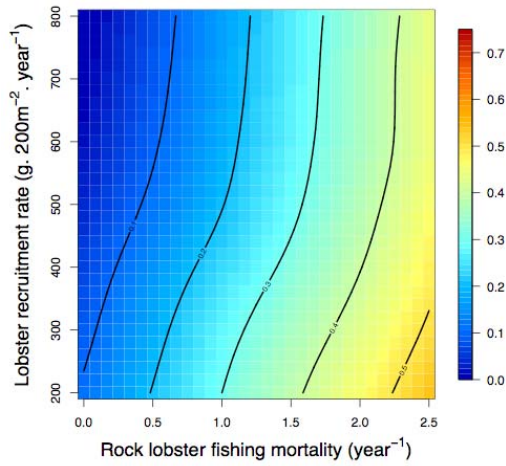


Figure 43. Effects of alternative management measures on the long-term probability of recovery of seaweeds on sea urchin barrens. (a) Extended FAST sensitivity indices showing the relative influence of all inputs on model behaviour (based on first axis of the PCA on normalised mean biomass densities for the last 10 years of simulations). Probability of seaweed bed recovery against lobster fishing mortality (b) under different management interventions (direct removal of sea urchins, or imposing a maximum legal size [carapace length = 145-155 mm] for lobsters). All Monte-Carlo simulations are initiated in the sea urchin barren state. ‘Current lobster fishery practice’ refers to a minimum legal size. The fishery is also managed by a catch quota that, in recent years, equates with a rock lobster fishery mortality of $\sim 1.5 \text{ y}^{-1}$.

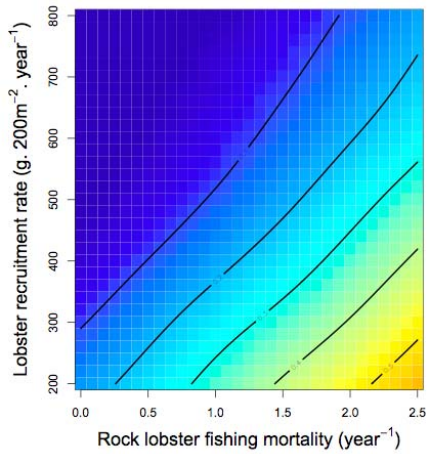
a) Current lobster fishery practice



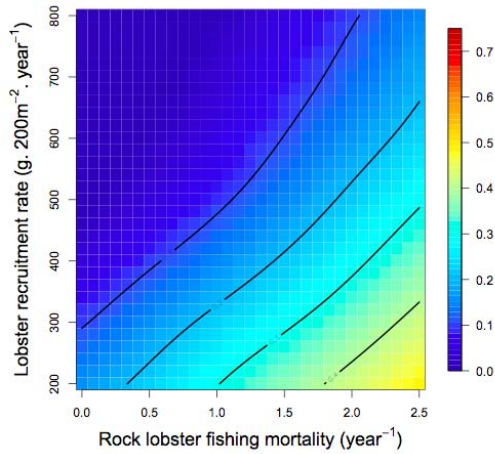
b) Maximum legal size for lobster



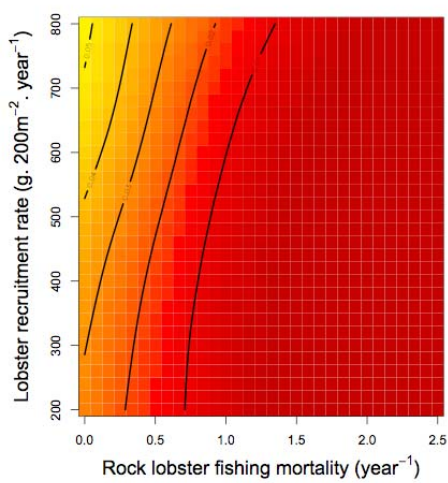
c) Moderate sea urchin culling



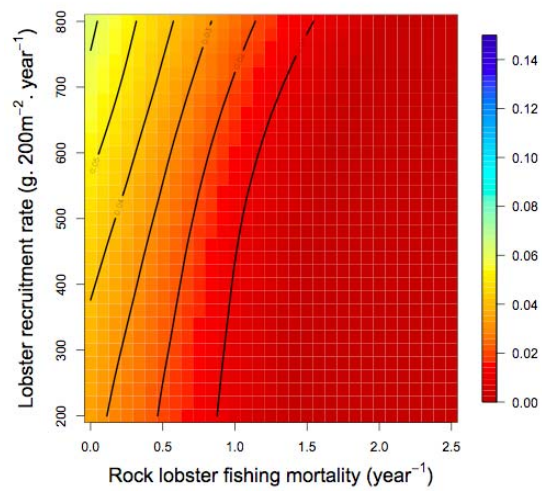
d) Moderate sea urchin culling and maximum legal size for lobster



e) Current lobster fishery practice



f) Maximum legal size for lobster



g) Moderate sea urchin culling

h) Moderate sea urchin culling and maximum legal size for lobster

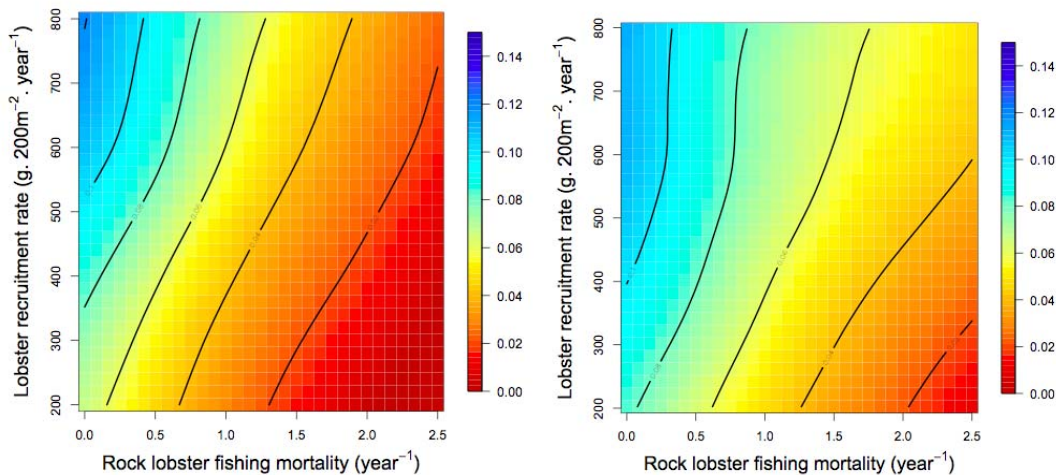


Figure 44. Probability of the modelled community shifting (a-d) forward from dense seaweed cover to sea urchin barrens, or (e-h) backward from sea urchin barrens to recovery of dense seaweeds as a function of rock lobster fishing mortality and mean lobster recruitment rate. Surface plots were produced using the 'krig' function from R's 'field' package and each refers to a different scenario: (a, e) under current rock lobster fishery practice (i.e. minimum legal size); (b, f) with implementation of a maximum legal size for rock lobster [carapace length = 145-155 mm]; (c, g) under moderate sea urchin culling ($F_{CR} = 0.5 - 1.5 \text{ year}^{-1}$); and, (d, h) under a combination of the two latter. Note that the mean time for the modelled community to shift (200-320 months for barren formation against 300-440 months for seaweed recovery) decreases as the likelihood of the shift increases.

All our results depict the presence of a hysteresis in community dynamics, which has strong implications for management. Preventing the further establishment of sea urchin barrens in eastern Tasmania arguably remains a realistic possibility (Figs. 42 and 44a-d), however once extensive barrens habitat has formed, restoration efforts palatable to the lobster fishing industry are likely to be ineffective (Figs. 43 and 44e-h), and TRITON indicates that even total cessation of lobster fishing on barrens habitat (Fig. 43b) may not realise recovery of seaweeds.

Of all the parameters related to management intervention, fishing of rock lobster and sea urchins demonstrate the highest influence on the model's ability to shift forward (Figs 42a, 44c) or backward (Figs. 43a, 44g) between states. Culling of sea urchins is particularly effective when combined with a marked reduction in lobster fishing. We acknowledge however that at current levels of activity in the *C. rodgersii* fishery, extensive harvesting of sea urchins is unlikely to occur at a sufficient scale to be effective in mitigating risk of barrens formation at a whole-of-coast scale. Despite repeated examples of large scale depletion, and sometimes collapse, of sea urchin populations elsewhere in the world through overfishing (Andrew *et al.* 2002), *C. rodgersii* does not currently have high market value and rapid escalation of the fishery in Tasmania appears unlikely. More importantly, the greatest extent of *C. rodgersii* barrens is in waters 20-40 m depth (Johnson *et al.* 2011), which greatly limits accessibility of divers to the resource.

On its own, protection of large predatory lobsters by imposing a maximum legal size only marginally reduces the risk of sea urchin barren formation (by ~10%), and has little effect in improving the likelihood of restoring dense productive seaweed beds (Fig. 44f). However, implementing a maximum legal size can reduce the probability of barrens formation by up to 20% when associated with a reduction in lobster fishing (F_{RL} between 0.5-1.5 year^{-1} ; Figs. 42b, 42d and 44b). Note that at low fishing pressure ($F_{RL} < 0.5$) on rock lobster, the maximum legal size has marginal effects (Figs. 42d) because sufficient animals reach

predator-capable size with or without an upper size limit. Additionally, TRITON's low sensitivity to initial abundances of lobster (Figs. 42a, 43a) suggests that single one-off events of translocating large lobsters onto shallow exposed reefs have virtually no influence on the long-term mitigation of sea urchin destructive grazing of seaweed beds. If there is ongoing fishing at translocation sites then translocated animals decline quickly while, as we observed at the two reserve sites (ERRR and NBRR) in the present study, if translocation sites are protected from fishing the translocated population is soon overtaken by growth of residents into predatory-capable size classes. In contrast, regular artificial enhancement of lobster populations through translocation (see Gardner & Van Putten 2008), captured in Figs. 44a-h as high lobster recruitment scenarios, can considerably improve outcomes against sea urchin destructive grazing. Importantly, Fig. 44 also illustrates how environmental factors, such as recruitment rates or seaweed growth rate, can affect the effectiveness of management interventions.

When a phase shift does occur in TRITON, transition times from one state to the other takes from two (forward shift) to three (seaweed recovery) decades (see previous section). This is consistent with the observed time between first occurrence of urchins and the establishment of widespread barrens in eastern Tasmania (Johnson et al. 2005, 2011). Under controlled experimental conditions where all grazers are totally excluded from small barren patches (a few m²), full recovery of dense seaweed beds takes about two years (Ling 2008a; see also Strain & Johnson 2013). In similar circumstances, the recovery of the seaweed bed in the absence of grazers also takes two years in TRITON (cf. Appendix A8; results presented in validating TRITON in the previous section). However, under persistent sea urchin recruitment and sufficient habitat complexity (e.g. shelter crevices), eradication of sea urchins on barren grounds to levels necessary to permit seaweed regrowth is likely to be unachievable at wider scales over just a few years. Thus, while preventing the establishment of sea urchin barrens in the first place is arguably feasible within current management schemes, implementing 30+-year management plans to restore seaweed beds is less realistic.

Caveats on management options

While model simulations provide valuable information about the effectiveness of different management levers to mitigate sea urchin destructive grazing, we keep in mind that TRITON is a model (i.e. a simplified representation of reality) and that the model's ability to shift 'forward' from dense seaweed bed to sea urchin barren was formally used as a calibration factor (see previous section on TRITON calibration and validation). Thus, while recovery of seaweed beds on extensive sea urchin barrens will certainly be more challenging than preventing extensive barrens in the first place, it may in reality be easier to achieve than suggested by TRITON's simulations. This is one reason why it is sensible to address the same questions – of the likelihood of preventing and recovering from extensive barrens – using alternative modelling approaches, as is tackled in the last section of this report. Additionally, the responses of real Tasmanian rocky reef communities to management intervention may prove more complex and variable than the mean patterns observed through simulation.

An important result is that the modelled community is nearly as sensitive to mean recruitment rates of both lobsters and sea urchins, and to the intrinsic growth rate of the seaweed assemblage, as to practical management levers associated with lobster fishing mortality or sea urchin culling mortality (Figs. 42a, 43a). Thus, it is possible that environmental factors can significantly counter the impact of management intervention, e.g. changes in future levels of regional lobster recruitment (see Johnson *et al.* 2011) can considerably influence the outcome of management intervention (Fig. 44). Spatial variability in lobster and sea urchin recruitment rates, and in seaweed growth rates, often reflects heterogeneity of habitat (e.g. suitability of substratum for recruiting newly metamorphosed individuals, exposure to storms, depth and light exposure, nutrient levels to drive seaweed growth). While our results through Monte-Carlo simulations capture the mean dynamics across the spatial variability of Tasmanian reef communities, patchy heterogeneous reef habitat will display a gradient of responses to particular management interventions.

Additionally, while this study addresses the effectiveness of alternative management interventions in an

ecological context, we have not seriously addressed practical questions or made a formal cost/benefit analysis relating to their implementation. Nonetheless, a brief analysis of our findings in the context of the current management environment is appropriate. In recent years, lobster fishing mortality in eastern Tasmania has varied around 1-1.4 year⁻¹ (Hartmann *et al.* 2012). While a moderate reduction in lobster fishing pressure is possible for the east coast of Tasmania (e.g. down to ~ 0.8 year⁻¹), a sharp decrease (e.g. below 0.5 year⁻¹) is unlikely to be acceptable to many stakeholders. Additionally, practical and economic considerations will limit the success of sea urchin culling (see section on management responses to *C. rodgersii* at small scales outlined at the beginning of this report). Targetted culling of sea urchins by divers is challenging given the complexity of reef habitat, nocturnal activity of the sea urchins (Flukes *et al.* 2012), the depth limitation of diving operations, and the cryptic nature of small and medium-sized individuals. It is likely that culling can be effective to prevent barrens and restore seaweeds at a tactical level focused on particular circumscribed areas, but again a careful cost-benefit analysis is warranted. A small-scale fishing and processing industry for *C. rodgersii* launched recently in northeast Tasmania may have potential to expand further, but the possible extent and intensity of harvesting is yet to be assessed. Even so, commercial harvesting by divers is effectively restricted to shallow reefs (depth < 25 m) given depth limitations of diving, while extensive barrens extend to 40+m where there is available reef. Note also that developing a commercial dive-based fishery for *C. rodgersii* is likely to favour sustainable harvesting of urchins rather than restoration of dense seaweed beds (Byrne *et al.* 1998). Irrespective, the extent to which divers harvesting urchins will focus on extensive barrens habitat remains an open question. Even if they do, whether working to achieve optimal harvest rates for the industry will reduce densities on extensive barrens sufficiently to effect recovery of seaweeds is unknown.

With respect to other management options, the simulations indicate that establishing an upper legal size (~>140 mm CL) can only usefully mitigate barren formation if it is set at <155 mm CL and combined with a reduction in lobster fishing.

In summary, our simulations indicate that simultaneous implementation of a combination of measures is most likely to mitigate sea urchin barren formation. Reducing fishing mortality is fundamental, but will see greatest effect when conducted in conjunction with culling or harvesting and, to a lesser extent, imposition of an upper size limit in the lobster fishery. Assessing the practicability and cost-effectiveness of each potential management lever in a formal cost-benefit analysis would be a useful next-step to complement the ecological assessment presented here.

Ecosystem-based fishery management: Rock lobster fishery biological performance and the importance of accounting for the ecological role of fishery target species

Lobster catches dependent on fishing mortality estimated from simulations using the single species model (itself based on the population dynamics component of the current stock assessment model) are much higher than catch estimates from simulations using TRITON in which the potential for and consequences of sea urchin destructive grazing of seaweed beds are accounted for (Fig. 45a). As fishing intensifies, estimates based on the single species model asymptote, while catch estimates from TRITON are not only lower than those from the single species model, they begin to decline as fishing mortality (F_{RL}) rises above ~0.7 year⁻¹. This is because as sea urchin barrens start to form and the complex seaweed bed habitat is lost, the potential for juvenile lobsters to recruit becomes reduced in TRITON. Available data indicate that lobsters recruit to seaweed beds, and our results at the Elephant Rock Research Reserve show that extensive urchin barrens are poorly preferred by juvenile lobsters. While large predatory-capable lobsters can utilise barrens habitat, under moderate to heavy fishing pressure their abundances do not attain levels to be ecologically meaningful. In our results from TRITON, the optimal yield is displayed as a horizontal dashed line for each model and corresponds to the 95% quantile of all simulated annual catches (Fig. 45a). Under current management practises (minimum legal size), the Maximum Sustainable Yield (MSY) estimated with TRITON is reached at a lower fishing pressure ($F_{RL, MSY}$ ~ 0.4-0.6 year⁻¹ associated with the green dashed line) than the MSY estimated from the single species model ($F_{RL, MSY}$ ~ 0.7-0.9 year⁻¹ associated with the red dotted line). The 'MSY' from TRITON can be thought of as the Ecological Sustainable Yield (ESY). Notably, both models suggest that the maximum economic yield (MEY), delivering highest catches for least fishing effort,

is in the vicinity of 0.5-0.7 year⁻¹.

Comparison of long-term annual lobster catches dependent on fishing mortality under different options for management intervention indicates that the nature of the management approach will dramatically affect catch. These results are derived from simulations with TRITON in which the community was initialised in the seaweed bed state. Out of all management options and across the whole range of potential fishing pressure on lobster, direct removal of sea urchins delivers the highest lobster catches (green line; Figs. 45a,b). Implementing a maximum legal size (set between 145-155 mm of carapace length) (red line; Fig. 45b) enhances fishery productivity at moderate to high fishing mortality but does not significantly affect fishery productivity at low fishing pressure ($F_{RL} < 0.4 \text{ year}^{-1}$) relative to current practise (minimum legal size only; black line in Fig. 45b). Overall, any management intervention that reduces *C. rodgersii* destructive grazing and minimises the extent of barrens habitat (e.g. reduction in lobster fishing or sea urchin culling) acts to improve fishery productivity.

The Tasmanian southern rock lobster fishery serves as a useful example to emphasise the importance for fishery management to account for the broader ecological role of commercially fished species. Our analyses provide a powerful argument for Tasmanian lobster fishery management to adopt ecosystem-based reference points, and to focus on an ecologically sustainable yield (ESY) (Mace 2001; Zabel *et al.* 2003; Hall & Mainprize 2004; Walters *et al.* 2005). Small scale experiments and observations in marine protected areas (Ling *et al.* 2009a; Ling & Johnson 2012), and the results of the large scale manipulations at the reserve sites in this project, show that large rock lobsters contribute an important ecological service in maintaining functioning of productive seaweed beds by controlling sea urchins responsible for destructive grazing. Depletion of large predatory capable lobsters by fishing facilitates habitat loss with, almost certainly, a concomitant decline in recruitment of juvenile lobsters, which the single-species approach does not account for (Hartmann *et al.* 2012). While the barrens habitat is recognised as a state with reduced productivity for both abalone and lobster fisheries in eastern Tasmania (Johnson *et al.* 2005, 2011), the actual magnitude of this loss of fishery productivity as estimated by TRITON requires cautious interpretation. Regardless of these quantitative considerations, the fishing mortality associated with the ecologically sustainable yield and point of greatest catch for least fishing effort estimated using TRITON is notably similar to that achieving greatest catch for least fishing effort estimated using the single species model. The overall message is encouraging, and that is that the fishing effort to optimize ecological sustainability and economic efficiency in the fishery are similar ($F_{RL} \sim 0.6 \text{ year}^{-1}$; Fig. 45), however this requires a relatively large reduction in catch and effort than has occurred in recent years on the east coast.

In the context of Tasmanian reef communities exposed to *C. rodgersii*, and in addition to the management instruments implemented currently in the lobster fishery (e.g. transferable quota, defined fishing season, and minimum legal catch size), any management effort to mitigate sea urchin destructive grazing of seaweed habitat relative is likely to improve fishery productivity, even if only marginally (as is the case, for example, when implementing a maximum legal size; Fig. 45b). Culling sea urchins together with a moderate reduction in lobster fishing ($F_{RL} \sim 0.7-0.8 \text{ year}^{-1}$) can deliver both better performance in the lobster fishery (Fig. 45b) while reducing the risk of barrens formation to ~20% (Fig. 42c), which may prove acceptable to many stakeholders. Despite the representation of fishing as an instantaneous mortality term in TRITON, we contend that the different sets of Monte-Carlo simulations reveal the effectiveness of alternative management interventions on both long-term ecological state of rocky reef communities and productivity of the lobster fishery.

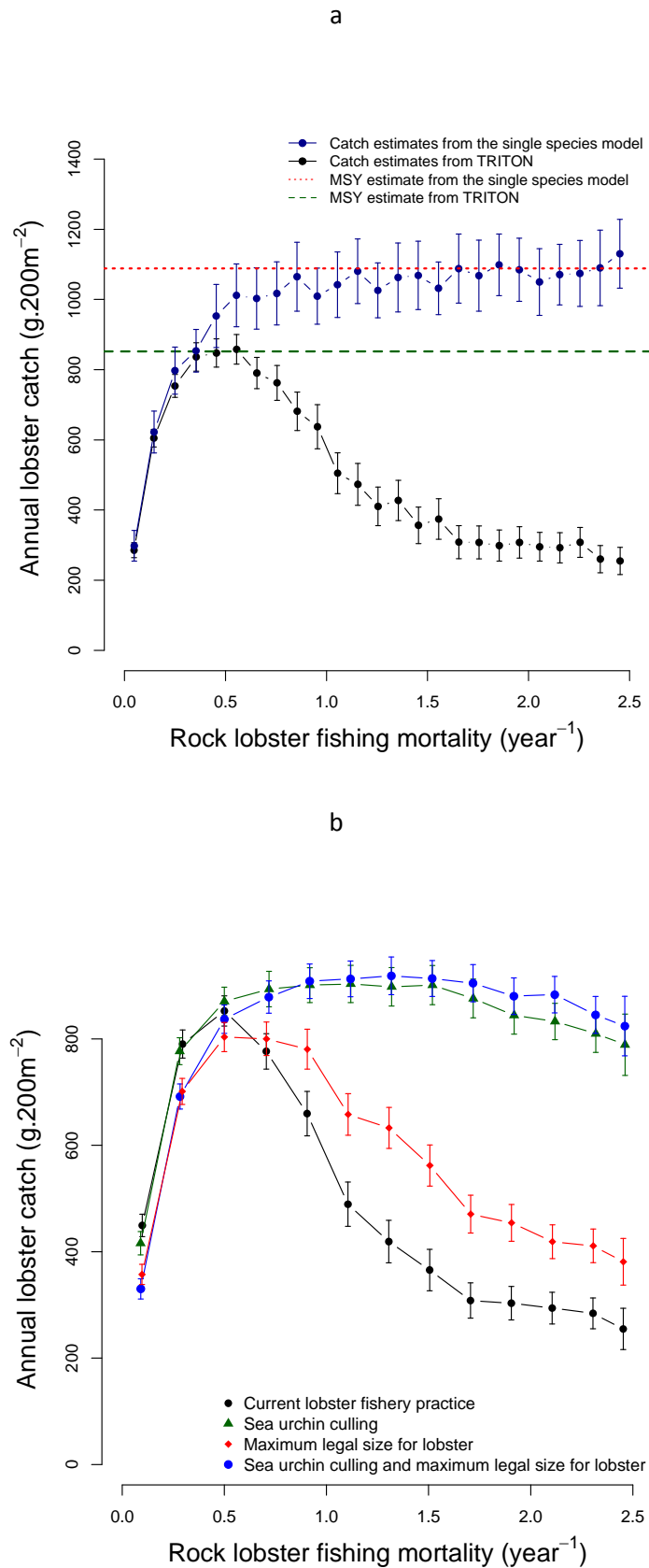


Figure 45. (a) Yield curves or annual equilibrium catches (g per 200 m² patch of reef) of rock lobster from simulations using a single-species lobster population model (based on the population dynamics component of the current rock lobster assessment model; blue), and with the TRITON model (black) that accounts for the risk and consequences of sea urchin barren formation and the consequences of this shift in community and habitat structure for lobster productivity. The red and green dashed lines show optimal yields estimated from Monte-

Carlo simulations based on the single species (Maximum Sustainable Yield) and the TRITON model (Ecologically Sustainable Yield) respectively. (b) Annual lobster catches estimated using TRITON under alternative management interventions (either removal of sea urchins, or imposing a maximum legal size for lobsters [carapace length = 145-155 mm] or both). 'Current lobster fishery practice' refers to a minimum legal size, and is shown by the black line. The fishery is also managed by a catch quota that, in recent years, equates with a rock lobster fishery mortality of $\sim 1.4-1.5 \text{ y}^{-1}$.

Conclusions

Using Monte-Carlo simulations with the TRITON model that specifically captures the potential for alternative community states in lobster-sea urchin-seaweed dynamics, we provide estimates of thresholds in Tasmanian rocky reef communities. These tipping points show clearly the presence of a hysteresis in community dynamics, and strongly emphasises the need to focus on preventing the formation of sea urchin barrens to circumvent the far more challenging task of restoring seaweed beds after extensive barren habitats have established. In addition to defining tipping points, we estimate more conservative management reference points to minimise the risk of barrens forming as a critical biomass density of large lobsters of $\sim 700-900 \text{ g. } 200 \text{ m}^{-2}$). Where it can be practically implemented, our results indicate direct culling or harvesting of sea urchins together with a reduction in lobster fishing is the most ecologically effective intervention to minimise the impact of the sea urchin grazing on Tasmanian reefs. At particular sites, direct control of sea urchins is likely to be more effective than intervention aimed exclusively at building the lobster population (e.g., by only reducing lobster fishing or implementing a maximum legal catch size). Simulations highlight the need for lobster fishery management to better account for the pivotal ecological role of lobsters in this system, and provide guidance to revise key target points accordingly. An important next step will be to perform a cost-benefit analysis across the various management scenarios available. This is addressed in part in the next section, which explores similar questions about management alternatives using an alternative modelling approach focused on population dynamics of the urchins (*C. rogersii*) and lobsters (*J. edwardsii*).

Assessing management strategies using population models of *Centrostephanus rodgersii* and rock lobsters

Preamble

While we do not include a formal risk assessment (which is beyond the scope of the study), in setting the bounds to and interpreting the results of the modelling we give explicit consideration to the notion of risk in the context of barrens formation. There are two elements to defining the level of risk associated with a particular event, *viz.* the probability of the event (i.e. barrens formation) occurring, and the consequences of the event should it occur. The key points are that risk is not defined solely by the likelihood of barrens forming, and that the consequences of extensive barrens forming are severe. Extensive *C. rodgersii* barrens result in local collapse of biodiversity (Andrew 1991, 1993; Andrew & O'Neill 2000; Johnson et al. 2005; Ling 2008) and, with the loss of habitat and decline in primary production, local decline of commercial fisheries (Andrew & Underwood 1992; Johnson et al. 2005, 2011; Strain & Johnson 2009; Strain 2010). This has the dual effect of reducing habitat available to the fishery and increasing the fishing pressure on the remaining fishable habitat. Moreover, as has already been indicated by the present project, it is difficult (and thus costly) to rehabilitate extensive barrens back to seaweed cover. Thus, extensive barrens need to be recognized as a long term phenomenon unless there is drastic intervention, which is only likely to occur at limited spatial scales. On a time scale of human generations and at a coast-wide spatial scale, formation of extensive barrens can be cumulative in a ratchet-like manner; the dynamic moves only in one direction. For these reasons, in setting the bounds to and interpreting the results of the modelling we assume that the overall level of risk – and therefore cost – associated with extensive *C. rodgersii* barrens is high. The subjective decisions required in scoping the model to identify target densities of urchins and lobsters to ensure low likelihood of extensive *C. rodgersii* barrens are considered in this light.

Long term dynamics of *C. rodgersii* at different levels of lobster predation

The model indicates that the relationship between asymptotic density of *C. rodgersii* and annual mortality is non-linear, described approximately by a negative exponential (Fig. 46). Thus, the greatest benefit in the impact of building lobster biomass to limit urchin numbers is at the beginning of any rebuilding phase, but as lobster numbers begin to build it becomes increasingly difficult to reduce urchin density further.

While the mean asymptotic density of *C. rodgersii* for a given level of mortality from lobster predation is important in informing target densities of lobsters, so too is the upper 95%CI of the mean asymptotic density when risk of barrens formation is considered. As a result of variability in urchin recruitment, and possibly variability in habitat characteristics such as exposure and the nature of the substratum, for a given level of annual mortality from lobster predation, it is inevitable that at some point in space and time the resulting urchin density will be greater than the predicted mean. A common approach to defining an upper limit is to use the upper 95% CI (red line, Fig. 46), so a conservative approach to minimise risk of barrens formation would base annual mortality rates of urchins as a result of lobster predation on the upper 95% confidence interval of the predicted mean asymptotic density. Given target densities of *C. rodgersii* identified previously, it is now possible to translate these to estimates of annual mortality from predation by lobsters based on the relationships in Fig. 46 (Table 24).

Long term ecological dynamics - target densities of lobsters

By combining (1) target densities of urchins, (2) predicted (asymptotic) densities of urchins for a given annual mortality rate, and (3) predation rates of large lobsters on urchins, we estimate the target density of large (>140 mm CL) lobsters necessary to rehabilitate existing extensive barrens and maintain *C. rodgersii* in healthy seaweed beds at sufficiently low densities to provide low risk of incipient barrens developing into extensive tracts of barrens habitat (Tables 25, 26). As outlined in the Methods section, for completeness we

used three approaches to estimate absolute predation rates of large lobsters on urchins at the two experimental reserves, but argue that the most reliable and robust estimate is that derived from changes in urchin abundance related to lobster abundance at the experimental reserve sites using data from all surveys of urchin abundance during the study. Accordingly, lobster target densities based on scaling these estimates are likely to be most reliable, and are reported below.

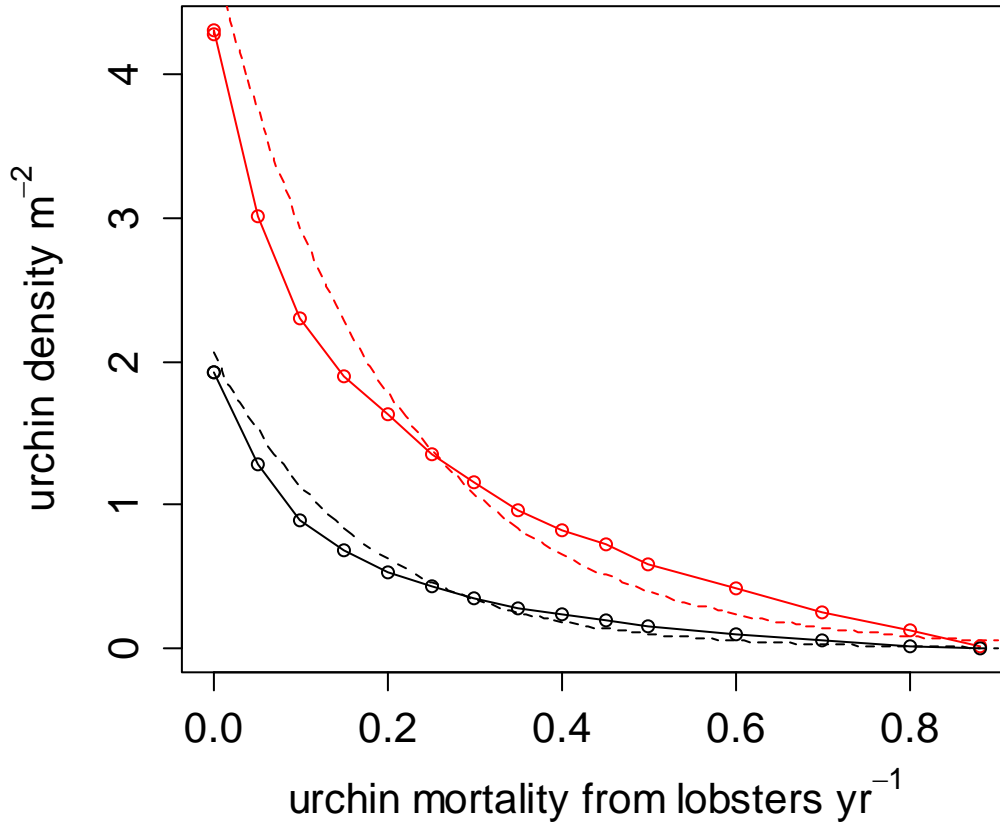


Figure 46. Output of the model showing the relationship between predicted mean asymptotic density of *C. rodgersii* (per m²; solid black line), and asymptotic density of the upper 95% confidence interval of the mean (solid red line), dependent on the annual rate of mortality of urchins resulting from predation by rock lobsters. The relationships are approximately exponential, given as $y = 0.721 * \exp(-5.948 x)$, $adj R^2 = 0.914$ for the mean density (black dotted line) and $y = 1.574 * \exp(-4.983x)$, $adj R^2 = 0.880$ for the 95%CI of the mean density (red dotted line).

Table 24. Estimated required annual mortality rates of *C. rodgersii* as a result of predation by rock lobsters (i.e. over and above background mortality) to achieve particular (maximum) target densities of urchins. Required annual mortalities are based either on the predicted mean asymptotic densities of urchins, or upper 95% confidence limit of predicted mean densities, for a given annual mortality rate from lobster predation (see Fig. 46).

<i>C. rodgersii</i> target density (m ⁻²)	Mortality based on mean	Mortality based on upper 95% CI
0.05	0.724	0.854
0.10	0.595	0.818
0.20	0.444	0.740
0.25	0.389	0.700

These simulations, focused on long term outcomes in incipient barrens or intact seaweed beds and assuming average urchin recruitment, indicate the need to maintain densities of large lobsters at the order of 30-35 lobsters ha^{-1} to ensure a relatively low risk of barrens formation (Table 25), while to counter extreme pulses in *C. rodgersii* recruitment lobster densities of $\sim 55 \text{ ha}^{-1}$ are required. Given spatial and temporal variability in urchin recruitment, lobster target densities determined from *mean* predicted asymptotic urchin densities, reflecting estimated long term mean urchin recruitment, must be considered as *minimum* target levels (Table 25). Attaining these densities of large predatory-capable lobsters does not eliminate the risk of extensive urchin barrens forming as a result of particular recruitment events greater than the long term average. Indeed, given variability in recruitment, it is certain that at some point in time and space extensive barrens will form if densities of large lobsters are at target levels determined from mean predicted asymptotic urchin densities. Attaining the target density of large lobsters determined from the upper 95% confidence limits of predicted asymptotic urchin densities (Table 26) will be more difficult to achieve as a management outcome, but will provide considerably greater certainty that extensive barrens will not form.

By comparison, predicted densities of large lobsters ($>140 \text{ mm CL}$) required to rehabilitate extensive urchin barrens are much greater, ranging from 180 - $>300 \text{ ha}^{-1}$ depending on whether urchin recruitment occurs at average or upper levels (Tables 25, 26). These densities are unlikely to be achieved without protecting affected areas from fishing lobsters for long periods. After 10 years of protection and during a period of high rock lobster recruitment (C. Gardner, pers. comm.), densities of legal-sized lobsters ($>113 \text{ mm CL}$) in the Maria Island Marine Reserve attained $\sim 375 \text{ ha}^{-1}$ (Barrett et al. 2009), but most of these were almost certainly $<140 \text{ mm CL}$ since analysis of data from 2004 two years later (i.e. 12 years after implementing the reserve) indicated the density of large lobsters ($>140 \text{ mm CL}$) at $\sim 80 \text{ ha}^{-1}$ (S. Ling, unpublished data), while in 2009 the density of large lobsters was estimated at $\sim 120 \text{ ha}^{-1}$ (unpublished MPA monitoring data).

Table 25. Target densities of large lobsters (>140 mm CL) to achieve particular targets of mean *C. rodgersii* density based on predicted mean asymptotic urchin densities, for different estimates of lobster predation rates. Target densities of urchins recommended for incipient barrens are <0.2 m⁻² (Table 4), while for extensive barrens we estimate that urchin density needs to be reduced to at least <0.25 m⁻² to effect recovery of seaweeds. Thus, for the level of risk of barrens formation associated with achieving predicted mean asymptotic urchin densities, preferred targets are underlined and in bold. ¹predation rates determined from fitted model of urchin population decline during the study using data from all survey times; ²predation rates determined from modelling the exact difference in mean urchin density from the beginning to end of the study; ³predation rates determined from DNA analysis of lobster faecal pellets; ⁴the estimated predation rate is too high to be sustained by the urchin population at this site, and must represent an overestimate. ⁵Average absolute predation rate estimated over the study period expressed per 3 day period, i.e. estimates derived from the DNA-based method and from the observed change in urchin abundance are equivalent.

⁵ Mean no. urchins per lobster per 3 day period (source)	Equivalent annual mortality rate	<i>C. rodgersii</i> target density			
		0.25 m ⁻²	0.2 m ⁻²	0.1 m ⁻²	0.05 m ⁻²
		Lobster target density (ha ⁻¹)			
Extensive Barrens					
0.359 (¹ fitted model)	0.0394	<u>183.1</u>	208.7	280.1	340.8
0.645 (² exact diff)	0.0664	108.8	124.0	166.4	202.5
0.46 (³ DNA)	0.0468	154.4	175.9	236.1	287.2
Incipient barrens					
0.087 (¹ fitted model)	0.4919	29.8	<u>34.0</u>	45.6	55.5
0.097 (² exact diff)	0.5425	27.0	30.8	41.3	50.3
0.28 (³ DNA)	⁴ NA				

Table 26. Target densities of large lobsters (>140 mm CL) to achieve particular targets of mean *C. rodgersii* density based on upper 95%CI boundaries of predicted mean asymptotic urchin densities, for different estimates of lobster predation rates. Target densities of urchins recommended for incipient barrens are 0.2 m^{-2} (Table 4), while for extensive barrens we estimate that urchin density needs to be reduced to at least 0.25 m^{-2} to effect recovery of seaweeds. Thus, for the level of risk of barrens formation associated with achieving predicted mean asymptotic urchin densities, preferred targets are underlined and in bold. ¹predation rates determined from fitted model of urchin population decline during the study using data from all survey times; ²predation rates determined from modelling the exact difference in mean urchin density from the beginning to end of the study; ³predation rates determined from DNA analysis of lobster faecal pellets; ⁴the estimated predation rate is too high to be sustained by the urchin population at this site, and must represent an overestimate. ⁵Average absolute predation rate estimated over the study period expressed per 3 day period, i.e. estimates derived from the DNA-based method and from the observed change in urchin abundance are equivalent.

		<i>C. rodgersii</i> target density			
		0.25 m ⁻²	0.2 m ⁻²	0.1 m ⁻²	0.05 m ⁻²
⁵ Mean no. urchins per lobster per 3 day period (source)	Equivalent annual mortality rate	Lobster target density (ha ⁻¹)			
Extensive Barrens					
0.359 (¹ fitted model)	0.0394	<u>329.2</u>	348.1	384.9	401.5
0.645 (² exact diff)	0.0664	195.6	206.8	228.7	238.6
0.46 (³ DNA)	0.0468	277.5	293.4	324.4	338.4
Incipient barrens					
0.087 (¹ fitted model)	0.4919	53.6	<u>56.6</u>	62.6	65.3
0.097 (² exact diff)	0.5425	48.6	51.4	56.8	59.2
0.28 (³ DNA)	⁴ NA				

Predicting barrens cover for a given lobster density

It is useful to also examine the inverse problem and, for a given density of large (>140 mm CL) lobsters, predict either (1) expected cover of barrens, or (2) the likelihood of reaching a sufficiently low density of urchins to enable seaweed recovery on extensive barrens.

General case – long term dynamics of incipient barrens

From estimates of *C. rodgersii* mortality as a result of predation by large lobsters in incipient barrens at North Bay, it is possible to estimate predation-related mortality across a range of lobster densities to predict asymptotic urchin densities (based on the relationships shown in Fig. 46), and from this the expected cover of barrens (based on the relationships depicted in Fig. 5). In these calculations it is assumed that urchin mortality as a direct result of lobster predation scales linearly with the density of large lobsters over the range of lobster densities considered. We have also assumed that the annual mortality rate of urchins at the North Bay site was 0.4919 (see Tables 25, 26).

Again, there are subjective choices to be made depending on the level of risk of barrens formation that is deemed acceptable. The prediction of urchin density for a given density of large lobsters can be based on the *mean* long term asymptotic urchin density (solid black line, Fig. 47) which essentially reflects expected mean densities over all sites and times. However, *particular sites at particular times* will support higher urchin densities (for a given density of large lobsters) than the predicted mean asymptotic density because of space-time variation in *C. rodgersii* recruitment. Taking into account variability in recruitment, the limit defined by the upper 95% CI of the mean asymptotic density (solid red line, Fig. 47) may be interpreted as a worst case scenario for any particular site. Note that these predictions at low densities of large lobsters (i.e. effectively zero in terms of their ecological impact) are consistent with recent observations on the east coast of Tasmania (see Fig. 5).

Further subjective choices are required in predicting the expected cover of barrens from a given urchin density based on the observed relationship between *C. rodgersii* density and the extent of urchin barrens (Fig. 5). If the estimate of barrens cover is based on the fitted relationship describing extent of barrens as a function of urchin density (solid black line, Fig. 5), it must be recognized that 50% of future observations – equivalent to 50% of local sites – are likely to demonstrate barrens cover greater than that predicted (note that the fitted line in Fig. 5 is a *median* given lognormal distribution of errors). If the prediction is based on the upper bound of the 95% prediction interval of the observed relationship between barrens cover and urchin density (upper dashed line, Fig. 5), then only 2.5% of future observations (local sites) would be expected to exceed the predicted extent of barrens cover.

For an accepted level of barrens cover, the targets of lobster density based on predicted long term mean asymptotic urchin densities and the median relationship describing barrens cover and urchin density (Fig. 48, black line) are the most readily achievable, but they will inevitably lead to a large proportion of sites supporting much higher barrens cover than that predicted (they will also lead to some sites supporting lower cover of barrens than predicted, but this is less of interest given the consequences of extensive barrens formation). For example, the scenario based on mean asymptotic urchin densities and the median relationship between extent of barrens and urchin density (Fig. 48, black line), predicts that at local scales (10^2 m) barrens cover cannot exceed ~50%, even with zero predation by large lobsters, and this quite clearly under-estimates the reality in eastern Tasmania where at some sites ~100% cover of urchin barrens is readily observed. Targets for densities of large lobsters based on the upper 95% confidence limit of predicted mean asymptotic urchin densities and the upper bound of the 95% prediction interval describing barrens cover and urchin density (Fig. 49) will ensure that no site is likely to support a greater cover of barrens than that predicted despite anticipated 'spikes' in urchin recruitment. However, these targets are likely to prove unrealistic to attain within an operating fishery given that the density of large lobsters (140+ mm CL) in the Maria Is marine reserve after 12 years of protection from fishing attained $\sim 80 \text{ ha}^{-1}$ (S. Ling, unpublished data), and after 17 of protection $\sim 120 \text{ ha}^{-1}$ (unpublished MPA monitoring data), and this during a period of elevated lobster recruitment (C. Gardner, pers. comm.).

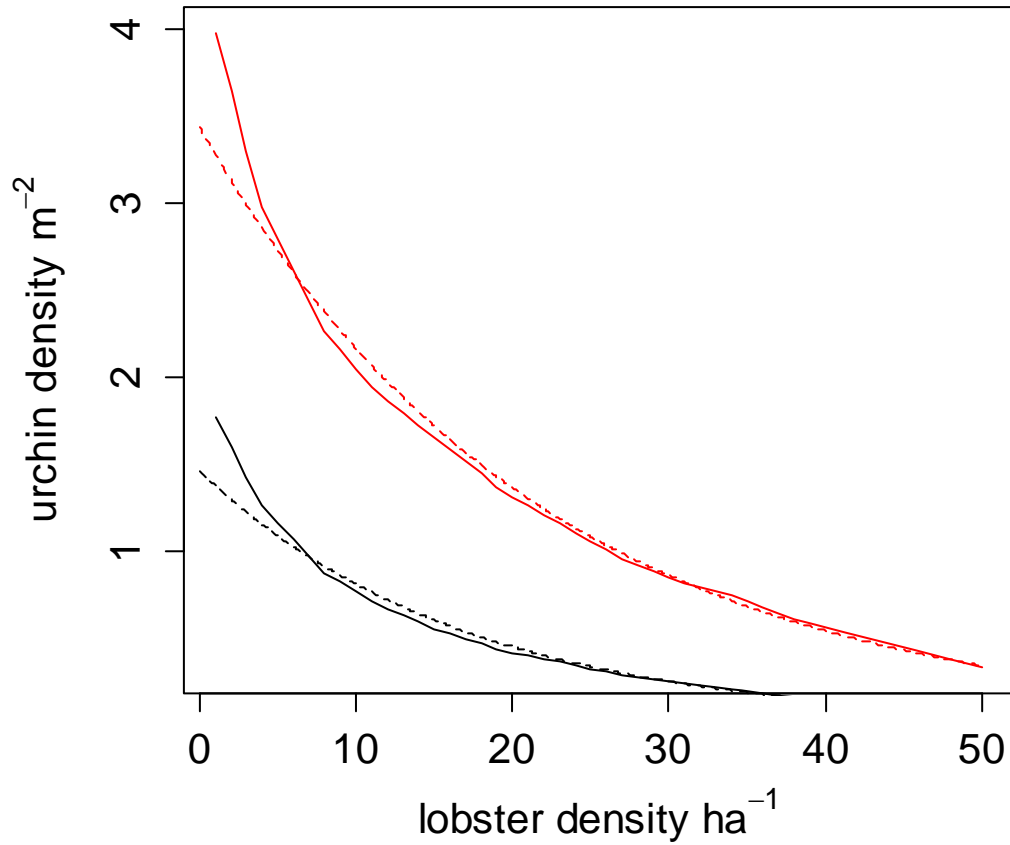


Figure 47. Predicted long term density of *C. rodgersii* depending on the density of large (>140 mm CL) lobsters. The black line is based on the mean asymptotic density of *C. rodgersii*, while the red line is based on the upper 95% CI of the mean asymptotic density. The relationships are approximately exponential (dotted lines), given as $y = 1.457 \cdot \exp(-0.059x)$, $\text{adj } R^2 = 0.993$ for the mean density (black dotted line) and $y = 3.436 \cdot \exp(-0.046x)$, $\text{adj } R^2 = 0.995$ for the 95%CI of the mean density (red dotted line). Imperfections in solid curves reflect data based on Monte Carlo simulation.

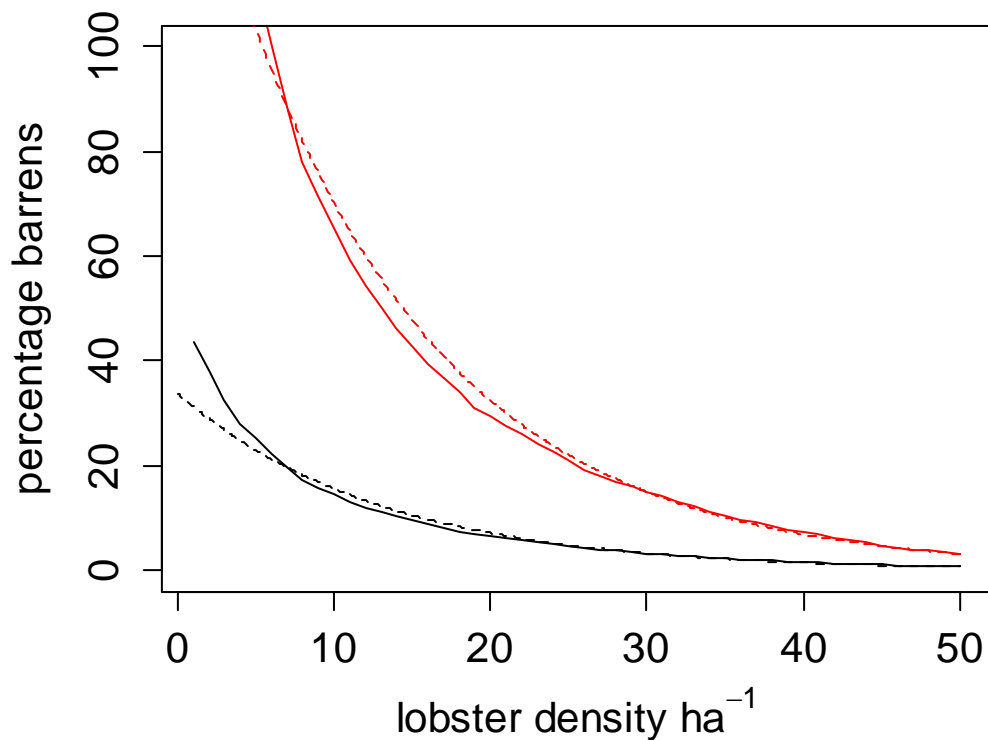


Figure 48. Predicted percentage cover of *C. rodgersii* barrens at local sites depending on density of large (>140 mm CL) lobsters. These predictions are based on mean asymptotic urchin densities, i.e. expected mean densities averaged across all sites and times, and thus they do not allow for observed *local* elevations in urchin numbers as a result of space-time variability in recruitment. The black line is based on the median relationship between percentage cover of barrens and *C. rodgersii* density as observed on the east coast of Tasmania (Fig. 5), while the red line is based on the upper bound of the 95% prediction interval of this relationship (Fig. 5). The relationships are approximately exponential (dotted lines), given as $y = 33.849 \cdot \exp(-0.077x)$, adjusted $R^2 = 0.993$ for the observed median relationship between barrens cover and urchin density (black dotted line) and $y = 151.77 \cdot \exp(-0.077x)$, adjusted $R^2 = 0.993$ for the upper bound of the 95% prediction interval of this relationship (red dotted line).

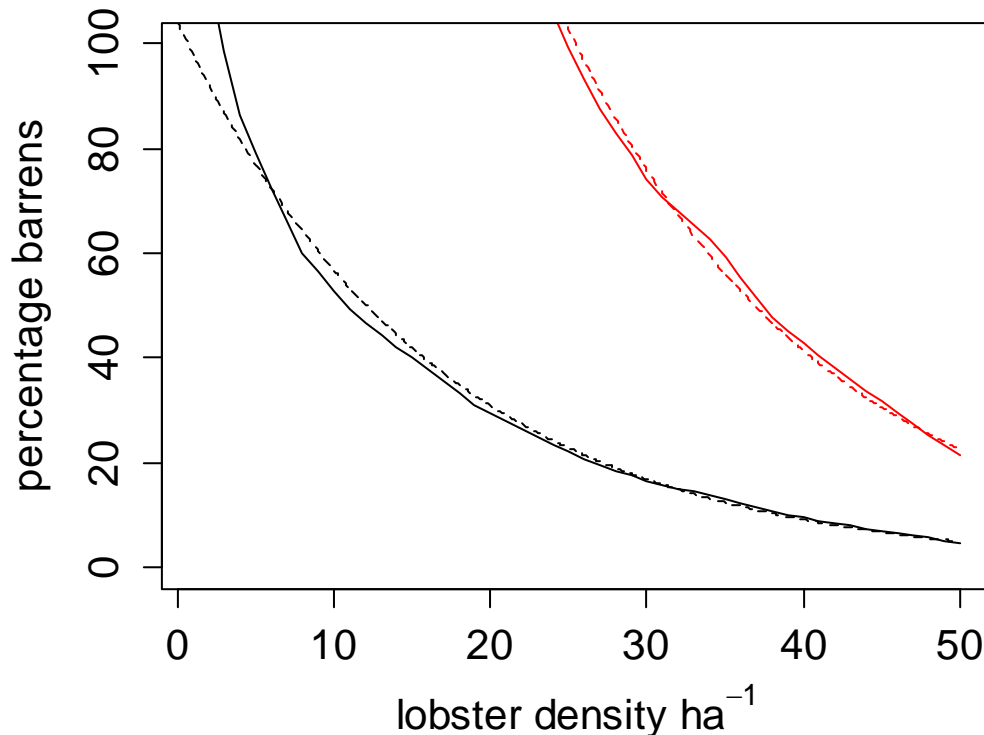


Figure 49. Predicted percentage cover of *C. rodgersii* barrens at local sites depending on density of large (>140 mm CL) lobsters. These predictions are based on the upper 95% CI of mean asymptotic urchin densities, i.e. they allow for expected elevations in urchin numbers at particular sites as a result of space-time variability in recruitment. The black line is based on the median relationship between percentage cover of barrens and *C. rodgersii* density as observed on the east coast of Tasmania (see Fig. 5), while the red line is based on the upper bound of the 95% prediction interval of this relationship (Fig. 5). The relationships are approximately exponential (dotted lines), given as $y = 104.06 \cdot \exp(-0.061x)$, adjusted $R^2 = 0.995$ for the observed median relationship between barrens cover and urchin density (black dotted line), and $y = 464.97 \cdot \exp(-0.06x)$, adjusted $R^2 = 0.995$ for the upper bound of the 95% prediction interval of this relationship (red dotted line).

Specific management scenarios

The fishery for southern rock lobster (*Jasus edwardsii*) in eastern Tasmania is currently at a cross roads. There are compelling economic reasons, independent of issues concerned with formation of barrens habitat by *C. rodgersii*, to rebuild biomass in the fishery in general and in the east coast region in particular (Hartmann et al. 2012). This would bring the fishery closer to its maximum economic yield, provide a buffer against interannual fluctuations in recruitment, and increase recreational fishing utility. These considerations seek an optimal compromise across social, economic and ecological imperatives, and it is well recognized that change to current management arrangements are likely to have social, economic and ecological consequences that may be perceived differently by different stakeholders. In considering *particular* alternative management strategies for the rock lobster fishery in eastern Tasmania into the future, the effect of those strategies on *C. rodgersii* populations and likely extent of development of barrens habitat on shallow reefs in eastern Tasmania is an important consideration. Thus, we consider specific management scenarios for the rock lobster fishery to assess (1) the likelihood of barrens cover for existing 'healthy' seaweed beds and incipient barrens, and (2) the likelihood of reducing densities of *C. rodgersii* on extensive barrens to levels that will permit recovery of seaweeds.

The approach uses projections of densities of rock lobsters >140 mm CL (based on the current rock lobster stock assessment model; Hartmann et al. 2012) for particular alternative management strategies. Potential management measures considered separately and together include a cap on the total harvest from the east

coast, imposition of an upper size limit, and measures to limit the recreational fishery which is particularly intensive on shallow reefs in eastern Tasmania (Table 27).

Table 27. Comparison of management scenarios defined by combinations of total allowable commercial catch statewide (TACC), imposition of a maximum legal size limit ('Max Size'), a cap on the commercial harvest on the east coast of Tasmania ('East Cap'; applies across fishery areas 1-3), and changes to the recreational fishery harvest ('Δ Rec'). Options to (a) 'Cease commercial fishing' and (b) take 'no cut' to the pre 2011 TACC (of 1323.9 t) and not to invoke any other management measures, provide 'extreme' reference points for comparison. The effect of each management strategy on east-coast (fishery areas 1-3) and state-wide biomass of 140+ mm CL lobsters, catch per unit effort (CPUE) across all size classes, and net present value (NPV) calculated over 20 years is given. Calculations are based on the current rock lobster stock assessment model. Colour code reflects changes relative to the 'no cut' strategy, where yellow indicates 'little or no' change, green indicates 'better' and red indicates 'worse'.

Management Strategy				East Coast							State-wide						
				Biomass			CPUE (all sizes)			NPV	Biomass			CPUE (all sizes)			NPV
TACC	Max Size	East Cap	ΔRec	2010	2015	2020	2015	2018	2020		2010	2015	2020	2015	2018	2020	
1103.24	160	150	-30%	115	319	1001	1.2	1.8	2.1	82	1078	1332	2204	1.1	1.2	1.3	546
1103.24	160	150	30%	113	239	707	1	1.4	1.6	68	1077	1252	1910	1	1.2	1.3	532
1103.24	160	150	None	114	270	831	1.1	1.6	1.9	75	1077	1283	2034	1	1.2	1.3	539
1103.24	160	175	-30%	111	261	822	1.1	1.6	1.9	87	1077	1324	2126	1.1	1.3	1.4	561
1103.24	160	175	30%	109	188	536	0.8	1.2	1.4	65	1075	1250	1840	1	1.2	1.3	539
1103.24	160	175	None	109	216	656	0.9	1.4	1.6	76	1076	1279	1960	1	1.2	1.3	551
1103.24	160	200	-30%	106	208	647	0.9	1.4	1.6	86	1076	1321	2054	1.1	1.3	1.4	566
1103.24	160	200	30%	105	143	377	0.7	1	1.2	47	1074	1256	1784	1	1.2	1.3	527
1103.24	160	200	None	105	168	488	0.8	1.2	1.4	69	1075	1281	1895	1	1.2	1.4	549
1103.24	160	225	-30%	102	161	481	0.8	1.2	1.4	76	1074	1324	1993	1	1.3	1.4	559
1103.24	160	225	30%	101	107	241	0.5	0.8	0.9	13.9	1073	1271	1751	0.9	1.1	1.2	469
1103.24	160	225	None	101	127	335	0.7	1	1.1	40	1073	1290	1847	1	1.2	1.3	523
1103.24	160	None	-30%	115	182	368	0.9	1.1	1.2	118	1080	1336	1990	1.1	1.3	1.4	580
1103.24	160	None	30%	113	153	288	0.7	0.9	1	84	1079	1260	1778	1	1.2	1.3	549
1103.24	160	None	None	114	163	317	0.8	1	1.1	99	1079	1291	1866	1	1.3	1.4	564
1103.24	150	150	-30%	115	344	1053	1.1	1.5	1.7	75	1078	1356	2256	1	1.2	1.3	539
1103.24	150	150	30%	113	266	759	0.9	1.2	1.4	59	1077	1279	1962	1	1.2	1.2	523
1103.24	150	150	None	114	297	884	1	1.4	1.5	67	1077	1310	2087	1	1.2	1.3	531
1103.24	150	175	-30%	111	287	874	1	1.4	1.5	77	1077	1350	2178	1.1	1.2	1.3	551
1103.24	150	175	30%	109	216	586	0.8	1	1.2	51	1075	1278	1890	1	1.2	1.3	526
1103.24	150	175	None	109	244	708	0.9	1.2	1.4	65	1076	1306	2012	1	1.2	1.3	539
1103.24	150	200	-30%	106	235	699	0.9	1.2	1.4	73	1076	1348	2106	1	1.3	1.4	553
1103.24	150	200	30%	105	171	423	0.6	0.9	1	25	1074	1284	1830	0.9	1.1	1.3	505
1103.24	150	200	None	105	196	537	0.7	1	1.2	53	1075	1308	1944	1	1.2	1.3	533
1103.24	150	225	-30%	102	188	529	0.7	1	1.2	58	1074	1352	2041	1	1.3	1.4	540
1103.24	150	225	30%	101	135	282	0.5	0.7	0.8	52.4	1073	1298	1792	0.8	1	1.2	430
1103.24	150	225	None	101	155	380	0.6	0.8	1	14	1073	1318	1891	0.9	1.2	1.3	496
1103.24	150	None	-30%	115	222	477	0.8	1	1.1	102	1080	1365	2056	1.1	1.3	1.4	568
1103.24	150	None	30%	113	190	381	0.7	0.9	1	69	1079	1287	1837	1	1.2	1.3	537
1103.24	150	None	None	114	201	416	0.8	0.9	1	84	1079	1319	1928	1	1.2	1.3	552
1103.24	140	150	-30%	115	389	1144	0.9	1.2	1.3	61	1078	1402	2347	1	1.2	1.2	525
1103.24	140	150	30%	113	314	853	0.7	1	1.1	40	1077	1326	2056	1	1.1	1.2	505

1103.24	140	150	None	114	344	979	0.8	1.1	1.2	51	1077	1357	2182	1	1.1	1.2	515
1103.24	140	175	-30%	111	334	968	0.8	1.1	1.2	58	1077	1397	2272	1	1.2	1.3	533
1103.24	140	175	30%	109	263	678	0.6	0.8	0.9	25	1075	1325	1981	0.9	1.1	1.2	499
1103.24	140	175	None	109	291	802	0.7	1	1	43	1076	1354	2106	1	1.2	1.2	517
1103.24	140	200	-30%	106	282	792	0.7	1	1	48	1076	1395	2199	1	1.2	1.3	528
1103.24	140	200	30%	105	217	509	0.5	0.7	0.8	15.8	1074	1330	1915	0.9	1.1	1.2	464
1103.24	140	200	None	105	243	629	0.6	0.8	0.9	20	1075	1355	2035	0.9	1.1	1.2	500
1103.24	140	225	-30%	102	235	620	0.6	0.8	0.9	21	1074	1398	2131	1	1.2	1.3	504
1103.24	140	225	30%	101	178	358	0.4	0.6	0.6	-120	1073	1340	1866	0.8	0.9	1	362
1103.24	140	225	None	101	200	464	0.5	0.7	0.8	36.5	1073	1363	1975	0.9	1.1	1.2	446
1103.24	140	None	-30%	115	289	663	0.7	0.9	1	78	1080	1413	2176	1	1.2	1.3	548
1103.24	140	None	30%	113	250	541	0.6	0.8	0.8	46	1079	1333	1945	1	1.1	1.2	516
1103.24	140	None	None	114	264	588	0.7	0.8	0.9	60	1079	1366	2042	1	1.2	1.3	531
1103.24	None	150	-30%	115	287	961	1.4	2.2	2.9	88	1078	1300	2163	1.1	1.2	1.3	552
1103.24	None	150	30%	113	202	667	1.1	1.7	2.2	78	1077	1215	1870	1	1.2	1.3	542
1103.24	None	150	None	114	236	791	1.2	2	2.5	83	1077	1248	1994	1.1	1.2	1.3	548
1103.24	None	175	-30%	111	226	782	1.2	2	2.5	96	1077	1289	2086	1.1	1.3	1.4	570
1103.24	None	175	30%	109	148	498	0.9	1.4	1.8	80	1075	1210	1802	1	1.2	1.3	555
1103.24	None	175	None	109	178	617	1.1	1.7	2.1	89	1076	1241	1921	1.1	1.3	1.4	563
1103.24	None	200	-30%	106	170	610	1.1	1.7	2.1	100	1076	1283	2017	1.1	1.3	1.5	580
1103.24	None	200	30%	105	100	342	0.8	1.2	1.4	73	1074	1213	1749	1	1.2	1.4	553
1103.24	None	200	None	105	127	452	0.9	1.4	1.7	88	1075	1240	1859	1.1	1.3	1.4	568
1103.24	None	225	-30%	102	121	446	0.9	1.4	1.7	97	1074	1284	1958	1.1	1.3	1.5	580
1103.24	None	225	30%	101	62	207	0.6	0.9	1.1	35	1073	1225	1718	0.9	1.2	1.3	517
1103.24	None	225	None	101	84	302	0.7	1.1	1.4	73	1073	1247	1814	1	1.3	1.4	555
1103.24	None	None	-30%	115	117	243	0.9	1.2	1.3	141	1080	1293	1925	1.1	1.4	1.5	595
1103.24	None	None	30%	113	90	183	0.8	1	1.1	105	1079	1217	1722	1	1.3	1.4	565
1103.24	None	None	None	114	99	206	0.8	1.1	1.2	121	1079	1247	1808	1.1	1.3	1.4	579
Cease commercial fishing				114	528	1774	2.2	3.9	5.1	5.2	1079	3462	7778	3	5.1	6.5	49
No Cut (1323.9)				114	77	139	0.8	0.9	1	103	1079	1101	1445	1	1.1	1.2	560

Not surprisingly, and consistent with the results of the TRITON model, the largest and thus most rapid increases in biomass of predatory-capable lobsters on the east coast occur when an upper size limit is imposed coincident with a cap on the commercial catch on the east coast, and when the recreational catch is reduced (Table 27). These measures have only a small effect on statewide NPV (which to 2020, across the various options examined, reduced by ~4% on average compared to the ‘no cut’ strategy), but relative to the ‘no cut’ strategy, invoking these measure would realize a drop in the NPV of the east coast fishery by almost 50% on average (note however that NPV calculations include only rock lobster fishery profits and does not include any effects on the fishery of ongoing loss of seaweed habitat). On this basis alone, and following discussion with managers and industry representatives, these measures are deemed not to be acceptable³. Imposing an upper size limit on its own, depending on whether at 160 or 140 mm, realizes ~2-4 fold increases respectively in biomass of 140+ mm CL lobsters on the east coast, while introducing a cap on the commercial catch of between 225-150 t pa as the only new management instrument over and above current regulations realizes ~2-6 fold increases respectively in biomass of large lobsters. Moreover, for a similar impact on the NPV of the east coast fishery, capping the catch realizes much bigger increases in

³ Note that calculations of NPV are sensitive to the discount rate (here set at 6.5%, although the nominal rate at time of writing is ~9.5%). Thus, decisions to set, and acceptance of, particular management strategies are also likely to be sensitive to the discount rate.

lobster biomass than imposing upper size limits. Again, the finding that setting an upper size limit on its own has limited effect is in line with results of the TRITON model. Overall, these results reflect the known limitation of having minimum and maximum size limits (i.e. a so-called 'slot size limit'), namely that gains in biomass within the 'slot' need to be substantial to compensate for loss of access to biomass to larger size classes following introduction of an upper limit. Another concern with establishing an upper size limit is that catch is displaced and concentrated on the 'slot' rather than removed, which can ultimately reduce catch rates. For these reasons, in considering the projections outlined in Table 27, a meeting in 2011 of fishery managers, stakeholders in the fishery and fishery scientists agreed that imposing a cap on the east coast fishery was an acceptable approach to rebuilding lobster biomass. Accordingly, a variety of scenarios were examined in which the total catch (i.e. combined across the commercial and recreational sectors) in areas 1-3 varies between 160-240 t pa, and these were compared with the 'extremes' of maintaining the current management regime for the fishery (the *status quo* with a state wide TACC of 1103.2 t pa) and complete closure of the fishery in eastern Tasmania.

First, we consider the predicted effects of these management scenarios on barrens development in intact kelp beds or incipient barrens (Figs. 50-56, Table 28; i.e. these simulations are not relevant to areas that currently exist as extensive *C. rodgersii* barrens). In these figures, the histograms can be interpreted as either the likelihood of a given site supporting a particular level of barrens (i.e. assuming a 'coastwide average site'), or the likely distribution of barrens habitat across all sites that are currently unaffected by urchins or supporting only incipient barrens. Estimates of the average cover of *C. rodgersii* barrens (Table 28) indicate the expected average for the east coast of Tasmania where urchins and at least incipient barrens occur currently (i.e. for rocky reef ~10-30 m depth between Eddystone Pt and Fortescue Bay).

Over the next decade all scenarios result in an increase in the extent of seaweed destruction by *C. rodgerii* in areas currently supporting intact seaweed beds or low-level incipient barrens. For scenarios with total catch quotas in the range of 200-240 t pa there is very little difference in the expected distribution of urchin barrens and size of urchin populations over the next 10 years. In this time frame, scenarios based on total catch in the range of 160-180 t pa realize a better outcome in terms of the expected extent of urchin barrens, but the difference to other scenarios based on larger TACs is small (Figs. 50-56, Table 28).

By 2032 the picture looks significantly more optimistic, with urchin numbers declining from the expected densities in 2021 for all scenarios in the range 160-240 t pa total catch. Not surprisingly, the smaller the total catch the larger is this effect, but there is no sharp non-linearity across the range of TACs considered. In short, urchin populations can be expected to increase over the next decade before they subsequently decline. However it needs to be recognized that these simulations do not take into account the hysteresis effect in the system. Given the hysteresis effect, any sites that develop into extensive barrens over the next decade (e.g. which can arbitrarily be defined as >50% barrens cover) are unlikely to recover in the manner predicted (Figs. 50-56) over 2021-2032.

These results suggest clearly that, within the bounds of these options as nominated feasible management scenarios, the most productive and sustainable long term outcome for the fishery in terms of least loss of habitat to urchin barrens would be to impose the most stringent measures it can cope with over the next decade (e.g. 160 t pa), with a view to increasing the TAC thereafter after recovery of lobster biomass.

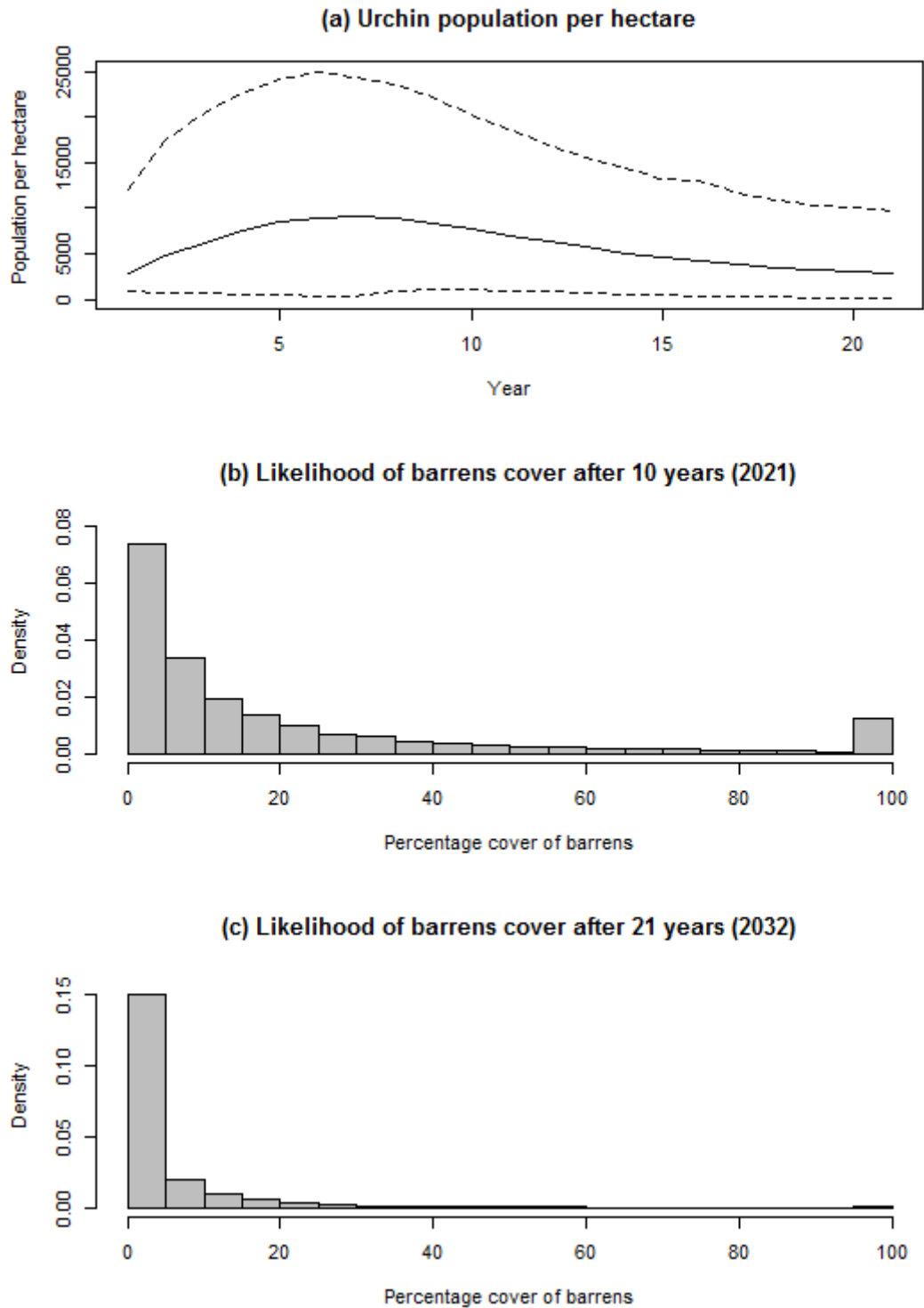


Figure 50. Predicted (a) *C. rodgersii* population size per hectare, and probability density distributions of the magnitude of *C. rodgersii* barrens at (b) 10 and (c) 21 years from present (2012) under the extreme scenario of **complete cessation of fishing** rock lobster in areas 1-3. In (a), the solid line is the mean predicted population, while dotted lines indicate the 95% confidence interval of the mean. Results are from Monte Carlo simulations of 5000 runs.

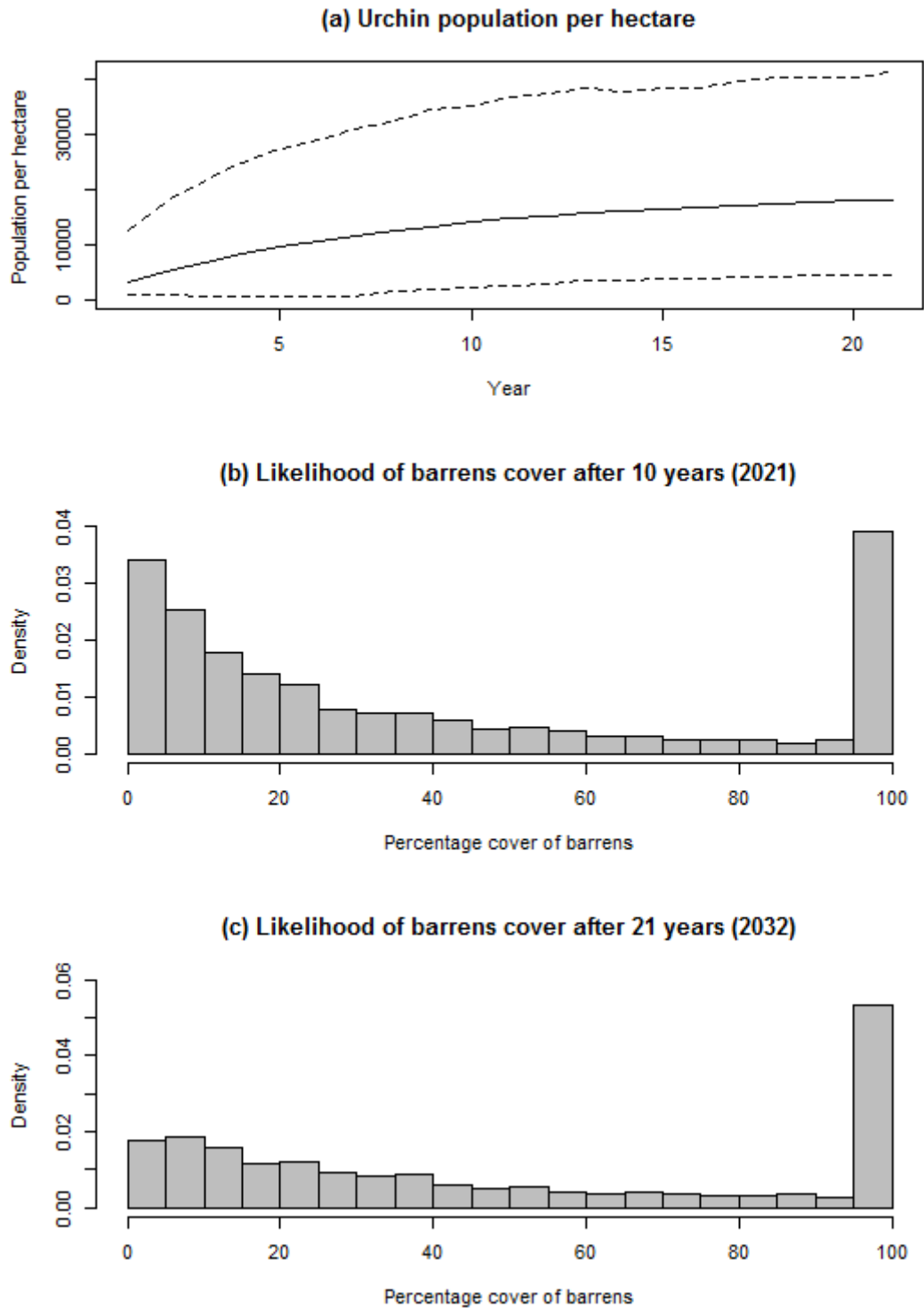


Figure 51. Predicted (a) *C. rodgersii* population size per hectare, and probability density distributions of the magnitude of *C. rodgersii* barrens at (b) 10 and (c) 21 years from present (2012) under ***status quo management*** of fishing rock lobster in areas 1-3. In (a), the solid line is the mean predicted population, while dotted lines indicate the 95% confidence interval of the mean. Results are from Monte Carlo simulations of 5000 runs.

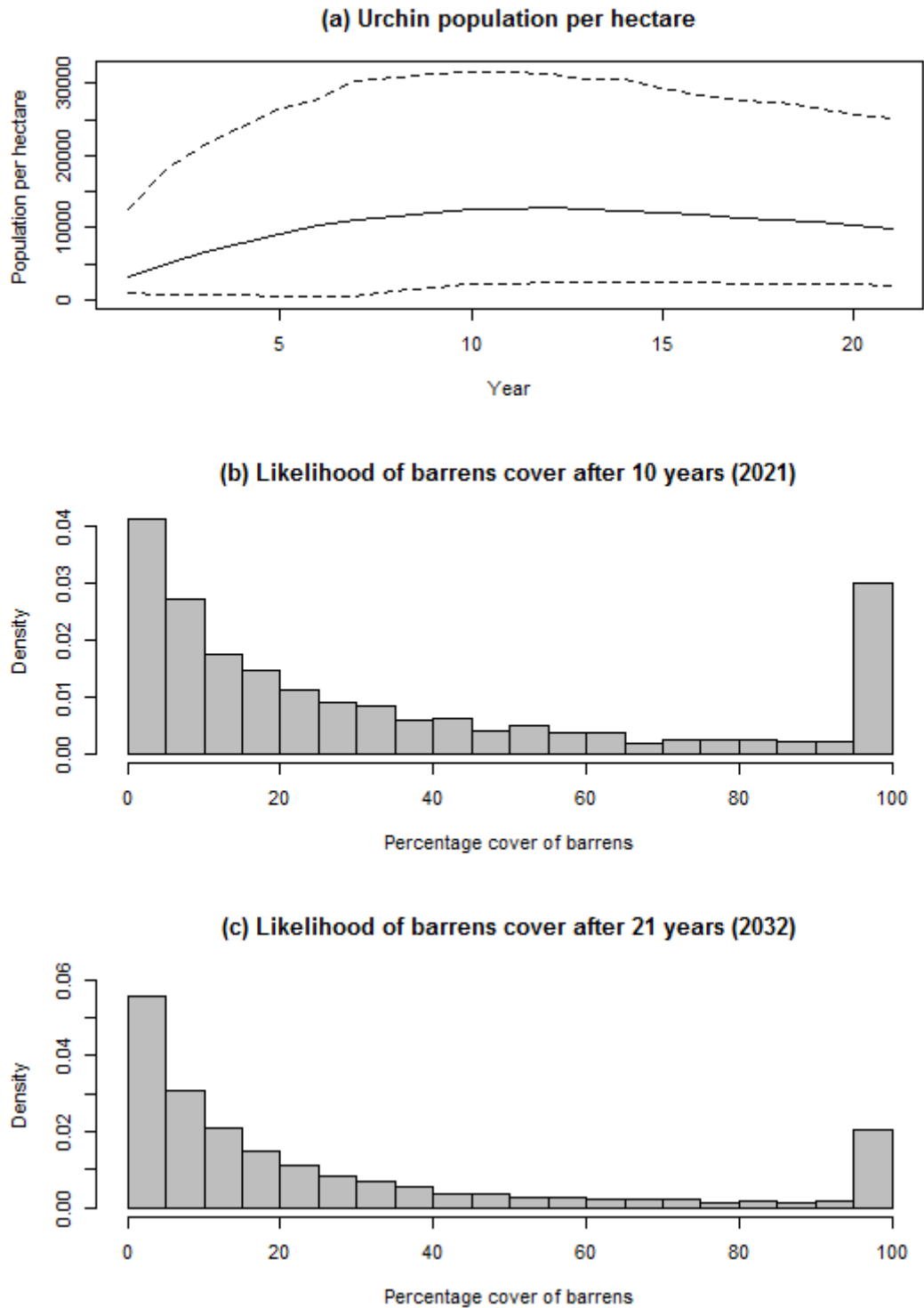


Figure 52. Predicted (a) *C. rodgersii* population size per hectare, and probability density distributions of the magnitude of *C. rodgersii* barrens at (b) 10 and (c) 21 years from present (2012) with a **total catch of 240 tonnes** p.a. rock lobster in areas 1-3. In (a), the solid line is the mean predicted population, while dotted lines indicate the 95% confidence interval of the mean. Results are from Monte Carlo simulations of 5000 runs.

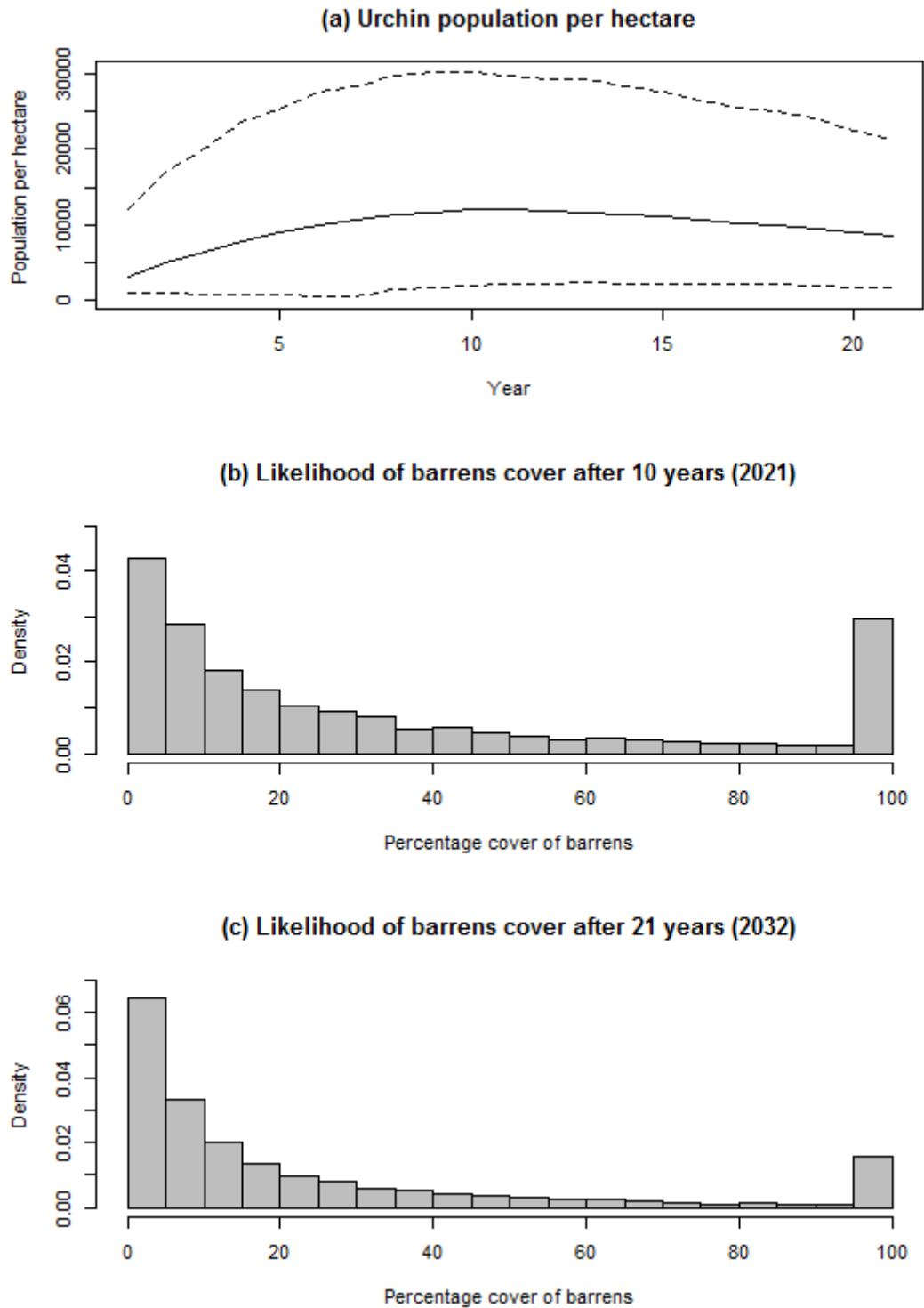


Figure 53. Predicted (a) *C. rodgersii* population size per hectare, and probability density distributions of the magnitude of *C. rodgersii* barrens at (b) 10 and (c) 21 years from present (2012) with a **total catch of 220 tonnes** p.a. rock lobster in areas 1-3. In (a), the solid line is the mean predicted population, while dotted lines indicate the 95% confidence interval of the mean. Results are from Monte Carlo simulations of 5000 runs.

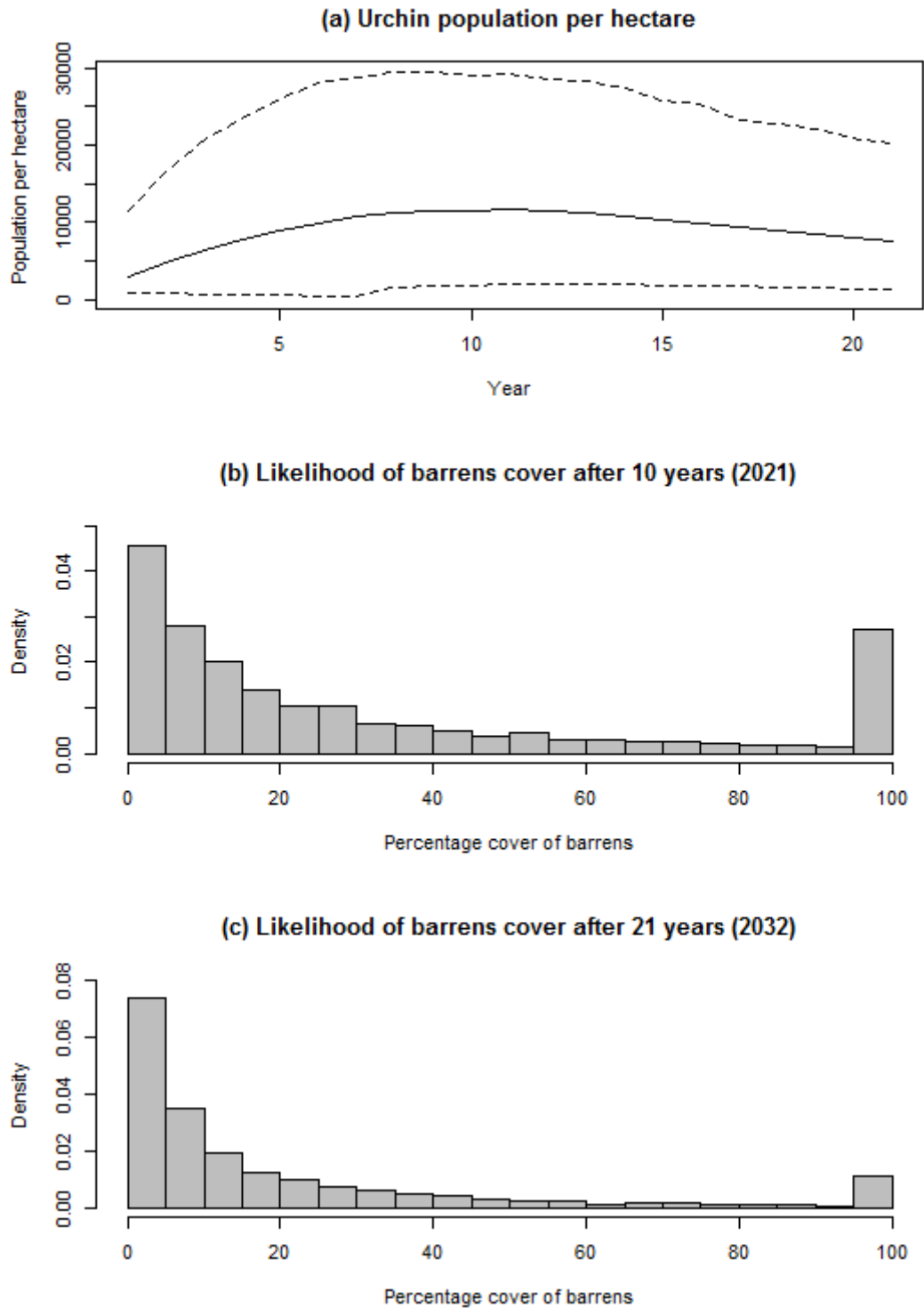


Figure 54. Predicted (a) *C. rodgersii* population size per hectare, and probability density distributions of the magnitude of *C. rodgersii* barrens at (b) 10 and (c) 21 years from present (2012) with a **total catch of 200 tonnes** per rock lobster in areas 1-3. In (a), the solid line is the mean predicted population, while dotted lines indicate the 95% confidence interval of the mean. Results are from Monte Carlo simulations of 5000 runs.

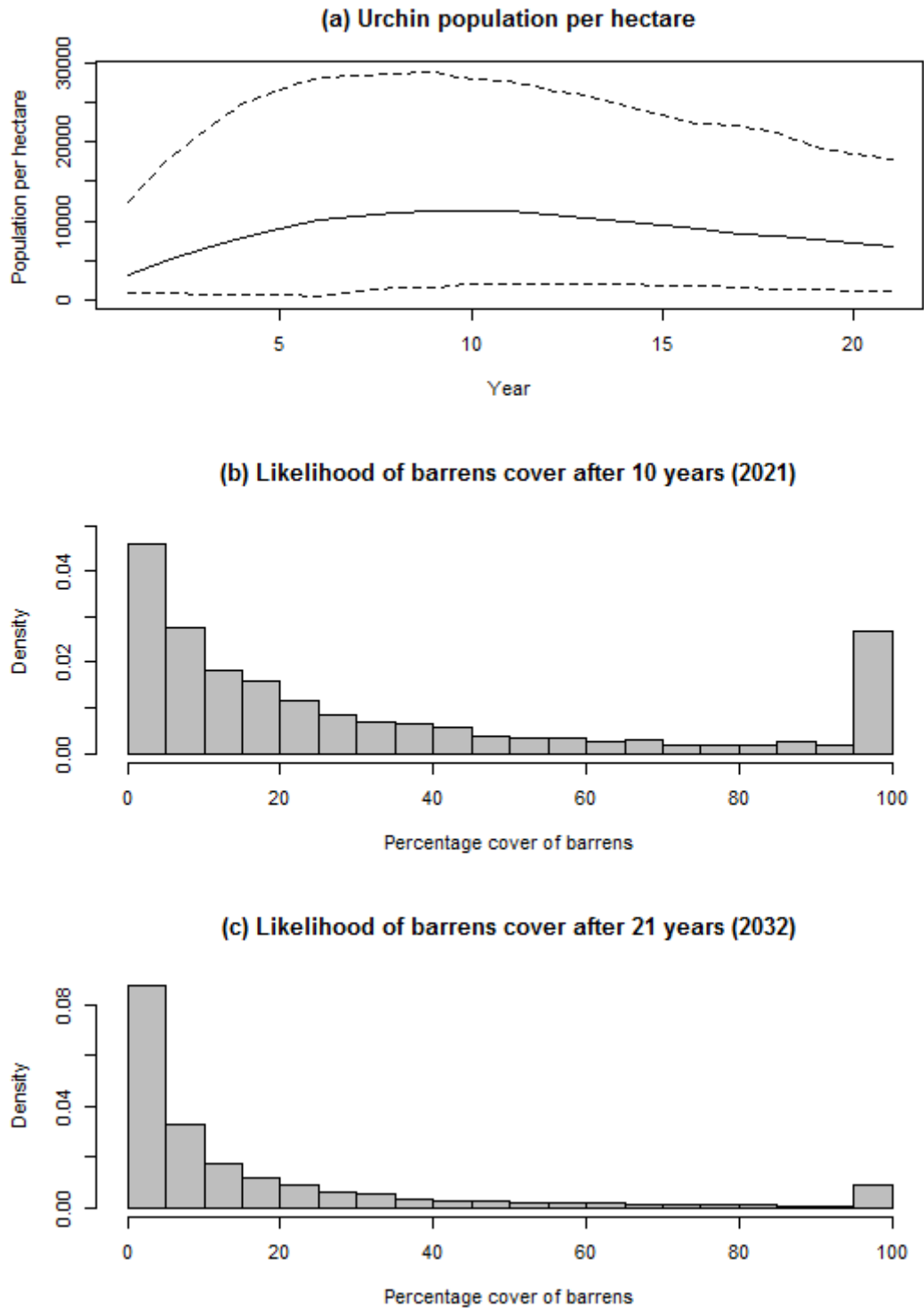


Figure 55. Predicted (a) *C. rodgersii* population size per hectare, and probability density distributions of the magnitude of *C. rodgersii* barrens at (b) 10 and (c) 21 years from present (2012) with a **total catch of 180 tonnes** pa rock lobster in areas 1-3. In (a), the solid line is the mean predicted population, while dotted lines indicate the 95% confidence interval of the mean. Results are from Monte Carlo simulations of 5000 runs.

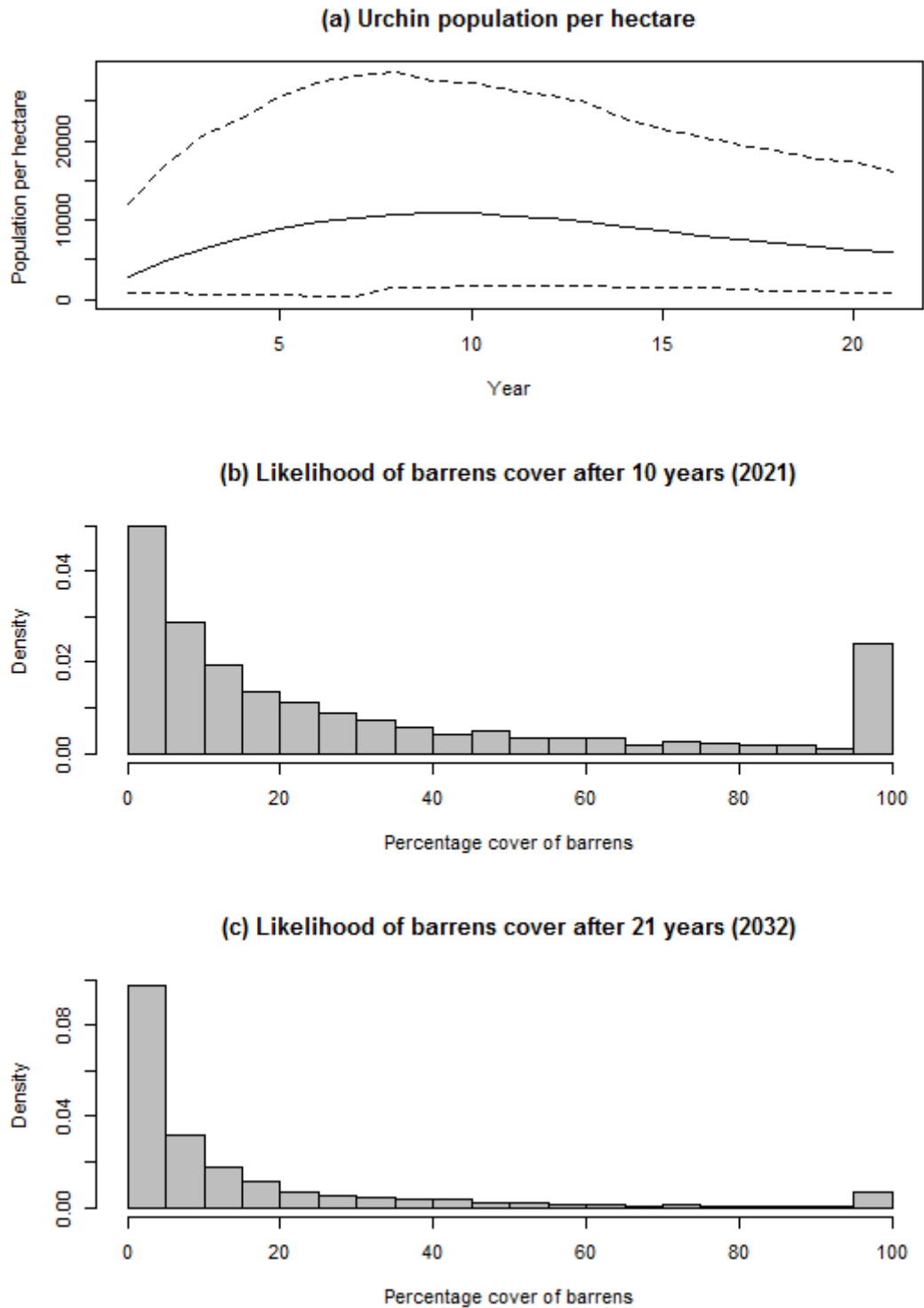


Figure 56. Predicted (a) *C. rodgersii* population size per hectare, and probability density distributions of the magnitude of *C. rodgersii* barrens at (b) 10 and (c) 21 years from present (2012) with a **total catch of 160 tonnes** pa rock lobster in areas 1-3. In (a), the solid line is the mean predicted population, while dotted lines indicate the 95% confidence interval of the mean. Results are from Monte Carlo simulations of 5000 runs.

Table 28. Estimates of the expected average cover of *C. rodgersii* barrens in 2021 and 2032 on the eastern Tasmanian coastline in the region where urchins and incipient barrens occur currently (i.e. for rocky reef ~10-30 m depth between Eddystone Pt and Fortescue Bay). The different scenarios for management of the rock lobster fishery apply to fishery areas 1-3 in eastern Tasmania (see Fig. 7).

Management Scenario for Rock Lobster Fishery (total catch)	Predicted mean % cover barrens 2021	Predicted mean % cover of barrens 2032
Cease fishing	21	5
160 tonnes total catch pa	30	15
180 tonnes total catch pa	31	17
200 tonnes total catch pa	32	20
220 tonnes total catch pa	34	24
240 tonnes total catch pa	35	27
Status-quo	39	49

For extensive barrens, the critical question is how quickly urchin numbers can be reduced to the point where seaweed recovery can commence, which occurs at an estimated threshold *C. rodgersii* density of no more than $\sim 0.25 \text{ m}^{-2}$. The simulations address this by comparing this threshold target with the predicted probability density of urchin density in 2021 and 2032 (Figs. 57-60).

None of the scenarios examined, including ceasing rock lobster fishing altogether, indicate that recovery of seaweed growth in areas currently supporting extensive barrens is likely within the time frame to 2032 if control of urchin populations relies solely on rebuilding rock lobster populations. Since there is very little difference in the predictions for scenarios of TACs of 160-240 t pa in the context of rehabilitation of extensive barrens, results of estimates for intermediate caps between these limits are not presented. These results are in close agreement with the TRITON ecosystem model, which showed that minimum recovery times from extensive barrens are of the order of 3 decades, even with ceasing lobster fishing altogether, and even then, the likelihood of recovery is relatively small. These results emphasise the hysteresis from a management perspective, i.e. in keeping with the results of the TRITON model and of our large scale translocations of lobsters to North Bay and Elephant Rock, it is clear that management responses to rebuild lobster biomass that will greatly reduce the risk of further barrens formation in eastern Tasmania are unlikely to have any material effect in effecting recovery of seaweed cover on extensive barrens.

Overall, the results of the population based modelling are in close agreement with field observations at the reserve sites, and with results of the independent TRITON ecosystem based model (which was developed using a completely different conceptual basis to the population based approach used here). All three approaches show that (1) rebuilding populations of large predatory capable lobsters, within the parameters of acceptable and feasible scenarios canvassed by rock lobster fishery managers and other stakeholders, is in most areas likely to be effective in preventing development of extensive barrens from a starting point of an intact seaweed bed or incipient barrens, but that (2) rehabilitating extensive barrens based solely on predatory control of urchins by rock lobsters will require much longer time frames and have a lower likelihood of success.

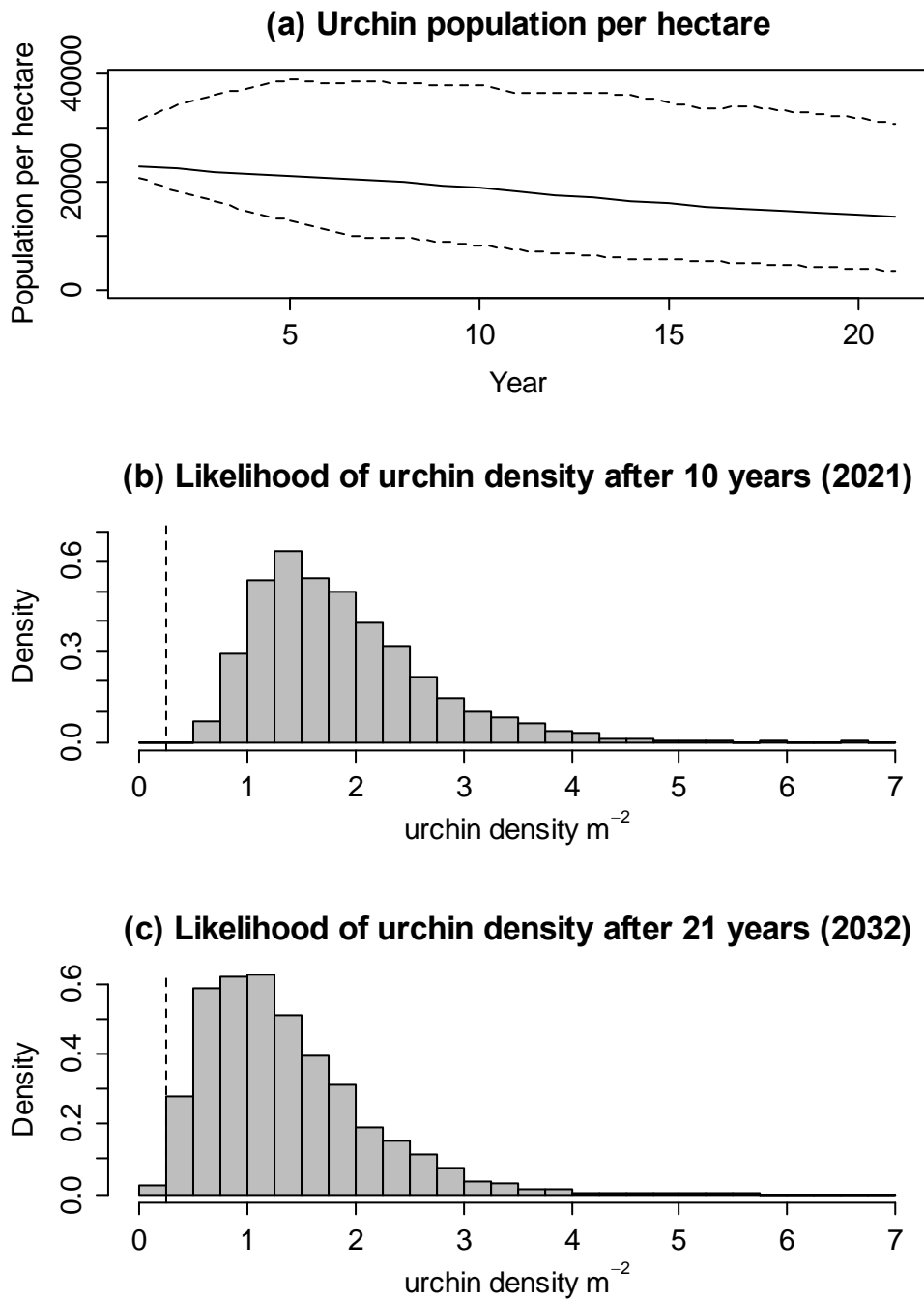


Figure 57. Predicted (a) *C. rodgersii* population size per hectare, and probability density distributions of *C. rodgersii* density on extensive barrens at (b) 10 and (c) 21 years from present (2012) assuming **complete cessation of fishing** rock lobster in areas 1-3. In (a), the solid line is the mean predicted population, while dotted lines indicate the 95% confidence interval of the mean. In (b) and (c) the vertical dotted line shows the estimated threshold *C. rodgersii* density for re-establishment of seaweed cover on extensively overgrazed reefs. Results are from Monte Carlo simulations of 5000 runs.

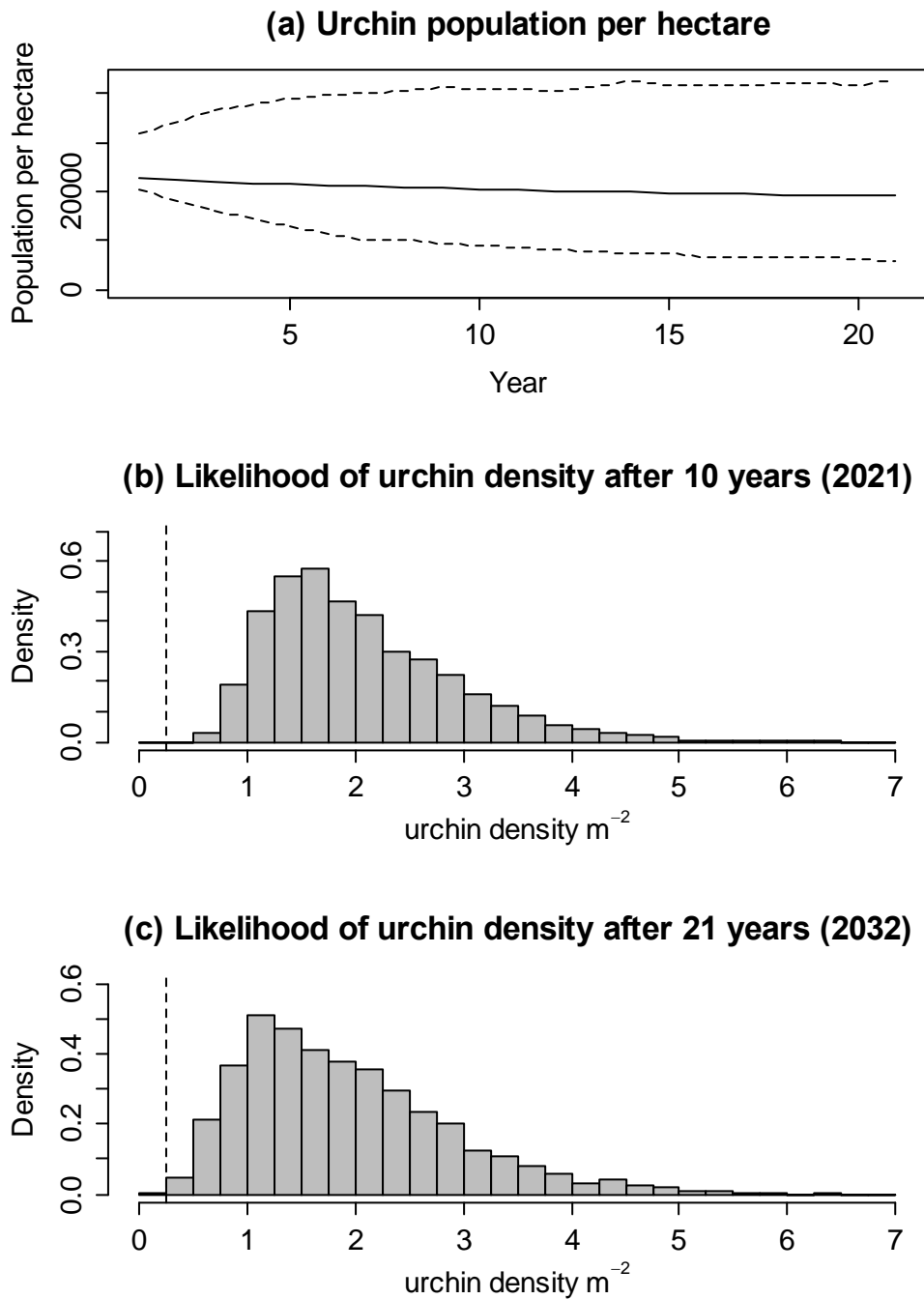


Figure 58. Predicted (a) *C. rodgersii* population size per hectare, and probability density distributions of *C. rodgersii* density on extensive barrens at (b) 10 and (c) 21 years from present (2012) assuming management of rock lobster in areas 1-3 with *status quo* settings. In (a), the solid line is the mean predicted population, while dotted lines indicate the 95% confidence interval of the mean. In (b) and (c) the vertical dotted line shows the estimated threshold *C. rodgersii* density for re-establishment of seaweed cover on extensively overgrazed reefs. Results are from Monte Carlo simulations of 5000 runs.

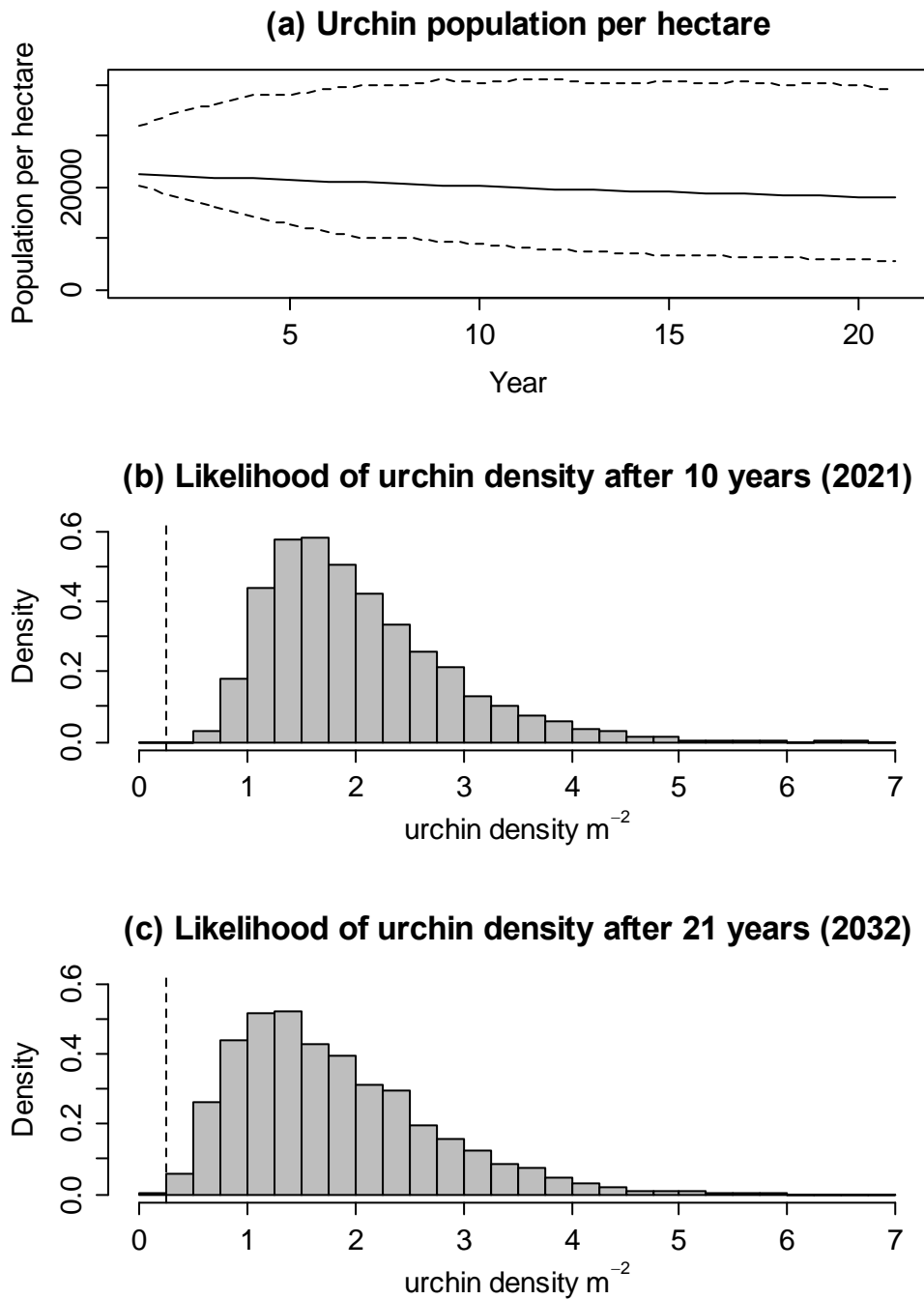


Figure 59. Predicted (a) *C. rodgersii* population size per hectare, and probability density distributions of *C. rodgersii* density on extensive barrens at (b) 10 and (c) 21 years from present (2012) with a total allowable catch of rock lobster in areas 1-3 of **240 t pa**. In (a), the solid line is the mean predicted population, while dotted lines indicate the 95% confidence interval of the mean. In (b) and (c) the vertical dotted line shows the estimated threshold *C. rodgersii* density for re-establishment of seaweed cover on extensively overgrazed reefs. Results are from Monte Carlo simulations of 5000 runs.

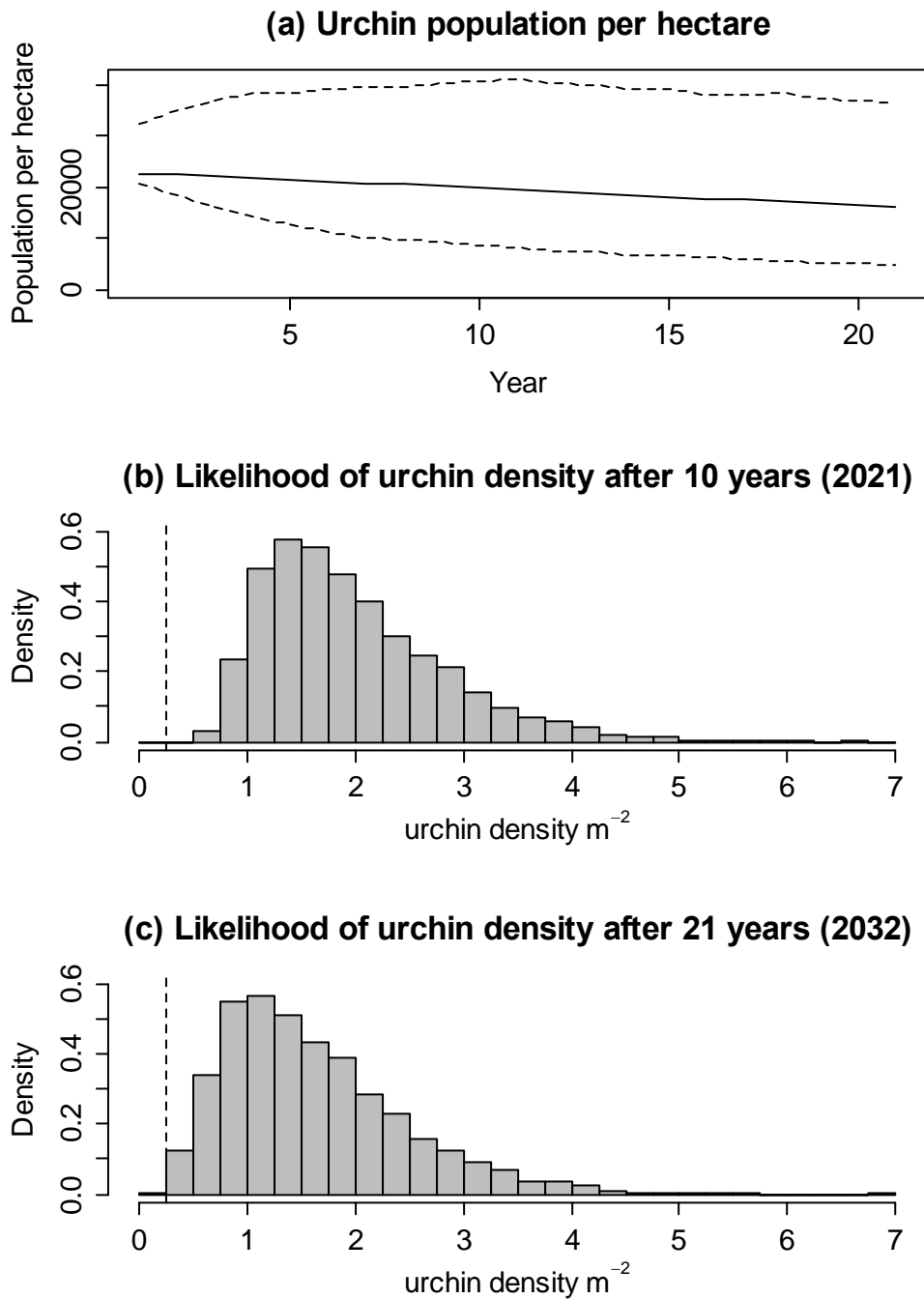


Figure 60. Predicted (a) *C. rodgersii* population size per hectare, and probability density distributions of *C. rodgersii* density on extensive barrens at (b) 10 and (c) 21 years from present (2012) with a total allowable catch of rock lobster in areas 1-3 of **160 t pa**. In (a), the solid line is the mean predicted population, while dotted lines indicate the 95% confidence interval of the mean. In (b) and (c) the vertical dotted line shows the estimated threshold *C. rodgersii* density for re-establishment of seaweed cover on extensively overgrazed reefs. Results are from Monte Carlo simulations of 5000 runs.

Conclusions

In many respects the ecosystem-level TRITON model and single species modelling provide similar outcomes. They both show that, at coastwide scales, rebuilding populations of predatory capable (>140 mm CL) rock lobsters to minimize risk of extensive urchin barrens forming will be much easier and occur much more quickly (and thus be much less costly) than rehabilitating extensive barrens once they form. Rehabilitation of extensive *Centrostephanus rodgersii* barrens will require a sustained and massively expensive intervention, and is likely to require at least 2-3 decades if dependent on predatory control. Both the TRITON model (Figs. 42, 45) and single species rock lobster model (current stock assessment model; Table 27) indicate that establishing an upper size limit on its own will have a relatively small effect, and that reducing lobster catch on the east coast is fundamental to rebuilding stocks of large lobsters, and thus fundamental to rebuilding resilience of kelp bed systems in eastern Tasmania in the face of the threat posed by *C. rodgersii*.

The principle difference in the TRITON model and the single species population model currently used as the basis of rock lobster stock assessments is in their prediction of future rock lobster catches dependent on fishing mortality. TRITON predicts notably lower catches than the rock lobster stock assessment model (Fig. 45) because TRITON accommodates the potential for and consequences of destructive grazing of seaweed beds by *C. rodgersii*. This outcome highlights the need for lobster fishery management to better account for the pivotal ecological role of lobsters in this system, as managers are currently attempting to do, and the model provides guidance to revise key target points accordingly.

TRITON also indicates that a combination of reduced lobster fishing and harvesting or culling urchins will be most effective at reducing urchin densities, particularly on extensive barrens. In this context, further development of the fledgling commercial harvest of *C. rodgersii*, and cost-benefit analysis of targeted culling by divers or use of quicklime (Bernstein & Welsford 1982; Wilson and North 1983) is warranted.

It seems clear that (1) imposing spatial management of the rock lobster fishery (i.e. implementing a separate total allowable catch for the east coast region), and (2) setting achievable and acceptable reductions in the total allowable catch of rock lobster on the east coast will significantly mitigate ongoing formation of extensive urchin barrens on reefs currently supporting intact seaweed cover or incipient barrens within a 20 year time frame. Perhaps most importantly, the modelling suggests that this can be achieved while maintaining a viable – albeit initially reduced – rock lobster fishery in eastern Tasmania. However, it is also clear that the best outcome in terms of minimizing risk of ongoing barrens formation, and thus providing an optimal long term outcome for the fishery, will be to reduce catch in eastern Tasmania as quickly as possible and by as much as can be tolerated, with a view to increasing the total allowable catch again once stocks rebuild. Given that rates of fishing mortality to position the fishery at maximum economic yield also achieve high levels of ecological stability of the seaweed beds on which the fishery depends, there is strong imperative to work toward this target. This approach would represent ‘world’s best practice’ for ecosystem-based reef fishery management, and thus present a strong marketing opportunity.

Our results from the large scale translocation of lobsters to incipient barrens, and of the TRITON and single species modelling, are entirely consistent in demonstrating that rebuilding stocks of large lobsters will greatly assist to rebuild the resilience of seaweed beds to the threat of *Centrostephanus rodgersii* in eastern Tasmania. Arguably, the most challenging element in attempting this stock rebuilding in eastern Tasmania – and which is not addressed in this study – is to limit the harvest by the recreational fishery to ensure that as legal sized biomass recovers there is not a compensatory increase in harvested biomass from the recreational sector. Given the urgency of the rebuilding task and what is at stake, this question warrants immediate attention.

8. BENEFITS and ADOPTION

This work provides clear directions for management to consider in responding to the threat of *C. rodgersii* continuing to overgraze seaweed beds on shallow rocky reefs in eastern Tasmania, with concomitant deleterious effects on biodiversity, productivity and the important abalone and rock lobster fisheries.

Throughout the conduct of the project, results, progress and implications were communicated regularly to the abalone and rock lobster fishery industry, recreational fishing and conservation peak bodies, fishery managers, scientists, and to the general public at local, national and international levels, as follows (numbers in parentheses refer to the number of presentation 'events', amounting to a total of 100 presentations, not including the published scientific papers):

Presentations to the Project Steering Committee (6)

Presentations and briefings to fishing- and management-related stakeholders:

- Tasmanian Abalone Council (5)
- Tasmanian Rock Lobster Fisherman's Association (3)
- Tasmanian Seafood Industry Council (4)
- Tasmanian Crustacean Fisheries Advisory Committee (4)
- Tasmanian Abalone Fishery Advisory Committee (1)
- Tasmanian Recreational Fisheries Advisory Committee (2)
- Derwent Estuary Program (1)
- TAFI and IMAS research overviews (5)
- *Centrostephanus* reference group (1)
- Articles in *Fishing Today* (3)
- Mail out to all registered recreational fishers and professional rock lobster fishers in Tasmania

Presentations to Ministers, other parliamentary delegates and parliamentary forums (3)

Presentations to the public:

- Public forums (5)
- Radio interviews (local and national) (22)
- Television news segments, local and national (6)
- Television features (2)
- International television (4)
- Newspaper (local and national) (4)

Presentations to the scientific community:

- International conferences (8)
- Invited international lectures (5)
- Invited national conferences and workshops (6)

The findings of the present work have been influential in the deliberations which have led to the recent approval by the Minister for Fisheries to, for the first time, implement spatial management of the rock lobster fishery in Tasmania including a reduced total allowable catch for the east coast region with the express purpose of rebuilding stocks of rock lobster in eastern Tasmania. This recommendation has the support of the fishery managers, key representatives of the rock lobster fishing industry and recreational fishing interests.

9. FURTHER DEVELOPMENT

While this project has provided clear answers to the key questions it set out to address, greater precision in some of the predictions and in identifying key thresholds and targets will deliver greater certainty to management decisions and outcomes, and to their cost effectiveness. Key areas where further effort is warranted are outlined below, in order of priority.

1. Much of the recommendations emanating from this work are underpinned by the modelling. While these models are 'fit-for-purpose', relatively sophisticated and have used the most up-to-date information, they are nonetheless simplifications of the natural systems they hope to represent. The only way to properly validate these models and improve their parameterisation is to ensure that they are based on, and compared with, empirical observation. To a large extent this critical information and empirical benchmark relies on the dynamics unfolding at the two scientific reserves (at North Bay and Elephant Rock) declared for the purposes of the project. Given the time scales of response predicted from the models, it is vital that the experiments commenced in these areas are continued into the medium term. Maximum benefit of the considerable investment in this work thus far will only be achieved by maintaining and monitoring (preferably on an annual basis) the closed areas over the next 5 years.
2. It is clear that the most effective response to the threat of ongoing formation of *C. rodgersii* barrens in eastern Tasmania will involve a diversity of responses, among them harvesting and/or culling of urchins. Liaison with and monitoring of the effects of the developing *C. rodgersii* harvest industry in Tasmania, and work to assess the cost effectiveness and to define optimal allocation of effort in culling urchins, either by divers or alternative approaches such as application of quick lime (Bernstein & Welsford 1982; Wilson and North 1983), is warranted. Arguably there is some urgency to progress this work.
3. A critical parameter in model predictions is the threshold density to which urchins on extensive barrens need to be reduced to allow regrowth of seaweeds. Currently there is no empirical work to identify this threshold, and the estimate is obtained from the TRITON model. We strongly urge undertaking experiments on extensive urchin barrens in which urchins are maintained in experimental plots across a range of densities to identify this threshold and validate the estimate from TRITON. It will be important to monitor urchin behaviour in a manner similar to that undertaken by Flukes et al. (2012) to determine any density-dependent compensatory changes in grazing behaviour as urchin density is reduced.
4. Estimating predation rates of lobsters on urchins by following temporal trajectories of predatory capable lobsters and urchin populations at particular sites requires very considerable effort, expense and time commitment. Model predictions depend entirely on this parameter. It is far easier and cheaper to obtain these estimates from DNA analysis of lobster faecal material. However, as we have shown in this study, lobsters have the possibility to ingest urchin DNA from sources other than direct predation, and there are subjective decisions in interpreting the output from the qPCR procedure. It is possible however – and would be worthwhile – to estimate and calibrate these effects so that reliable estimates of absolute predation rates can be obtained using the molecular approach. This would enable space-time variability in predation to be better quantified, and thus improve the predictions from modelling.
5. The TRITON model is currently developed for local implementation. There is clearly potential to use TRITON as the basis of a spatially explicit regional model for eastern Tasmania to predict system dynamics – including lobster catch and risk of barrens formation – at coastal scales of 10^4 - 10^5 m.

10. PLANNED OUTCOMES

The intended outcome of the work is that management authorities in Tasmania (i.e. the Department of Primary Industries, Parks, Water and Environment) will consider the results and recommendations of the work in developing and implementing strategies and policy to minimise loss of productive reef from overgrazing by *C. rodgersii* in eastern Tasmania. Thus, the ultimate outcome is to provide a sure footing for the sustainability of the abalone and rock lobster industries in particular, but also several smaller fisheries, that are dependent on shallow reefs by ensuring that these areas continue to support dense seaweed cover, and thus maintain their ecological integrity, biodiversity and productivity.

As already mentioned, results from this project have been considered and contributed significantly to the the Minister for Fisheries recent approval to, for the first time, introduce spatial management in the Tasmanian rock lobster fishery and a reduced total allowable catch for the east coast region. There are also compelling economic and stock productivity reasons to reduce catch towards rebuilding rock lobster biomass in eastern Tasmania.

We anticipate that the results and recommendations from this report will be considered carefully in ongoing discussions among managers and stakeholders to determine the total allowable catch of rock lobsters in eastern Tasmania. To this end the PI has agreed to release the population dynamics model for *C. rodgersii* to fisheries scientists informing management, which predicts urchin population dynamics and the likely extent of urchin barrens for a given temporal trajectory of predatory capable rock lobsters. This modelling framework will be used to update predictions against updated estimates of rock lobster dynamics in the region, which can then be considered by the relevant Fisheries Advisory Committee and departmental managers in setting future TACs for the industry.

11. CONCLUSION

The sum total of the work points to a number of clear conclusions:

- Implementing management responses to minimise prevention of extensive overgrazing by *Centrostephanus rodgersii* in the first place is far more tractable and achievable than rehabilitating extensive barrens once they form; 'a little prevention is worth a vast amount of cure'. Once extensive barrens form, if recovery occurs at all, it is likely to be of the order of at least 3 decades if dependent on rebuilding populations of large predatory lobsters alone, and it will require a drastic and expensive management response.
- Reducing the likelihood of incipient barrens developing into extensive barrens by managing rock lobster populations is feasible, and reducing the catch of lobsters on the east coast while maintaining a viable commercial fishery emerges as a suitable means to rebuild populations of predatory capable lobsters.
- Managing catch of lobsters in eastern Tasmania to adequately rebuild stocks of large (>140 mm CL) lobsters will greatly assist to both rebuild the resilience of seaweed beds to the threat of *C. rodgersii* in eastern Tasmania, and shift the industry closer to its maximum economic yield.
- Implementing an upper legal size limit in the rock lobster fishery will, on its own, have relatively little effect in increasing populations of large (>140 mm CL) lobsters. While imposing an upper size limit *together* with reducing catches is the most effective way to rebuild biomass of large lobsters, this approach may be more costly to the fishery than restricting catch on its own.
- Catch limits of rock lobsters in eastern Tasmania likely to be palatable to the industry won't prevent extensive barrens from developing in some areas.
- Acknowledging that reducing the lobster catch in eastern Tasmania to levels that may prove acceptable to the industry will significantly mitigate (but not universally prevent) ongoing development of extensive barrens, the best medium and long term outcomes for both the state of shallow reefs and for the medium- and long-term sustainability of the fishery will be realized by immediately reducing the lobster catch by as much as is tolerable with a view to increasing the allowable catch once lobster biomass has recovered.
- Despite that extensive barrens can readily support large populations of large predatory capable lobsters (but not small ones), rehabilitation of seaweed cover on extensive barrens is likely to need additional intervention through harvesting and /or culling of urchins if results are desired within 3 decades.
- The most effective way to reduce the risk of ongoing barrens formation is to simultaneously rebuild populations of predatory capable lobsters and harvest or cull urchins. Attention to developing the harvest industry and quantifying the cost effectiveness of culling by divers is warranted. Abalone divers should be encouraged to cull urchins while fishing for abalone, particularly at high-yielding sites.
- Further exploration of means to reduce urchin populations on extensive barrens, e.g. by applying quicklime, is warranted.
- Maintaining management of the lobster fishery in eastern Tasmania at *status quo* settings will inevitably realize significant ongoing destruction of seaweed beds by urchins and thus significantly reduced catches in key fisheries into the future.

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APPENDIX 1: Intellectual Property

There are no overriding intellectual property issues.

APPENDIX 2: Staff

The following staff contributed to the project:

1. Institute for Marine and Antarctic Studies (IMAS), University of Tasmania

- Prof Craig Johnson (lead PI)
- Dr Scott Ling
- Dr Craig Sanderson
- Dr Neville Barrett
- Kylie Cahill
- Rauri Colquhoun
- Juan (Gabriel) Dominguez
- Prof Graham Edgar
- David Faloon
- Dr Stewart Frusher
- Dr Caleb Gardner
- Dr Klaas Hartmann
- Justin Hulls
- Louisa Lyall
- Chris McKinley
- Mike Porteus
- Adam Stephens
- Simon Talbot
- Dr Simon Wotherspoon

2. Other University of Tasmania staff

- Richard Holmes

3. Staff from other institutions

- Dr Jeff Dambacher (CSIRO)
- Dr Malcolm Haddon (CSIRO)
- Dr Simon Jarman (Australian Antarctic Division)
- Dr Rich Little (CSIRO)
- Dr Jean-Christophe Soulié (CIRAD, France)

The following IMAS students at the University of Tasmania were engaged on the project:

- Emma Flukes (Honours program)
- Dr Martin Marzloff (PhD program)
- Kevin Redd (PhD program)

APPENDIX 3: Forming sea urchin barrens from the inside-out: an alternative pattern of overgrazing.

Here is presented the full technical account of the approach, analysis and interpretation of the component of the project that examined *Centrostephanus rodgersii* behaviour to obtain a clear understanding of the process of barrens habitat formation and the likely effectiveness of culling sea urchins at local spatial scales. The work has been published in an international peer-reviewed journal, and can be cited as:

Flukes, E.B., Johnson, C.R. & Ling, S.D. (2012). Forming sea urchin barrens from the inside-out: an alternative pattern of overgrazing. *Marine Ecology Progress Series*, 464: 179-194.

Abstract

Overgrazing by sea urchins on temperate reefs can effect a phase shift from macroalgal beds to sea urchin 'barrens' habitat largely devoid of seaweeds. Existing models of barrens formation are derived largely from observations of stronglycentrotid urchins, which typically show a behavioural shift from cryptic feeding to exposed grazing fronts that move through and 'mow down' macroalgal beds. Foraging by the temperate diadematid urchin *Centrostephanus rodgersii* triggers a similar transition from intact macroalgal bed to widespread barren grounds, but does not appear to involve a behavioural shift. Fine-scale foraging movements were observed using time-lapse photography across the urchin's range-extension region and described with respect to a random walk model. Foraging was highly nocturnal, with individuals homing strongly to available crevices. *In situ* monitoring of tagged individuals suggests strong fidelity to and thus high stability of barren patches, while similar behavioural patterns across habitat types representing a gradient of foraging intensities indicate no behavioural shift associated with overgrazing. Laboratory experiments showed that *C. rodgersii* lacks a directional chemosensory response to either macroalgae or conspecifics. Combined evidence suggests a model of barrens formation fundamentally different to the well-established 'feeding front' model, with formation of widespread barrens by *C. rodgersii* occurring from the 'inside-out' via growth and coalescence of small barrens patches that form within macroalgal beds as a result of additive localised grazing radiating from crevice shelter. Regulation of urchin density at the spatial scale of individual barrens patches is proposed as a viable option to manage the formation of widespread barrens habitat within the urchin's recent range-extension to eastern Tasmania.

Introduction

Marine ecosystems worldwide are subject to increasing anthropogenic stress, lowering their resilience to 'catastrophic shifts' (after Scheffer et al. 2001) in ecological structure and function (Beisner et al. 2003). Grazing by herbivores is frequently implicated as a driver of phase shifts in marine environments via the removal of primary producers and biogenic habitat. In shallow temperate waters, sea urchins are one of the most dominant and conspicuous habitat-structuring taxa on rocky reefs, particularly through their propensity for intensive grazing that triggers a shift from dense macroalgal beds to 'barrens' habitat largely devoid of fleshy macroalgae (e.g. Lawrence 1975, Bernstein & Mann 1982, Harrold & Reed 1985, Andrew & Underwood 1989, Johnson et al. 2005, Johnson et al. 2011). Sea urchin barrens are characterized by decreased habitat complexity, biodiversity and productivity relative to adjacent seaweed beds (Chapman 1981, Himmelman et al. 1983, Tuya et al. 2005, Ling 2008). Unlike terrestrial herbivores that frequently overgraze their food, sea urchins are capable of maintaining high density populations on barrens by switching to alternative food sources including microalgae, non-geniculate coralline algae, drift algae (Johnson et al. 1981) and invertebrate material (Ling 2008). The transition to barrens habitat is particularly problematic because it represents a catastrophic phase shift between alternative stable states with hysteresis (e.g. Ling et al. 2009a), requiring extensive reductions in sea urchin densities for kelp beds to recover (Harrold & Reed 1985, Carpenter 1990).

Few studies have employed an experimental approach to elucidate the mechanism of grazing dynamics leading to the creation of barrens habitat. Among these, most have focussed on species of sea urchins in the family Strongylocentrotidae (e.g. Mattison et al. 1977, Dean et al. 1984, Dumont et al. 2007, Lauzon-Guay & Scheibling 2007b, Feehan et al. 2012). This focus in research is due in part to the wide geographical distribution of strongylocentrotids and their close proximity to northern hemisphere researchers, in combination with a spectacular and highly conspicuous mode of overgrazing that involves the formation of three-dimensional 'feeding fronts' at the interface between kelp bed and barren habitat. Manifestation of this phenomenon appears to coincide with a switch in behaviour from low-impact sedentary and / or cryptic foraging to destructive motile and exposed feeding aggregations (e.g. Harrold & Reed 1985). The likelihood of barrens formation is therefore usually associated with complex behaviour involving threshold densities, and this pattern has been widely accepted and generalised across sea urchin taxa (e.g. Mattison et al. 1977, Dean et al. 1984, Lauzon-Guay & Scheibling 2007). Our casual observations over several thousand person hours of diving across hundreds of kilometres of coastline in Tasmania indicate that *C. rodgersii* does not form grazing fronts in creating extensive sea urchin barrens, but that it forms relatively small patches which can eventually become sufficiently numerous to grow, coalesce and form extensive areas of barrens habitat. In this paper we identify behaviour consistent with our general observation of forming barrens habitat from the 'inside out' without the formation of grazing fronts. These findings indicate that well-established models of barrens formation do not apply universally across all systems and sea urchin taxa.

The role played by the diadematid sea urchin *Centrostephanus rodgersii* in structuring shallow rocky reef communities is unparalleled by any other benthic herbivore in south eastern Australia (reviewed by Andrew & Byrne 2001, Johnson et al. 2005, Johnson et al. 2011). Throughout the species' historical range in New South Wales (NSW) it maintains widespread and persistent barrens habitat across approximately 50% of all near-shore rocky reef (Andrew & O'Neill 2000). In recent decades the sea urchin has extended its range southward to Tasmania, driven primarily by increased poleward penetration of the East Australian Current (Johnson et al. 2005, Ling et al. 2009b), and establishment of reproductively viable populations in Tasmanian waters has further facilitated its spread and establishment (Johnson et al. 2005, Ling et al. 2008, Banks et al. 2010). Widespread barrens are now found extensively in the northeast of Tasmania, with a gradient of decreasing grazing intensity with latitude manifesting as patchy barrens decreasing in size and frequency down the east coast of Tasmania (Johnson et al. 2005, 2011). Continued barrens formation throughout the range-extension region in Tasmania poses a major threat to local biodiversity (Ling 2008) and to the lucrative reef-based abalone and rock lobster fisheries dependent on macroalgal production and habitat (Johnson et al. 2011). Importantly, removal of predatory spiny lobsters from Tasmanian rocky reefs via commercial and recreational fishing has reduced the resilience of kelp beds, increasing the risk of

catastrophic shift to widespread barren habitat (Ling et al. 2009a).

In common with other diadematid sea urchins (Nelson & Vance 1979, Lissner 1980, 1983), divers observe *C. rodgersii* to shelter in crevices during the day and emerge to forage at night (reviewed by Andrew & Byrne 2007). In Tasmania, *C. rodgersii* within dense macroalgal beds graze discrete patches surrounding their crevices to form local barren patches, termed 'incipient barrens' (Johnson et al. 2005). Formation of widespread barrens occurs more frequently on boulder substratum where localised shelters are abundant, although barrens may also form on featureless flat-rock substrata (Johnson et al. 2005, Ling & Johnson 2012) which sea urchins will graze from nearby rudimentary 'shelter' when all available crevices are occupied or persist exposed on flat rock surfaces throughout the entire diel cycle (e.g. Andrew & O'Neill 2000). The availability of crevice structure has been shown to mitigate vulnerability of *C. rodgersii* to predation (Ling & Johnson 2012), with such crevice dependency found to influence the sea urchins grazing patterns to the extent that Andrew (1993) suggested that availability of crevices for shelter within kelp beds is a pre-requisite condition for barren formation. Thus the development from incipient through extensive barrens on boulder substratum and finally to widespread barrens habitat on extensive areas of flat rock represents an increasing gradient of foraging intensity that is effectively spatially mapped out along the urchin's recent range-extension region in eastern Tasmania. The prevalence of incipient barrens on this coast therefore represents a crucial point in the initial transition from kelp bed to widespread barren habitat (Johnson et al. 2005, Ling et al. 2009a). Thus, isolating the mechanisms underpinning the dynamics of these patches is likely to be of key importance in understanding the phase shift caused by *C. rodgersii*.

This study explores movement of *Centrostephanus rodgersii* and its patterns of habitation persistence within incipient barren patches to infer foraging dynamics and thus the likely mechanisms by which these small-scale features form, grow and ultimately develop into widespread barrens. We describe (1) spatial and temporal patterns in foraging behaviour on three different types of barrens habitat representing a gradient in foraging intensity across the sea urchins' range-extension region in eastern Tasmania; (2) the extent of fidelity of sea urchins to individual barrens patches and how per capita grazing impact scales with increasing barrens patch size; and (3) sea urchin responses to chemosensory stimuli characteristic of patch boundaries. We assess whether incipient barren patches represent a series of largely independent local patches in a seaweed bed or a mosaic of patches interconnected by widely ranging sea urchins routinely moving among patches, and thus whether targeted management of patches can be used to limit their further expansion and ultimately the formation of widespread and ecologically undesirable barrens habitat.

Methods

Spatial and temporal patterns of movement across range extension region

Fine-scale movement of *Centrostephanus rodgersii* on rocky reefs in eastern Tasmania was assessed using time-lapse photography between November 2009 and February 2010 across a number of different sites with similar environmental and exposure regimes. These sites were chosen specifically for the type of barrens habitat they contained, with targeted monitoring carried out in three distinct habitat types: widespread barrens (grazed areas $> 10^4$ m²) composed of flat rock; widespread barrens composed of boulders; and incipient barrens (grazed patches 10^0 - 10^1 m²) representing the north-to-south gradient of decreasing grazing intensity across the sea urchin's range-extension region (Fig. A3.1). Each monitored reef was characterised by moderate topographic relief reaching a maximum depth of 12-16 m, with a macroalgal canopy (where present) dominated by the laminarian *Ecklonia radiata* and furoid *Phyllospora comosa*. Movement was recorded over 15 different nights with time-lapse sequences using Nikon D200 digital SLR and Pentax Optio W80 digital compact cameras equipped with red lighting to minimize disturbance of sea urchins throughout the nocturnal cycle (see Millot 1968, Gras & Weber 1983). Each sampling occasion was spatially independent, with a different area of reef and different sea urchins monitored in each of the photographic sequences. Cameras were mounted on adjustable aluminium tripods and deployed by SCUBA divers. The field of view photographed by the cameras varied from ~ 5 m² to 30 m² depending on both the camera system used and the adjusted height of the tripod (0.8 – 3 m from the

substratum, depending on topography) but this variation in FOV occurred haphazardly across the different habitat types. Field-of-view dimensions were determined from image calibration based on measurements taken between visible features on the benthos. Image sequences spanned a minimum of 12 hours between 19:30 and 07:30, with a single photograph taken every five minutes and sea urchin coordinates recorded using the 'Manual Tracking' plugin for ImageJ (v 1.42). The time frame over which individual sea urchins could be reliably tracked was estimated from pilot trials examining urchin velocity. A frequency of photographing at ~5 minute intervals permitted unambiguous tracking of each urchin in the view field.

The path followed by an animal through time was reproduced and divided into a series of steps, stops and moves. A step was defined as the vector connecting two successive positions (five minutes apart), a stop as an interval where an individual remained stationary for at least two frames (10 minutes), and a move as the vector between two successive stops (see Dumont et al. 2007 for detailed explanation). An arbitrary minimum step length of 10 mm was used, below which movement was considered to be measurement error or indicating local spine movement of otherwise stationary individuals.

Movement of *Centrostephanus rodgersii* was initially observed over the entire diel cycle (24 h) to properly quantify periods in which sea urchins were active. Preliminary analyses of these images indicated highly nocturnal foraging consistent with observations on mainland Australia, so all subsequent photography was from 19:30 to 07:30 (overnight, daylight-to-daylight). Images from the different habitat types were examined separately for temporal patterns in speed of movement. The frequency of sea urchins moving faster than the nightly average within each hourly period was calculated to identify times throughout the night corresponding with peaks in activity. Quantitative comparisons between distributions from each habitats type were made using pair-wise Kolmogorov-Smirnov tests, with Bonferroni adjustments made to α to protect against compounding of Type I error. Net displacement and total distance moved over the night were calculated for the subset of sea urchins within each habitat that remained in the field of view for the entire duration of nocturnal footage. Sea urchin density was estimated for each night of footage as the mean of five density measures taken at three hour intervals between 19:30 and 07:30. All response variables were initially examined using one-way nested ANOVA with sampling occasions (replicates) nested within habitats. Sampling occasion (night of camera footage) was found to be non-significant ($P > 0.25$ for all response variables), so replicates were *post-hoc* pooled (removal of the factor 'sampling occasion' from the model) in accordance with Underwood (1997). One-way ANOVA with associated REGWQ *a posteriori* multiple range tests as appropriate were then performed on all response variables across three levels of barren habitat type using SAS[®] (v 9.1).

To characterise movement in *Centrostephanus rodgersii*, observed movement paths were compared with paths simulated by an established walk model. Kareiva & Shigesada (1983) give an equation for a correlated random walk (CRW) models that is frequently used to characterize the foraging behaviour of animals in homogenous environments (Byers 2001, Austin et al. 2004, Lauzon-Guay et al. 2006, Dumont et al. 2007):

$$R_n^2 = nm_2 + 2m_1^2 \frac{\psi}{1-\psi} \left(n - \frac{1-\psi^n}{1-\psi} \right)$$

where R_n^2 is the net squared-displacement of a path, n is the number of moves in a path, m_2 is the mean of the squared move length, m_1 is the mean move length, and ψ is the mean cosine of the turning angle. The distribution of observed *C. rodgersii* turning angles was initially analysed and found to be uniform (i.e. the mean cosine of angles was not significantly different to 0), hence the model was by definition reduced to a simple random walk (RW) equation:

$$R_n^2 = nm_2$$

As the RW model assumes no autocorrelation between either the length or direction of consecutive moves, turning angles were tested for first- and second-order autocorrelation within each habitat type using the

method described by Conradt & Roper (2006) and Turchin (1998). The presence of first-order autocorrelation between successive move lengths was also tested for using Spearman rank tests (Zar 1999, Dumont et al. 2007).

Observed paths from within each habitat were compared with 1,000 paths simulated by the RW model using the software MATLAB (v 7.3.0). A maximum of 6 moves per path were used in model simulation, as this was equal to the maximum number of moves made by at least 10 sea urchins within each habitat. For every iteration of the simulation, n move lengths and n turning angles were drawn randomly (with replacement) from the respective empirical distributions for each habitat, and a single path was generated (Bootstrap method, Turchin 1998). Once 1,000 simulated paths were obtained for each habitat, the mean net squared-displacement (\overline{R}_n^2) was calculated for every value of n as the mean of these 1,000 paths.

Variation around the expected \overline{R}_n^2 was examined using the technique recommended by Turchin (1998), with 95% confidence intervals estimated using the percentile method (Crowley 1992, Manly 1997, Turchin 1998). Net squared-displacement (R_n^2) of individual sea urchins was classified as local, directional or random based on whether it fell below, above or within the confidence intervals of the walk model (Austin et al. 2004). An individual track was considered significantly different from the model when the observed R_n^2 fell outside the confidence intervals for at least half of all moves (Dumont et al. 2007).

Assessing fidelity to incipient barren patches

To assess the long-term stability of incipient barren patches, the fidelity of *Centrostephanus rodgersii* to individual patches was evaluated by measuring movement and dispersal of tagged sea urchins at Fortescue Bay, Tasman Peninsula. Three incipient barrens patches in close proximity (~20 m from nearest adjacent barren) were selected haphazardly from within the kelp bed at depths of 6-8 m. The patches varied in area (1.2 - 3.9 m²), perimeter (15 - 30 m), and the number of urchins they contained (6 - 22), and were broadly representative of the typical scale of patches in incipient barrens habitat. All *C. rodgersii* found within these patches ($n = 14, 22, 6$ individuals for patches I-III, respectively) were tagged at the commencement of the experiment by drilling two small holes through the test with a hypodermic needle (100 mm long by 1.25 mm diameter), threading a 150 mm length of monofilament line (0.45 mm diameter) with a uniquely numbered spaghetti tag through the needle, and crimping the line ends together with a leader sleeve (Ling et al. 2009a). Despite previous findings of minimal mortality and tag loss (< 5%) associated with *ex situ* tagging in this way (Pederson & Johnson 2006, Ling et al. 2009a), all tagging was conducted *in situ* by SCUBA divers, and animals were returned to within 10 cm of their initial position immediately following application of the tag. *In situ* tagging in this way avoided any risk of behavioural changes that might result from removal to the surface and subsequent release.

Patches were searched for tagged sea urchins one week after tagging, and again every three weeks over a period of 90 days (total of six encounter occasions). The area of kelp immediately surrounding the patch was also searched on each occasion using a 5 m circular sweep around a central fixed point within the patch. Each time a tagged sea urchin was sighted, its identity was recorded, test diameter measured, and its location within the patch or surrounding kelp bed was triangulated with respect to two fixed pickets hammered into the reef. The position of each sea urchin was also recorded as 'shallow' or 'deep' depending on its location relative to the shore and pickets. These three measurements provided a unique set of coordinates, allowing calculation of the net distance moved since an animal's previous sighting and displacement from its initial tagging position for each individual. The relationship between cumulative total distance moved (the sum of net movements between consecutive sightings) and overall displacement from the original position was examined for every resighting occasion and used to assess patch fidelity. Given evidence for a strong positive relationship between movement and body size in stronglycentrotid sea urchins (Dumont et al. 2004), size-specific movement was examined by quantile regressions of test diameter against net movement using the 'quantreg' package (Koenker 2009) for the 'R' software. To verify that fidelity and movement estimates were not biased by some sea urchins moving beyond the boundaries of the experimental area, daily survival and resighting probabilities of individuals were assessed using a Cormack-Jolly-Seber (CJS) mark-recapture model with the factors 'plot', 'time', and covariate of 'size'. Data

were analysed using the CJS routine of the MARK (v 6.1) software (White & Burnham 1999), whereby the saturated model was tested for goodness-of-fit and the most parsimonious model identified using the quasi-likelihood form of the Akaike Information Criterion, *as per* Ling et al. 2009a).

Role of chemosensory cues in determining patch dynamics

The potential role of food and conspecific chemosensory cues in stimulating movement of *Centrostephanus rodgersii* across the barren-macroalgal interface at the perimeter of patches were investigated in a series of laboratory choice experiments. Sea urchins were collected between February and March 2010 and housed in flowing sea water tanks without food for a minimum of four weeks before trials commenced. Given an average gut passage time of 24-60 hours under normal feeding regimes across a number of sea urchin taxa, and a maximum food retention time of 1-2 weeks in starved sea urchins (see De Ridder & Lawrence (1982) and references within), a four week starvation period was assumed to be sufficient to ensure significant motivation to feed. Experiments were conducted in a 250 mm diameter Y-shaped maze constructed from PVC piping with section lengths of 0.5 m (arms) and 0.7 m (trunk). Each arm was connected to a header tank containing either a 'stimulus' or 'blank' seawater. A flow rate of 21 L min⁻¹ (velocity 0.24 m min⁻¹ in the main stem) was maintained throughout all trials, with dye experiments conducted regularly to verify minimal mixing of water upstream of the junction point. Initial trials indicated that large individuals (in which the lateral diameter of the spine canopy spanned the width of the experimental apparatus) tended not to move within the maze, so only sea urchins with spine canopies less than 250 mm were retained for analysis since they moved freely in the maze and were not impeded by the dimensions of the apparatus. The first two sets of trials tested the potential role of food cues in stimulating sea urchins to cross the barren-macroalgal boundary by using fresh *Ecklonia radiata* (simulating attached plants) and damaged/decomposing *E. radiata* (representing detached drift algae), both of which are known to be consumed by *C. rodgersii* (Andrew 1993, 1994, Hill et al. 2003). The third set of trials addressed the hypothesis that patch fidelity of *C. rodgersii* is maintained by attraction to conspecifics, and in these trials 15-20 sea urchins (depending on size, 0.3-0.4 urchins L⁻¹) were held in one of the header tanks. All trials were conducted at night between 21:00 and 05:00 in complete darkness during the peak of *C. rodgersii* feeding activity.

Trials commenced with a single sea urchin placed in the centre of the main Y stem. Its location was monitored every 10 minutes for a period of 40 minutes, and a choice was considered to have been made when an individual moved either side of the junction and its centroid crossed the entrance to one arm of the maze. Each sea urchin response was scored as positive (towards stimulus), negative (away from stimulus), or no response (no choice made between either arm). Water inflows were swapped after every second trial to eliminate any potential bias in the apparatus. For trials in which sea urchins made a choice between arms of the apparatus, the exact probability of the observed outcomes was analysed using χ^2 tests.

Scaling per capita grazing impact with barrens patch size

The grazing impact of *Centrostephanus rodgersii* individuals at the forefront of the urchin's range-extension region was assessed by broad-scale diver surveys in incipient barrens habitat across nine sites in eastern Tasmania (Fig. A3.1). Over a total of 20 geo-referenced timed swims (surface GPS towed by diver for 30-45 minutes, $n = 4$ swims per site for North Bay and $n = 2$ swims for all other sites) between 5 and 15 m depth, divers searched for incipient barrens patches and carried out *in situ* estimations of patch sizes using a 1 x 1 m quadrat for calibration. Abundance of *C. rodgersii* within each patch was estimated for patch sizes up to a maximum of 5 by 5 m (25 m²) in area; beyond this size patches became too large to efficiently estimate urchin abundance (see Fig. A3.1 caption for more detail). The relationship between planar grazed area of each barrens patch and *C. rodgersii* abundance was assessed using linear regression analysis. To assess overall impacts urchin grazing on kelp beds (beyond individual patches considered above) diver belt-transect data from Johnson et al. (2005) was re-analysed by linear regression to determine the relationship between mean *C. rodgersii* density and mean percentage cover of barrens habitat for 13 sites across the sea urchins' range-extension region (means of $n = 3$ sub-sites per site, with sub-site estimates obtained

from the mean of 4 belt transects, see Johnson et al. 2005 for full method).

Results

Spatial and temporal patterns of movement

A total of 368 sea urchins were tracked across the three barren habitat types, each of which contained a similar density of sea urchins (Table A3.1). Movement of *Centrostephanus rodgersii* was strongly nocturnal with peaks in velocity occurring immediately following sunset and just before sunrise (Fig. A3.2A). This broad pattern was common to all habitat types, although sea urchins consistently moved fastest on flat-rock surfaces and slowest in incipient barrens patches on boulder habitat (Fig. A3.2B). The mean speed of animals on widespread flat-rock barren was fastest from approximately 01:00 relative to other habitats (see Fig. A3.2B); however this was driven primarily by a small number of individuals returning late to shelter towards the end of the night. After standardising by the frequency of animals moving faster than the nightly average (assessed across hourly bins), differences among habitat types in the distribution of movement patterns across hourly time intervals during the night were not significant (Bonferroni adjusted $\alpha = 0.017$, $P > 0.23$ for all pair-wise comparisons).

A total of 189 sea urchins remained within the field of view of the camera for the entire duration of filming, and approximately equal proportions of the 179 excluded transitory animals moved into (44%) and out of (56%) the field of view ($\chi^2 P = 0.12$). The total nightly distance travelled by sea urchins on widespread flat-rock barrens (5.1 ± 0.3 m) was significantly greater than that of animals on either widespread boulder (3.5 ± 0.2 m) or incipient (2.8 ± 0.2 m) barrens habitat on a boulder substratum ($F_{2,188} = 15.62$, $P < 0.001$) (Fig. A3.3A). Similarly, sea urchins on flat-rock were significantly further from their starting position at the end of the night ($F_{2,188} = 13.75$, $P < 0.001$) and their overall homing tendency to their site of origin at the beginning of the night was weaker relative to animals on incipient or widespread boulder barren (Fig. A3.3B). The net displacement of sea urchins on incipient barrens was not significantly different to that of animals on widespread boulder barrens; however 98% returned to within 0.8 m of their starting position compared with 84% in widespread boulder barren and just 24% on widespread flat-rock barren habitat. Sea urchins in incipient barrens also spent significantly less time moving ($F_{2,367} = 9.91$, $P < 0.001$) than their counterparts on widespread boulder or flat-rock barrens (Table A3.1). The total distance moved by sea urchins within each habitat was generally less than the minimum field of view dimension for filming on that habitat. While many foraging animals display classic Lévy flight movements (i.e. local random movement with occasional large 'jumps' to new sites), there is no evidence to suggest that *C. rodgersii* exhibits this mode of behaviour, as indicated by high recovery of tagged urchins from circumscribed sites after 12-14 months (Ling & Johnson 2009). Using this evidence, combined with a moderate to strong homing tendency across all habitats (average net displacement < 0.6 m) (Fig. A3.3B, see also section below), we are confident that exclusion of animals leaving the camera field of view did not influence our estimates total distance moved and net displacement.

Of all the sea urchins tracked, 292 paths were composed of at least three moves and were thus appropriate for use in the random walk analysis. The average length of moves varied significantly between habitats ($F_{2,291} = 25.6$, $P < 0.001$), with sea urchins on flat-rock barren travelling approximately 50% further in a single move than those on widespread boulder barren, and more than twice as far as the average length of move in incipient barren patches. A strong autocorrelation in the length of successive moves was detected for sea urchins on flat-rock barren (Spearman rank correlation, $r_s = 0.605$, $P < 0.001$) but not in either of the other two habitats ($P > 0.1$ for both incipient and widespread boulder barrens). This violates one of the assumptions of the RW model (Turchin 1998), however it likely reflected the occurrence of distinct behavioural types (active and passive movers) that was evident only in sea urchins on flat-rock habitat. Also, no 1st or 2nd order autocorrelation in turning angles was detected ($\chi^2 P > 0.07$ for all habitats) and hence it was deemed reasonable to proceed with the random walk analysis.

The random walk model significantly overestimated the net squared-displacement of sea urchins in all

habitats (Fig. A3.4). Despite variation in individual movement parameters (see Table A3.1), the relationship between observed and predicted net squared-displacement was similar across habitats. The observed net squared-displacements of pooled paths was within or close to the 95% confidence limits of model predictions for the first and second move of a path, but displacement increased very little beyond these two initial moves. The value at which the observed mean net squared-displacement ($\overline{R_n^2}$) stabilised varied from $\sim 1 \text{ m}^2$ in flat-rock barrens to ~ 0.35 and $\sim 0.15 \text{ m}^2$ in widespread boulder barrens and incipient barrens habitats, respectively (Fig. A3.4). A smaller stabilising value of $\overline{R_n^2}$ for animals in incipient barrens relative to widespread boulder barrens reflects a shorter average move length and less frequent movement overall (see Fig. A3.3, Table A3.1). The majority of movement within each habitat was local (displacement less than random) due to active homing or movement of short distances within a restricted area. A greater proportion of individuals in incipient barrens patches followed movement paths that fell within the predictions of the random walk. However, sea urchins exhibited directed movement less frequently in this habitat, indicating a greater tendency for homing or localised movement relative to that observed on widespread flat-rock or boulder barrens (Table A3.2).

Fidelity to incipient patches

Of the 42 sea urchins tagged, 71.4% were recovered from within or immediately adjacent their respective incipient barren patches after three months of monitoring. Every individual was resighted on at least one occasion (i.e. they 'disappeared and reappeared'), suggesting that the 12 urchins not recovered at the end of the study were likely present in the reef matrix but simply not found by divers. The cumulative distance moved by animals between the 5 consecutive sampling periods was considerably greater than their net displacement (even with relatively infrequent sampling), indicating that while local movement and reshuffling of shelter sites continued to occur within patches over the monitoring period, most individuals remained within their particular patch over a period of three months (Fig. A3.5A). Correspondingly, the mean net displacement of sea urchins over the monitoring period did not exceed 2.5 m from the position of initial tagging, although this metric was clearly influenced by the physical dimensions of the patch (Fig. A3.5B). No more than six individuals (14% of total) were observed outside incipient patches on any one occasion, five of which were on the periphery of an incipient grazed patch following a seasonal flush of small ephemeral algae. After demonstrating satisfactory fit ($P = 0.469$) of the saturated mark recapture model [$\text{phi}(\text{plot} \times \text{time} \times \text{size}_{\text{cov}}) \rho(\text{plot} \times \text{time} \times \text{size}_{\text{cov}})$], analysis of encounter rates of individually tagged sea urchins revealed that the best supported CJS model contained urchin survival (phi) as being independent of plot, time or body size, while encounter probability (ρ) was dependent on sea urchin size only [$\text{phi}(\cdot) \rho(\text{size}_{\text{cov}})$]; Figs. A3.6A & B). Although large sea urchins had a greater potential for movement than smaller ones (75th quantile regression, $P = 0.037$) (Fig. A3.6C), the strong positive relationship between size and encounter probability (Fig. A3.6B) shows that large individuals consistently remained within or nearby their 'home' patches, and that tagged animals that were resighted less frequently were predominantly small individuals that displayed restricted movement within patches (Fig. A3.6C) but were less easily found by divers among the reef matrix (Fig. A3.6B).

Response to chemosensory cues

A choice, towards or away from either a food or conspecific stimulus, in Y-maze trials was made by approximately 70% of all sea urchins tested. However, there was no trend in the pattern of choices so that the number of animals moving towards or away from each stimulus did not differ significantly for any of the stimuli trialled ($P > 0.5$ for all sets of trials, Table A3.3) indicating no directional movement in response to olfactory stimuli.

Per capita grazing impact versus barrens patch size

The relationship between incipient barrens patch size and the number of sea urchins contained within each patch was well described by linear regression, with each individual sea urchin member maintaining a grazed area of approximately 0.6 m^2 independent of the patch size, and thus independent of the number of

individuals per patch (Fig. A3.7A). Beyond individual barrens patches, the percentage cover of reef that is barrens across entire kelp beds also displayed a strong linear relationship with *C. rodgersii* density, suggesting existence of a fixed grazing impact that is a simple function of the local density of *Centrostephanus* at a site absent of any density-triggered behavioural shift (Fig. A3.7B).

Discussion

Patterns of foraging behaviour across barrens types

Our detailed observations of nocturnal behaviour of *Centrostephanus rodgersii* were consistent with previous observations *in situ* (Jones & Andrew 1990) and evidence of light sensitivity in other diademid sea urchins (Millott 1954, 1968, Gras & Weber 1983). Peaks in the velocity of their movement at the end of the night were most pronounced on widespread flat-rock barren, where the first appearance of daylight appeared to trigger a short burst of rapid and directional movement towards shelter in individuals not already occupying crevices or micro-crevices (fissures < 20 mm depth and width). This behaviour was observed less frequently in either of the boulder-based habitats, and may be explained by the relative scarcity of crevices on flat-rock substratum. Aside from subtle differences in the timing of peak velocity, time-related patterns in foraging were similar across habitats indicating a common response to ambient light levels and an inherent circadian cycle (e.g. Ogden et al. 1973, Bernstein et al. 1981, Hereu 2005).

A dramatic shift in behaviour from sedentary low-impact grazing to motile feeding aggregations is a consistent feature in the formation of widespread barrens habitat by strongylocentrotid sea urchins (Dean et al. 1984, Lauzon-Guay & Scheibling 2007a, Scheibling & Hatcher 2007). If *Centrostephanus rodgersii* exhibited a similar behavioural shift, we would expect it to occur between the progression from incipient “developing” to widespread “established” barrens, and that it would manifest as measureable differences in nocturnal (when the animals are active) foraging patterns between animals on these different habitats. However, the pattern of foraging activity was similar across all three habitat types, and the subtle habitat-specific patterns observed can be attributed to features of the substratum rather than the extent of barrens formation. For example, sea urchins on widespread flat-rock barren moved faster and over greater distances than their counterparts on boulder substratum (whether widespread or incipient barrens), and had a greater net displacement over the nightly foraging period. This may be explained by more rapid locomotion of sea urchins across flat-rock substrata in the absence of crevices and vertical surfaces (Laur et al. 1986). However, we note also that a systematic underrepresentation of movement on boulder substratum is unavoidable when movement on a complex 3-dimensional landscape is converted to a 2-dimensional planar measurement, hence the magnitude of the differences in movement parameters between flat-rock and boulder substrata would likely be somewhat reduced if rugosity was taken into account.

Homing behaviour: non-random movement

Movement of *Centrostephanus rodgersii* is highly localised relative to the predictions of the RW model. This suggests either that animals move in a restricted fashion remaining in close proximity to a particular focal point (i.e. a ‘home site’) or, alternatively, that they move predominantly randomly but with the addition of a distinct ‘outwards’ and ‘inwards’ phase away from and returning to a home crevice (i.e. homing behaviour). A homing strategy is a more parsimonious explanation of the observed foraging behaviour, with the observed net-squared displacement only deviating from the predictions of the RW model following the second move of a path (only tracks with at least three moves were retained for analysis, so an increasing proportion of tracked individuals returned to a home crevice and ‘ended’ a foraging path for move numbers ≥ 3). Homing behaviour has been well-documented in conspicuous marine invertebrates such as limpets (e.g. Underwood 1977, Sebastián et al. 2002), as has the alternation between random and homing ‘phases’ of movement (although with an overall strong homing pattern) (Mackay & Underwood 1977). The homing behaviour of *C. rodgersii* observed here contrasts with the predominantly random movement observed in *Strongylocentrotus droebachiensis* (Lauzon-Guay et al. 2006, Dumont et al. 2007).

While neither of these studies examined habitat-specific movement characteristics *per se*, movement was found to be random on both barren habitat and in grazing fronts, suggesting an inherent difference in foraging dynamics between *S. droebachiensis* and *C. rodgersii*.

Shelter-oriented homing behaviour has previously been observed and quantified in the diademid sea urchins *Centrostephanus coronatus* (Nelson & Vance 1979) and *Diadema antillarum* (Carpenter 1984). In general, a homing strategy is thought to be advantageous when predation pressure is reduced by occupying a shelter site, and when the availability of such sites is limited (Cook 1979, Nelson & Vance 1979). Shelter-centric homing behaviour is frequently observed in conjunction with nocturnal patterns of activity as a defence against predation during daylight hours (Ogden et al. 1973, Nelson & Vance 1979, Bernstein et al. 1981, Hereu 2005). The reasons for homing and nocturnal foraging observed in *C. rodgersii* however may be less clear. The principle predator of *C. rodgersii* in Tasmania is the rock lobster *Jasus edwardsii* (Johnson et al. 2005, Ling et al. 2009a) which is also a nocturnal forager, and thus a homing strategy and sheltering in crevices during the day is unlikely to confer any survival advantage against the threat of lobster predation. Importantly, the establishment of *C. rodgersii* in Tasmania is very recent (Johnson et al. 2005, 2011), and the sea urchins' behaviour may reflect that, historically at least, within its native NSW range its major predator is the large diurnally foraging grouper *Achoerodus viridis* (labridae) (see Andrew 1993). If so, then the persistence of nocturnal foraging and diurnal sheltering by *C. rodgersii* in Tasmania suggests that the behaviour is evolved and innate.

The only discernible differences in foraging patterns of *Centrostephanus rodgersii* between incipient and widespread barren habitats was in the absolute distance travelled in a time period (i.e. magnitude of net squared-displacement) and in the dominant movement 'type'. The three types of behaviour we considered were (1) random movement, fitting the RW model; (2) movement characterized by a return trip, i.e. the 'homers'; and (3) those undertaking long-distance directional movement away from a starting position, possibly guided by some chemosensory stimulus. Directional movement was rare in incipient barren patches relative to in widespread barrens. Sea urchins within incipient barrens seem to adopt local movement or random movement but within the boundaries of the patch, whereas animals on widespread barrens habitat may adopt the full spectrum of movement types including directional foraging. As with invariant nocturnal patterns in movement, there were no major differences in movement between incipient and widespread barrens as might be expected if *C. rodgersii* exhibited the kinds of behavioural shifts demonstrated in stronglylocentroid sea urchins (Mattison et al. 1977, Dean et al. 1984, Lauzon-Guay & Scheibling 2007a, Scheibling & Hatcher 2007). Importantly, observations of homing tendency around localised shelter sites on widespread barrens over short time scales are consistent with our observations of high levels of site fidelity over much longer time scales, as evident from up to 45% recovery of chemically tagged individuals within unfenced 8 x 8 m areas on extensive barrens over a 14 month time period (Ling & Johnson 2009).

Incipient barren patches as 'isolated' systems

Most sea urchins monitored over three months demonstrated high fidelity to incipient barren patches, with their net dispersal over this entire period less than the mean distance travelled during a single night of foraging. Previous work has indicated that large sea urchins may be particularly motile in kelp bed habitats (Ling & Johnson 2009); however, the majority of tagged animals that failed to be consistently re-located during the current study were small, cryptic individuals that persisted throughout the experiment but were less visible to divers. Net dispersal measurements are therefore biased towards the larger and more motile sea urchins, and hence our estimates of patch fidelity are likely to be conservative when considering the full range of cryptic and emergent size classes of the sea urchin. Observations of marked incipient barren patches in eastern Tasmania have indicated long-term persistence (2001-2011) of patches (S. Ling *unpub. data*), but previously it was unknown whether these patches were maintained by transitory animals from the surrounding kelp bed and neighbouring patches, or by sea urchins that largely remain resident within a given patch, as indicated by our results. Our observations reveal that individuals can readily cross the macroalgal boundary at the perimeter of patches, i.e. substratum discontinuities or abrasion by kelps sweeping the substratum (Andrew 1993, Konar 2000, Konar & Estes 2003) do not completely prevent

movement of sea urchins across the border of barren patches. The tendency of sea urchins to remain within patches therefore suggests strong fidelity to patches rather than inhibition of movement beyond patch boundaries. Importantly, this fidelity effectively renders each incipient barren patch an isolated system independent of other patches.

Aggregative behaviour does not drive patch dynamics

The absence of locomotory responses of *Centrostephanus rodgersii* to food cues in the laboratory trials is consistent with *in situ* observations by divers and from time-lapse photography that urchins do not demonstrate movement towards or aggregation around attached kelps. Sea urchins may stop at a high-quality food patch whilst foraging, but they appear either not to detect chemosensory stimuli emitted from macroalgae, or else do not respond to detected food cues with directional movement. This contrasts strongly with established models of strongylocentrotid foraging which involves strong attraction to food and subsequent formation of aggregations, as has been demonstrated in both laboratory (Bernstein et al. 1983, Mann et al. 1984, Prince & LeBlanc 1992) and field (Mattison et al. 1977, Lauzon-Guay & Scheibling 2007a) experiments. Using a modelling approach, Lauzon-Guay et al. (2008) suggested that chemoreception may not be a necessary prerequisite to formation of strongylocentrotid urchin aggregations along the margins of kelp beds, and that these aggregations could instead arise purely through random encounters. Using an extension of this model, Feehan et al. (2012) recently found that large stationary aggregations of urchins within cleared patches in kelp beds do not appreciably expand these patches, particularly on shallow and/or sheltered reefs, largely because they are supplied with drift algae and can access prostrate kelp fronds on the margins of patches. These findings contrast with an extensive body of literature on strongylocentrotid sea urchins based on both field observations (Breen & Mann 1976, Scheibling et al. 1999, Lauzon-Guay & Scheibling 2007a) and mathematical models (Lauzon-Guay et al. 2008, Lauzon-Guay et al. 2009) but, interestingly, appear to be more consistent with our own observations of *C. rodgersii* behaviour. A major difference, however, is the conspicuous absence of *C. rodgersii* feeding on drift algae, presumably because of an inability to effectively trap algae using tube feet on their aboral surface given their considerable spine length. The absence of a clear aggregation response of *C. rodgersii* to attached macroalgal food, in combination with their homing-like behaviour within patches and thus fidelity to particular patches, confers stability to incipient barren patches, since feeding by sea urchins on macroalgae at the periphery of patches will only arise through random encounters.

Centrostephanus rodgersii was similarly unresponsive to stimuli from conspecifics despite a natural tendency to cluster and a contagious dispersion when translocated to seemingly homogenous reef habitat (S. Ling *unpub. data*). Attraction to conspecifics as a potential mechanism by which formation of incipient barrens is initiated cannot be ruled out. However, chemosensory detection of conspecific cues does not appear to induce a locomotory response in *C. rodgersii*, and so the common observation of aggregated distributions around crevices in the field may instead be mediated via direct contact or, more likely, attraction to optimal local shelters (the importance of which has recently been demonstrated by Ling & Johnson 2012). The high frequency of sheltering behaviour of *C. rodgersii* in the field is consistent with the overriding tendency of large individuals in Y-maze experiments to remain stationary under laboratory conditions when their spine canopy spanned the diameter of the apparatus, mimicking a concave shelter (hence the decision to exclude these from analysis), and is indicative of the importance of crevice structure in determining local spatial patterns of sea urchin distribution (Andrew 1993).

An alternative model of sea urchin overgrazing

The behaviours of *Centrostephanus rodgersii* revealed in this study, coupled with our general observations made over thousands of person hours of diving in the system, indicate the likely mechanisms of widespread barren formation. Broad similarities in foraging behaviour across the range-extension region and thus all stages of barren development from incipient to widespread barren on all substratum types suggest no evidence of a distinctive behavioural shift leading to overgrazing by exposed individuals as has been described in other barren-forming sea urchins (e.g. Dean et al. 1984, Harrold & Reed 1985, Vadas et al. 1986). The fidelity of individual *C. rodgersii* to their particular incipient patch is strong, macroalgal cues

do not stimulate movement across the kelp-patch interface and, in particular, the aggregative behaviour thought to precipitate formation of feeding fronts in stronglycentrotid sea urchins (Mann et al. 1984, Dumont et al. 2007, Lauzon-Guay & Scheibling 2007a) is conspicuously absent. As a result, individual incipient barren patches are highly stable and each patch effectively behaves independently. The detailed behavioural observations and patch size dynamics presented here are consistent with broad-scale data from our general observations over several 100 km of coastline which suggest that the size of individual barrens patches increase as a linear function of sea urchin abundance and that density within patches is remarkably consistent (at one urchin per $\sim 0.6 \text{ m}^2$ of barrens area), and that eventual widespread barrens occur through the simple process of patch formation, expansion and eventual coalescence of multiple patches. Interestingly, this very mechanism has recently been suggested as a possible alternative behavioural model for *S. droebachiensis* (Feehan et al. 2012), however this is yet to be demonstrated experimentally in an unmanipulated stronglycentrotid system. The position and size of any particular *C. rodgersii* barrens patch is dictated by the individual grazing efforts of sea urchins contained within it and, for a given overall density, the local spatial distribution of the urchins is strongly influenced by the availability of shelter. Similarly, the likelihood of initial patch formation is also a direct consequence of local sea urchin density, and thus the distribution of sheltering sites, within a macroalgal bed (see Lauzon-Guay & Scheibling 2010). Thus, it appears that increases in population density of *C. rodgersii* across a reef manifest as an increased number of discrete incipient barren patches which, as they grow by the recruitment and grazing activity of additional urchins, eventually coalesce to form widespread barrens habitat from the 'inside-out'. This pattern, underpinned by high fidelity to patches and a homing tendency irrespective of habitat, sea urchin density or stage of barrens formation across the range-extension region, suggests that regulation of urchin density at the spatial scale of individual patches will reduce the likelihood of widespread barrens formation.

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Table A3.1. Sample sizes and movement characteristics of *Centrostephanus rodgersii* on incipient, widespread boulder and widespread flat-rock barren habitats. Means include S.E. in parentheses. Where ANOVA results are presented, all numerator df = 2. *Indicates value is significantly different from other means as indicated by 1-way ANOVA (for significant overall tests) and REGWQ multiple range tests.

Characteristics	Habitat			ANOVA		
	Incipient barren	Widespread boulder barren	Widespread flat-rock barren	df	F	P
Sampling period	Dec 09 - Feb 10	Nov 09 - Dec 09	Dec 09	-	-	-
Nights of movement observations	7	4	4	-	-	-
Total no. of sea urchins tracked	93	94	181	-	-	-
No. of sea urchins in field of view all night	53	51	85	-	-	-
Mean sea urchin density (m ⁻²)	1.99 (0.11)	1.88 (0.28)	1.93 (0.33)	14	0.06	0.946
Mean proportion of time spent moving (%)	49.9 (1.7)*	59.6 (1.5)	57.6 (1.2)	367	9.91	<0.001
Mean velocity (mm s ⁻¹)	0.16 (0.009)	0.15 (0.006)	0.19 (0.005)*	367	22.0	<0.001
No. observed paths ≥ 3 moves	54	60	99	-	-	-
Mean length of move (mm x 10 ²)	2.39 (0.17)*	3.37 (0.27)*	5.06 (0.31)*	291	25.6	<0.001
Mean cosine turning angle	0.08 (0.07)	0.06 (0.06)	0.05 (0.06)	291	0.05	0.955

Table A3.2. Relative frequency of *Centrostephanus rodgersii* movement types on incipient, widespread boulder and widespread flat-rock barren habitats. The number of tracks observed in each habitat is given by (n). Movement type of a given track is classified depending on the proportion of moves within the track that fall above, below or within the confidence limits of random walk model predictions. Sea urchins are classified as directional, local or random movers for tracks where at least half of all moves fall above, below, or within model confidence limits, respectively. Given a maximum of 6 moves per path, paths are classified as undetermined where the same number of moves are assigned to two or more different movement types (e.g. 3:3, 2:2:2).

Habitat	(n)	Move type (%)			
		Random	Directional	Local	Undetermined
Incipient barren patch	54	14.8	5.6	70.4	9.3
Widespread boulder barren	60	6.7	13.3	70.0	10.0
Widespread flat-rock barren	99	6.1	16.2	67.7	10.1

Table A3.3. Movement responses of *Centrostephanus rodgersii* to stimuli in Y-maze trials, indicating neither attraction to or repulsion from waterborne cues from food or conspecifics. The number of trials conducted for each stimulus set (*n*) is given in parentheses. The 'not choosing' response indicates individuals that did not move up the trunk of the maze and into either branch arm. Probabilities indicate likelihood of choices differing from no choice (i.e. ratio of 1:1 responses to both stimuli) by chance, estimated using the χ^2 statistic.

Pairs tested	(n)	No. of sea urchins		χ^2 probability of observed choices
		choosing	not choosing	
Blank	(24)	9	8	<i>P</i> = 0.617
<i>E. radiata</i> (fresh)		7		
Blank	(24)	9	7	<i>P</i> = 0.808
<i>E. radiata</i> (decomposing)		8		
Blank	(25)	7	8	<i>P</i> = 0.532
Conspecifics		10		

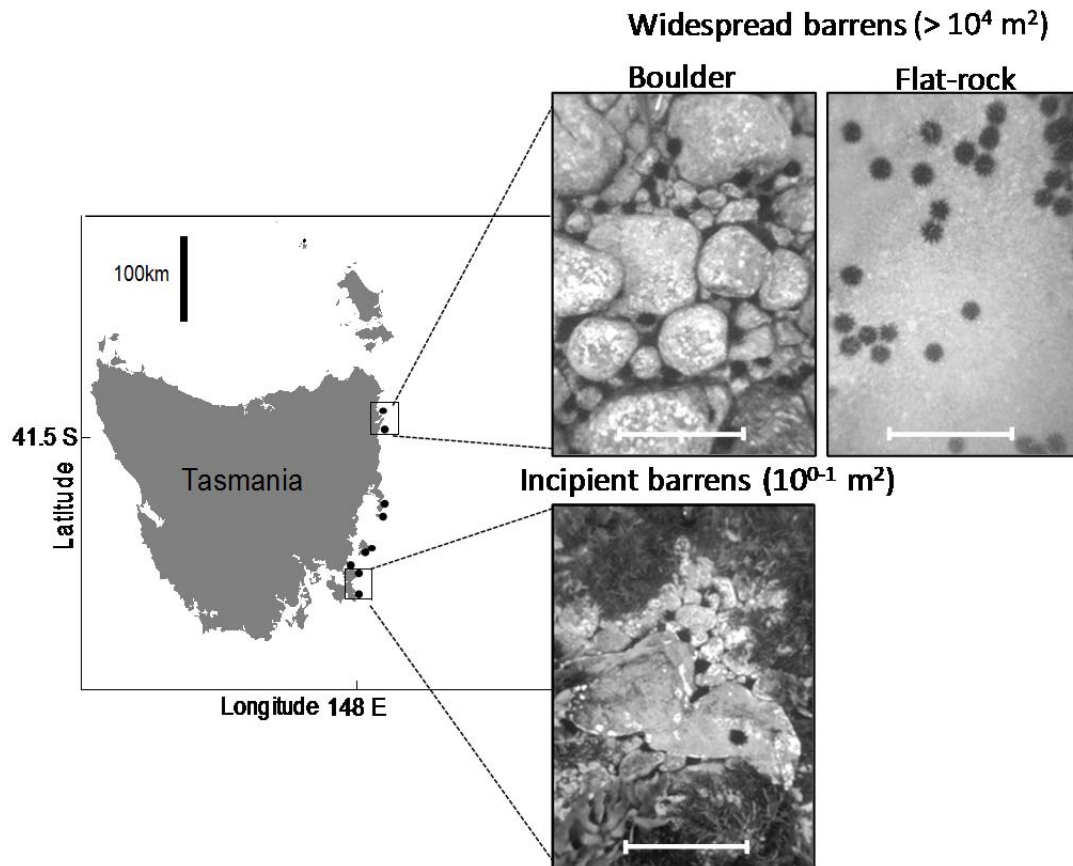


Figure A3.1. Map of south eastern Australia showing sites where movement of *Centrostephanus rodgersii* was assessed across different habitat types in eastern Tasmania. Abundance of *C. rodgersii* and prevalence of barrens declines with latitude southward along the eastern Tasmanian coast (Johnson et al. 2005, 2011; Ling et al. 2009a) with widespread barrens (10^4 m²) occurring in the north east region; while only smaller scale (10^{0-1} m²) barrens patches are currently present in southeastern Tasmania. Expanded boxes indicate the two regions where movement was examined: NE widespread flat-rock (minimal cracks and crevices) and widespread boulder barrens; SE incipient barrens patches only. White bars indicate spatial scale of 1 m. Overgrazing progresses from incipient barrens centered on boulder habitat to widespread boulder barrens and finally, where grazing is most intense, flat-rock habitats are stripped bare of kelp. Sites where barrens patch-size dynamics were recorded by geo-referenced timed-swims (Nov 2008 to June 2009) are shown as filled circles, ordered north to south the sites were: Sloop Rock, St. Helens Is, Wineglass Bay, Trumpeter Bay, Mistaken Cape, Bunker Bay, Cape Paul Lemanon, North Bay, Fortescue Bay.

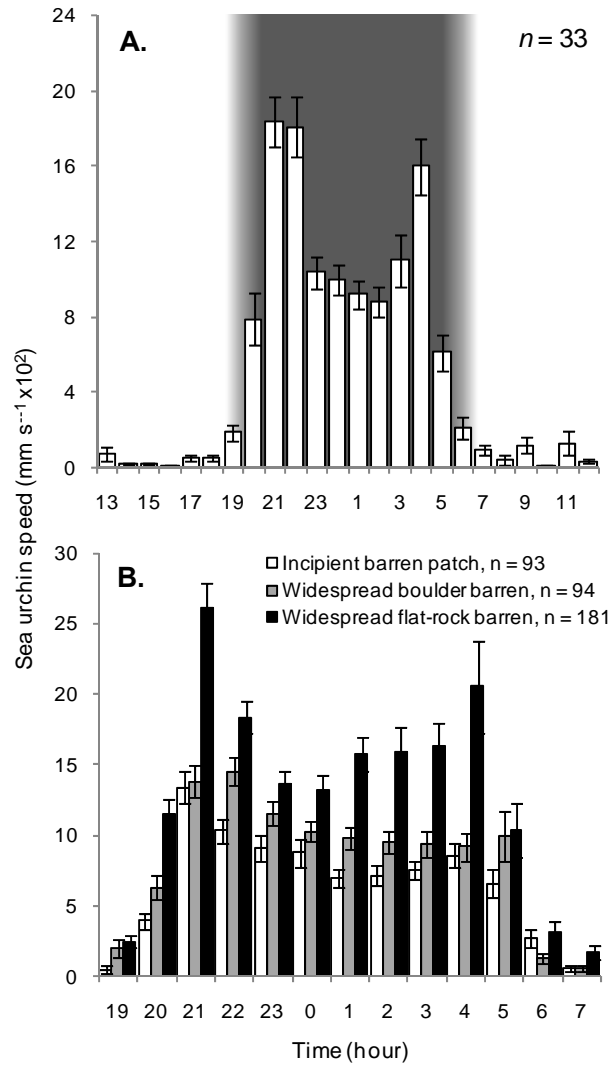


Figure A3.2. Mean (\pm SE) time-dependent velocity of *Centrostephanus rodgersii* on incipient, widespread boulder and widespread flat-rock barrens as recorded using time-lapse photography. Time is given in 24-hour format. (A) Movement over entire diel cycle and pooled across habitat types. Shading indicates estimated relative light levels based on the timing of sunset (20:38) and sunrise (05:27) averaged across recording dates. (B) Movement over nocturnal period separated into habitat types.

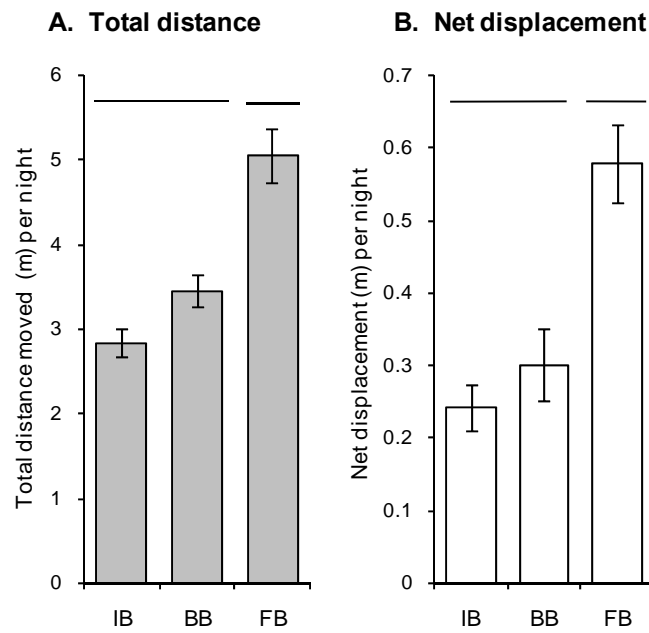


Figure A3.3. Movement of *Centrostephanus rodgersii* on incipient, widespread boulder and widespread flat-rock barrens between 19:30 and 07:30 hours as determined by time-lapse photography (data are means \pm S.E.). Only sea urchins remaining within the field of view for the duration of filming were considered; $n = 54, 51, 85$ for incipient (IB), widespread boulder (BB) and widespread flat-rock barrens (FB), respectively. Horizontal bars above indicate significant differences between habitat means determined by REGWQ tests after significant ANOVA. (A) Total distance moved throughout the recording period. (B) Net displacement (straight line distance) of sea urchins from their starting position after a night of foraging.

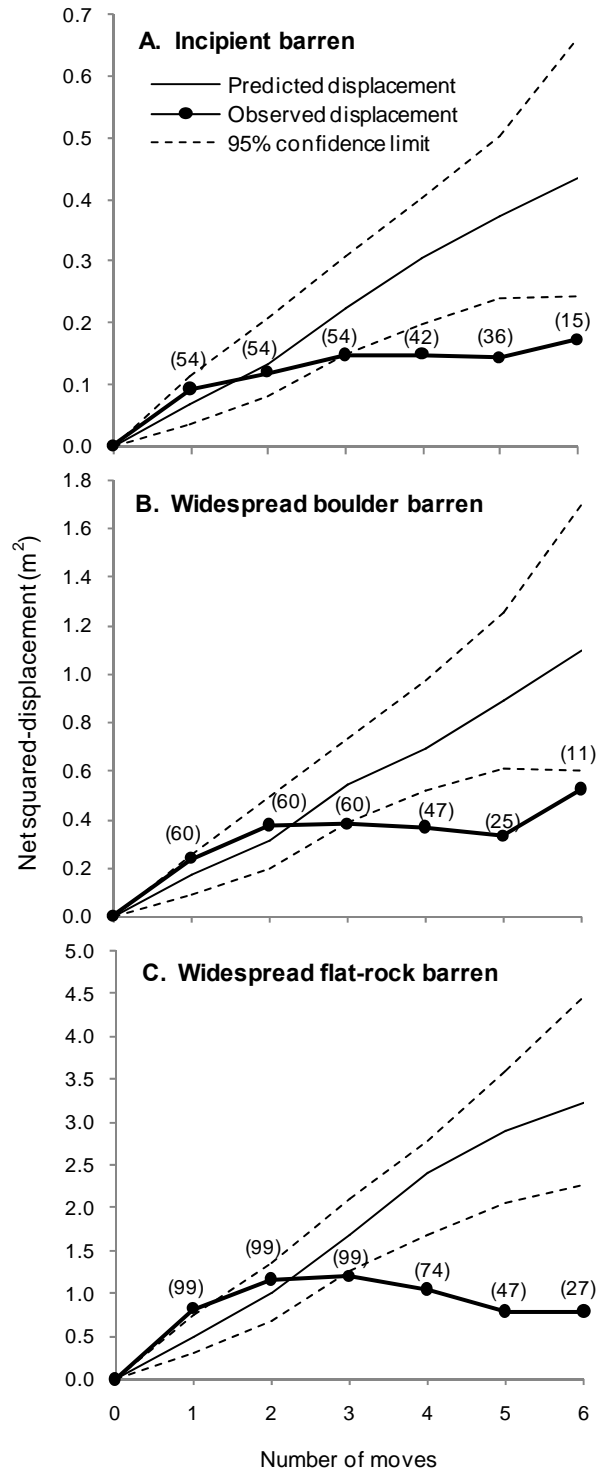


Figure A3.4. Examination of *Centrostephanus rodgersii* movement across habitats relative to predictions of a correlated random walk model. Mean net squared-displacement is calculated over six consecutive moves from predicted (solid line) and observed (closed circles) movement paths in three habitat types. Dashed lines are 95% confidence limits for the predicted net squared-displacement based on a random walk. Numbers in parentheses indicate the number of individuals observed.

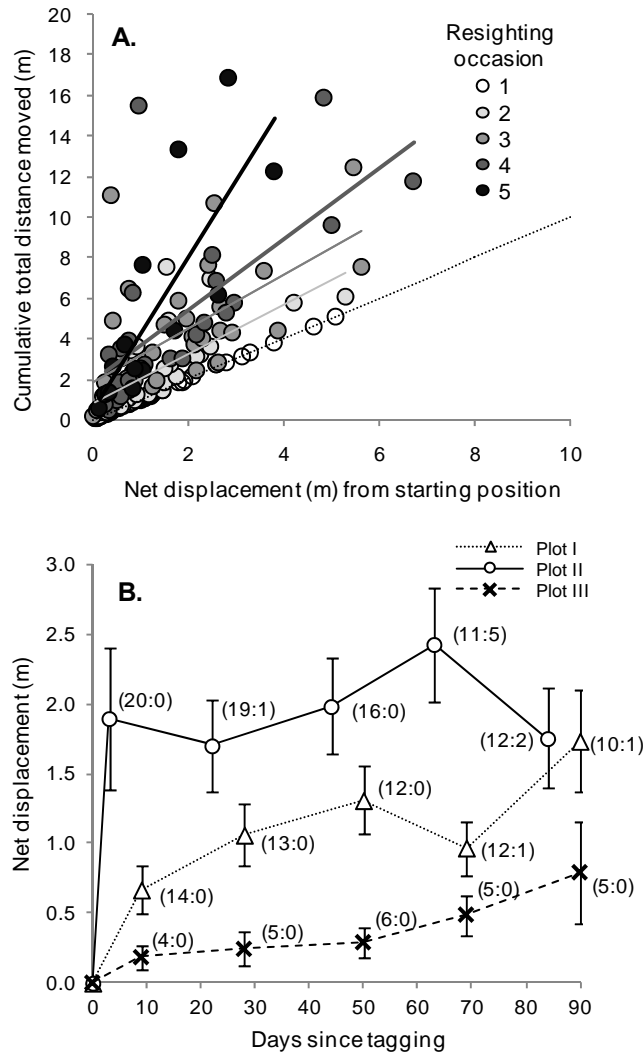


Figure A3.5. Movement of tagged *Centrostephanus rodgersii* over a three month monitoring period. (A) Cumulative total distance moved by individuals between sightings vs. net displacement from initial tagging position. Dashed line indicates perfect directional movement (1:1) away from the initial position, while perfect homing is represented by a vertical line passing through the origin. Gray scale of points and fitted lines darken with successive sighting occasions at 10, 28, 50, 69, 90 days since commencement of the experiment. Increasing slope of lines with successive sightings indicates persistent fidelity to incipient barren patches. (B) Mean (\pm SE) displacement of sea urchins from initial tagging position over time across monitored plots (barren patch plus surrounding kelp area). Numbers in parentheses indicate the number of individuals sighted on each monitoring occasion (inside patch : outside patch). Barren patch areas I-III are 2.41, 3.85 and 1.27 m², respectively.

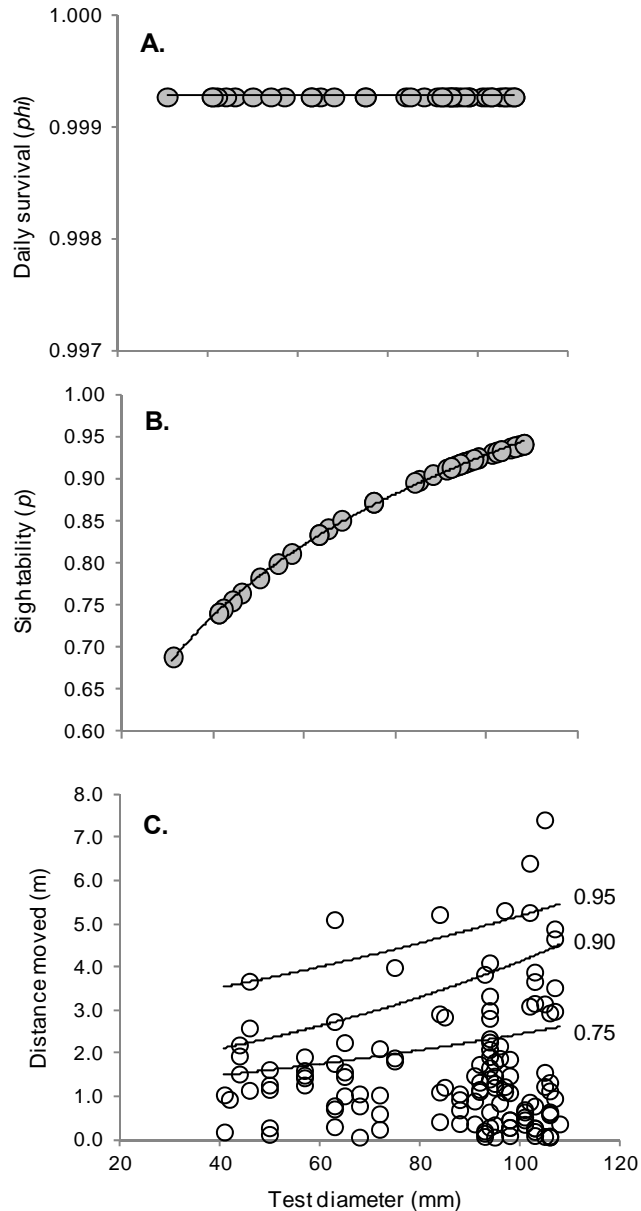


Figure A3.6. Size-specific characteristics of tagged *Centrostephanus rodgersii*. Relationship between (A) daily survival (ϕ) and test diameter; and (B) resighting probability (p) and test diameter; as estimated from the most parsimonious CJS model (variance inflation factor (\hat{c}) adjusted to account for overdispersion in sampling variation *as per* Pollock et al. 1990). (C) Net distance moved between consecutive sightings of individuals vs test diameter. 95th, 90th and 75th quantiles are given by $y = \exp(0.0065x + 0.9980)$, $P = 0.281$; $y = \exp(0.0113x + 0.2908)$, $P = 0.074$; and $y = \exp(0.0084x + 0.0573)$, $P = 0.037$, respectively.

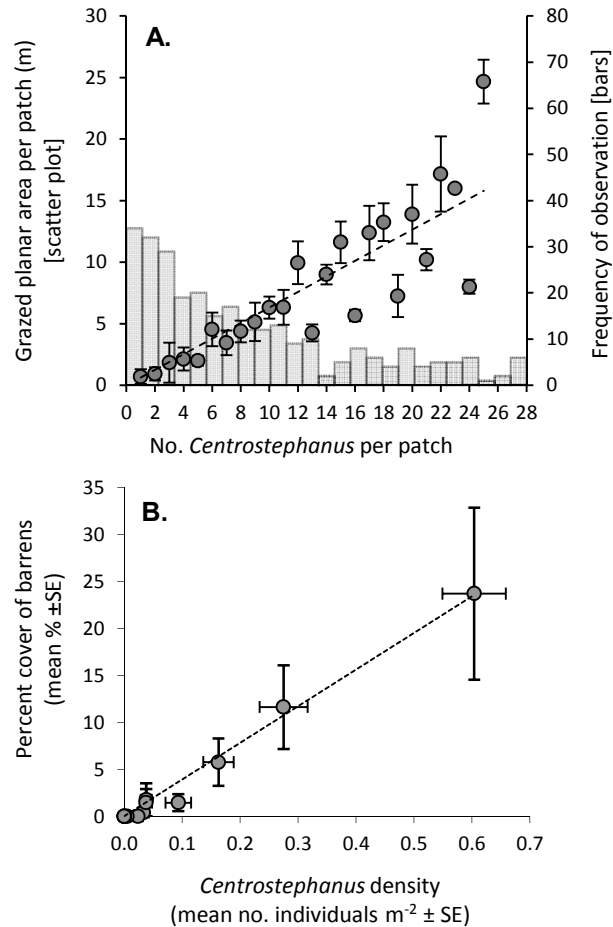


Figure A3.7. (A) Relationship between the grazed planar area of *Centrostephanus rodgersii* barrens patches and number of *C. rodgersii* per patch (data are means \pm S.E.) as assessed by timed geo-referenced diver swims ($n = 284$ individual patches). Linear regression given by $y = 0.631x$, $R^2 = 0.901$, $t(24) = 15.1$, $P < 0.0001$. Grey bars represent the observed frequency of each data point. (B) The percent cover of sea urchin barrens and *C. rodgersii* density across sites spanning the range-extension region, as assessed by $n = 156$ diver belt-transects (data from Johnson et al. 2005). Data expressed as means \pm S.E. Linear regression given by $y = 39.2x$, $R^2 = 0.99$, $t(12) = 37.5$, $P < 0.0001$. Note that because sea urchin barrens habitat on exposed eastern Tasmanian coast is caused exclusively by *C. rodgersii* with negligible contributions from grazing by the native *H. erythrogramma* (see Johnson et al. 2005), the intercept for the linear regression was set to 0.

APPENDIX 4: Assessing the effectiveness of abalone divers culling *C. rodgersii* while fishing

This work has been developed as a manuscript for publication, with a title and authorship as:

Title: Effectiveness of abalone divers at mitigating 'barrens' formation by culling sea urchins while fishing for abalone

Authors: Sanderson, J.C., Ling, S.D., Dominguez, J.G. & Johnson, C.R.

Given the simplicity of approach for this part of the project, an outline of methods is given in the main body of the report. This appendix presents an abstract of the paper, an outline of the broad context of the work, and a description of the statistical analyses of the data obtained in this component of the project.

Abstract

The incursion and spread of the long-spined sea urchin (*Centrostephanus rodgersii*) in eastern Tasmania, and its capacity to overgraze seaweeds to create 'barrens' habitat unable to support valuable fisheries, has prompted calls for strong management intervention. Here we examine the effectiveness of abalone divers at controlling *C. rodgersii* at local scales by smashing them while they fish for abalone. Diver behaviour suggests that fishing yield, not smashing sea urchins, is a primary motivator. At sites where catch rates of abalone were high, divers focussed on fishing and conducted long dives, while they abandoned dives early at sites where catch rates were low. Smash rates of sea urchins correlated negatively with fishing success, so the highest absolute numbers of sea urchins smashed were on shorter dives when fishing was poor. Despite that several thousand sea urchins were culled, overall densities of sea urchins at the cull sites and benthic community structure did not change significantly, and no change was detectable in the density or size frequency distribution of incipient barrens patches, reflecting that divers were able to cull urchins in only a small proportion of patches before quitting areas when catch rates declined. However, divers were effective in culling most urchins in the particular patches that they targeted, and these patches quickly reduced in size after culling due to algal regrowth. Professional divers culling sea urchins may help reduce risk of sea urchins barrens forming at particular local sites, but this activity will not be effective at controlling urchins at spatial scales much larger than $\sim 10^1$ m.

Context

The transformation of diverse and productive seaweed-dominated habitat on rocky reefs to poorly productive 'barrens' habitat largely devoid of seaweeds as a result of overgrazing by sea urchins has been reported from temperate coasts worldwide (Lawrence 1975; Chapman and Johnson 1990; Jackson et al. 2001; Steneck et al. 2002). In addition to causing loss of productivity and diversity, overgrazing to cause and maintain barrens habitat by sea urchins can threaten commercial fisheries associated with rocky reef habitat. Tasmania's two most valuable fisheries, black-lipped abalone (*Haliotis rubra*) and southern rock lobster (*Jasus edwardsii*), with a combined value of \sim \$AUD150M pa before processing, depend fundamentally on rocky reefs which support highly productive seaweed beds and a high diversity of associated other invertebrates. The single largest threat to the integrity of the shallow rocky reef system on the east coast of Tasmania is the long spined sea urchin (*Centrostephanus rodgersii*), which has only relatively recently established in Tasmanian waters (Johnson et al. 2005, 2011; Ling & Johnson 2009; Ling et al. 2008). This large diadematid sea urchin is problematic because it has the capacity to overgraze seaweeds and invertebrates on rocky reefs,

effecting a transition from highly productive and diverse seaweed-based systems to poorly productive 'barrens' habitat largely devoid of seaweeds, with greatly reduced invertebrate biomass and diversity, unable to support commercial fisheries for abalone or rock lobster (Johnson et al. 2005, 2011; Ling 2008).

Importantly, sea urchin populations are able to persist on and maintain barrens habitat indefinitely, and are themselves not threatened by the lower productivity of barrens (Johnson & Mann 1982). In line with the results of removal experiments around the globe focussed on other species (e.g. *Arbacia dufresnii* in southern Chile, Newcombe et al. 2012; *Heliocidaris erythrogramma* in Tasmania, Ling et al. 2010; *Paracentrotus lividus* in the western Mediterranean, Palacin et al. 1998; *Strongylocentrotus droebachiensis* in Eastern Canada, Himmelman et al. 1983), removal of *C. rodgersii* from barrens inevitably results in recovery of seaweeds (e.g. Hill et al. 2003; Andrew & Underwood 1993). Similar experiments in Tasmania indicate that seaweed cover and community structure in plots from which sea urchins are removed converges with that of ungrazed control sites within ~18 months of their removal (Ling 2008). However, while responses to small scale manipulative removals are unequivocal, attempts to control sea urchin numbers at larger spatial scales to reduce risk of formation of barrens habitat or rehabilitate seaweed beds, e.g. by application of quick-lime (Bernstein & Welsford 1982; Wilson and North 1983), removing fishing pressure on sea urchin predators (Tegner & Levin 1983; Tegner & Dayton 2000), or by developing targeted fisheries (Sala et al 1998; Guidetti et al 2004), has proven challenging.

All evidence to date indicates that barrens formation in eastern Tasmania, which occurs when populations of emergent adult sea urchins increase to the point where overgrazing is initiated, is likely the direct result of fishing of rock lobsters (*J. edwardsii*) on rocky reefs since large lobsters have been identified as the principal predator of *C. rodgersii* in Tasmania (Ling et al. 2009). This circumstance is not unique; it is already well established that *J. edwardsii* is the key predator of the smaller native sea urchin (*Heliocidaris erythrogramma*) in eastern Tasmania (Pederson & Johnson 2006), and there is a wealth of evidence from elsewhere in the world to suggest that development of sea urchin barrens is linked to fishing of predators (e.g. Steneck 1997, 1998; Sala et al. 1998; Pinnegar et al. 2000; Jackson et al. 2001; Steneck et al. 2002; Tegner and Dayton 2000; Shears and Babcock 2003). On the basis that formation of extensive tracts of barrens habitat is related to human activity, management intervention to limit the extent of sea urchins barrens, particularly when the transition from kelp bed to barrens habitat threatens valuable fisheries, is justified.

The southward incursion of *C. rodgersii* from NSW and its successful establishment in Tasmanian waters is most likely initially the result of transport of larvae, reflecting changes in the behaviour of the East Australian current driven by climate change (Johnson et al. 2005, 2011; Ling et al. 2008). Evidence suggests that this species established in the Kent Group in Bass Strait in the 1960s and in northeast Tasmania in the 1970s (Johnson et al. 2005, 2011). In the Kent Group ~50% of shallow reefs now exist as *C. rodgersii* barrens, reflecting the state of reefs on most of the NSW coast (Andrew & O'Neill 2000). Off Tasmania proper, *C. rodgersii* is now established along the entire east coast, and has latterly been discovered on the south and south west coasts (Ling et al. 2008). This relatively rapid range expansion and spread along the east coast of Tasmania, the extent of *C. rodgersii* barrens habitat in NE Tasmania, and the extent and rapidity of spread of 'incipient' barrens occurring as bare overgrazed patches in seaweed beds in eastern Tasmania has prompted calls to better manage the threat.

A meeting of stakeholders in December 2005, including representatives of the rock lobster and abalone fisheries, State fisheries managers, peak industry and community groups, and scientists, moved that management responses to formation of *C. rodgersii* barrens in Tasmania should be evaluated. Two broad classes of options for management were identified, namely strategic control of *C. rodgersii* populations at large scales by manipulation of their key predators, and tactical control at

local scales by the targeted activities of abalone divers. This paper specifically addresses the question of whether abalone divers can be effective in culling *C. rodgersii* at local scales while they fish for abalone. Focus on testing the effectiveness of abalone divers controlling urchin numbers while engaged in otherwise normal fishing activity reflects the motivation of the industry to respond to the problem in areas important to the abalone fishery, and the considerable expense of mobilising divers exclusively to cull or harvest sea urchins.

'Incipient' *C. rodgersii* barrens arise initially as small barrens patches, or holes in the kelp canopy, and individual barrens patches may be caused by as few as one or two sea urchins (Flukes et al. 2012). Progression in barrens formation is from initially sparse 'incipient barrens' patches, which increase in size and frequency with sea urchin density to form a reticulated network of barrens patches which eventually coalesce to create extensive barrens covering several tens of hectares in size and supporting hundreds of thousands of sea urchins. The question of the effectiveness of using abalone divers as a management response was focussed on incipient barrens given that extensive barrens do not support a viable abalone fishery (i.e. there is no motivation for divers to fish for abalone on extensive barrens), that incipient barrens are now a widespread feature of the Tasmanian coastline, and that control of urchin populations creating incipient barrens is likely to be far more tractable than addressing the challenge of rehabilitation of extensive barrens (Marzloff et al., submitted MS; Johnson et al. unpublished data).

Statistical analysis of results of culling

Given the simplicity of the approach required for this component of the project, the methods are largely outlined in the main body of the report. Here is summarized the approach to analysis of the data.

Parametric univariate ANOVA was used to estimate the significance of differences in sea urchin and abalone densities, extent of barrens cover, cover of canopy algae, and number of patch barrens between the start and the end of the experiment (based on the data from transect assessments and timed swims), and changes in size of the marked incipient barrens patches over the experimental period. For these tests data were checked for homogeneity of variances and a suitable transformation determined using Box-Cox plots. Transformations are expressed in terms of the untransformed variate, Y . Community structure at the sites before and after the culling periods, as defined by multivariate descriptors obtained from the transects, was depicted using a 2-dimensional ordination produced from canonical analysis of principal coordinates (CAP routine, PRIMER6) based on Bray Curtis similarities calculated after 4th root transformation of data. PERMANOVA (PRIMER 6) was used to assess the significance of differences in community structure. Comparison of frequency distributions of patch sizes from the timed swims was performed using the Kolmogorov-Smirnov test. The statistical package 'R' was used for the univariate analyses (v. 2.12.2). Where errors are presented, these are standard errors of means.

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APPENDIX 5: Assessing lobster translocations and the effect of protection from fishing: Lobster dispersal, population dynamics and behaviour post translocation

This element of the work has been prepared as a paper for submission to the *Proceedings of the National Academy of Sciences USA*.

Title: Rebuilding predatory lobsters on sea urchin barrens: Reducing undesirable and increasing desirable resilience among alternative reef states

Authors: Ling, S.D., Johnson, C.R., Sanderson, J. C. & Pederson, H. G.

The abstract of the paper, an explanation of the broader context of this work, and a detailed outline of the methods and technical appendices in support of the results and discussion presented in the main body of the report is given below.

Abstract

Ecosystem change can be typified by break point transitions after which return to prior ecosystem states may be very difficult or virtually impossible to achieve if the new state imposes strong feedbacks reinforcing its' own persistence. Such 'catastrophic phase shift', from productive kelp beds to impoverished sea urchin 'barren has occurred on reefs in eastern Tasmania caused by interaction of climate-driven range expansion of the sea urchin *Centrostephanus rodgersii* (Diadematidae) and ecological overfishing of rock lobsters (*Jasus edwardsii*) as the urchin's principal predator. Intensive fishing reduces the abundance of the predators and decreases the resilience of kelp beds against urchin overgrazing. While an abundance of large predatory spiny lobsters within kelp beds minimises the risk of forming extensive barrens, the ability of these predators to exist and function on reefs either already shifted to widespread barrens or catastrophic shift, has not been explored. By simultaneously mass translocating large predatory-capable lobsters (i.e. 'reverse-fishing') and protecting these reefs within no-take reserves, we show that large predatory lobsters persist by establishing home-ranges and normal foraging patterns on reefs supporting either extensive or incipient urchin barrens. Coupled with unrestrained growth of local resident lobsters within the protected areas to attain predatory-capable size, we show that large lobsters can be rebuilt to levels that effectively increase resilience of kelp beds at early stages of destructive grazing, and decrease resilience of extensive urchin barrens. Conversely, continued fishing on barren grounds will further enhance resilience of this undesirable state with a return to kelp beds exceedingly unlikely. Given the highly degraded state of many ecosystems, management for local-scale resilience of natural systems as a climate change adaptation measure must recognise alternative ecosystem configurations and act to both diminish resilience for undesirable states while promote resilience of remnant desirable ecosystem states.

Context

Global acceleration in the intensity and frequency of human perturbations on ecosystems threatens to exhaust the goods and services that have underpinned our populous rise as a species. While living systems are by their very nature renewable, there are increasing examples of altered ecosystems that no longer meet societal expectations for goods and services as experienced and depended upon by previous generations (e.g. Scheffer & Carpenter 2003; Hughes et al. 2005; Scheffer et al. 2012). With the majority of terrestrial and marine environments suggested to be approaching or at maximum exploitable capacity (e.g. Steffen et al. 2007; Rockström et al. 2009; Barnosky et al. 2011), there is an urgent need to sustain productive ecosystems by preventing further undesirable ecosystem shifts (which burdens remaining productive systems with even greater pressure), but to also identify the circumstances where remedial action will favour reversibility of degraded ecosystem states and the likely time scales involved.

Natural ecosystems are inherently renewable and robust to some level of stress, however major shift in the structure and function of these systems can occur if critical stress-thresholds are exceeded (reviewed by Scheffer et al. 2001). Particularly concerning for attempts to manage natural resources are ‘catastrophic phase-shifts’, whereby wholesale change in the underlying ecosystem dynamic occurs with a return to the former desirable ecosystem state exceedingly difficult or perhaps impossible once the critical stress-threshold has been passed (e.g. Lewontin 1969; May 1977; Holling 1973; Sutherland 1974; Petraitis & Dudgeon 2004; Scheffer et al. 2001, 2012; Fung et al. 2011). That is, once a threshold is exceeded, reversibility back to the preferred ecosystem configuration can be difficult, or virtually impossible to achieve if the new configuration imposes strong feedbacks (Ling et al. 2009a; Marzloff et al. 2011) reinforcing its’ own persistence (‘persistence stability’ *sensu* Holling 1973). Thus, defining the dynamics and mechanisms bestowing persistence stability, hereafter resilience, of both desirable and undesirable states is therefore essential if fundamental ecosystem dynamics are to be understood and ecosystems ultimately managed within a sustainable context.

Catastrophic phase-shift from productive kelp beds to impoverished barren reef has occurred in eastern Tasmania caused by recent climate-driven range expansion of the sea urchin *Centrostephanus rodgersii* (Diadematidae) (Johnson et al. 2005, 2011; Ling et al. 2008; Ling et al. 2009a&b). Transition from kelp beds to *C. rodgersii* barrens represents a catastrophic shift between alternative reef states because barrens display persistence stability, i.e. there are strong positive feedbacks (Marzloff et al. 2011) and return to the kelp-dominated state requires reducing sea urchin densities to much lower levels than the threshold at which destructive overgrazing occurs in the first place (Andrew & Underwood 1993; Ling et al. 2009a). The goods and services provided by rocky reefs are reduced in the barrens state due to loss of local biodiversity (Ling 2008) and the lucrative reef-based fisheries for abalone (*Haliotis rubra* ~AUD\$100M.year⁻¹ before processing; Andrew & Underwood 1992; Johnson et al. 2005, 2011; Strain & Johnson 2009). Furthermore, on near-shore reefs, commercially important spiny lobsters (*Jasus edwardsii* – Palinuridae) also appear to depend on kelp habitat (Fig. 25, main report) with lobsters generally found in low abundance when *C. rodgersii* occurs at high density and when sea urchin barrens become extensive (Fig. 25, main report).

The long-held consensus is that sea urchin barrens represent a degraded and undesirable temperate reef ecosystem state (lower productivity, Chapman 1981; and biodiversity e.g. Duggins et al. 1989) where benthic sea urchin predators (e.g. lobsters, Breen & Mann 1976; Mann 1977; Wharton & Mann 1981; Wahle & Incze 1997; Johnson et al. 2005; and fish, e.g. Vadas & Steneck 1995) occur in low abundance. While the negative correlation between extent of barrens and abundance of urchin predators is in several cases clear (e.g. Fig. 1b, main report), it begs the question of whether there are few predators on extensive barrens because they have been fished down, or because sea urchin barrens represent undesirable habitat for predators. In eastern Tasmania, large lobsters are the

principal predator of *Centrostephanus rodgersii* (Ling et al. 2009a) and the native sea urchin *Heliocidaris erythrogramma* (Pederson & Johnson 2006), but heavy fishing has reduced the abundance of functional sea urchin predators and decreased resilience of kelp beds against overgrazing by sea urchins (Johnson et al. 2004; Pederson & Johnson 2006; Ling et al. 2009a). While an abundance of functional predatory lobsters within kelp beds inside marine reserves has been shown to minimise risk of urchins commencing destructive grazing in the first instance (Ling et al. 2009a), for reef already shifted to extensive barrens the ability of lobsters to exist and function within this alternative configuration, which confers its own level of resilience, has not been explored.

For predator-driven recovery of seaweeds on extensive barrens habitat in eastern Tasmania, large predatory capable lobsters (>140 mm carapace length [CL]; Ling et al. 2009a) must either permanently or semi-permanently inhabit sea urchin barrens or at least undergo frequent foraging excursions from adjacent kelp habitat and, for incipient barrens existing as barrens patches within an otherwise intact kelp bed, they must visit barrens patches to prey on the urchins. Here we combine benthic habitat mapping, acoustic monitoring of individual lobsters, *in situ* surveys, and geo-referenced trapping arrays and mark-recapture methods over ~2.5 years to generate high-resolution information on lobster behaviour to determine whether lobster populations can be rebuilt on barrens habitat and thus affect the resilience of this alternative and undesirable rocky reef state. We achieved this by conducting a large-scale 'reverse fishing' experiment in which 933 large predatory-capable lobsters (≥ 140 mm CL, total biomass ~2,400 kg; see Table A5.1) were re-introduced to a widespread barrens ground (barrens 10^4 m² in size, see Table A5.2) that was simultaneously closed to fishing (the Elephant Rock Research Reserve, ERRR, in north east Tasmania). We ran a parallel experiment involving translocation of 732 large predatory lobsters (~2,194 kg, Table A5.1) to incipient barrens existing within otherwise intact kelp beds supporting ~1% cover of barrens patches at scales of 10^0 - 10^1 m² in size (the North Bay Research Reserve, NBRR, in south east Tasmania).

Methods

Correlative relationships between lobsters, kelp beds and sea urchin barrens

Relationships between abundance of southern rock lobsters (*Jasus edwardsii*) and percentage cover of seaweed, and between lobsters and extent of *Centrostephanus rodgersii* sea urchin barrens, were assessed across eastern Tasmania in 5m by 1m quadrats laid haphazardly on the reef surface. Assessed *in situ* by divers, quadrats were surveyed contiguously along each of 12 transect lines set perpendicularly from the shore (~6 m depth to a maximum of 18 m depth; $n = 11,455$ 5 m² quadrats in total) at 13 eastern Tasmanian sites (open to lobster fishing) and separated by approximately 20 km ranging in latitude from 40°55'S to 43°10'S, some 330 km of coastline (*for more details see* Johnson et al. 2005). Quantile regression was used to define the relationship between variables (Quantreg package in program R version 2.15.1).

Experimental re-introduction of large predatory-capable lobsters

Large predatory capable lobsters (≥ 140 mm Carapace Length [CL]) caught from commercial vessels fishing baited traps on deepwater reefs in NE and NW Tasmania were purchased and translocated to research reserves in NE and SE Tasmania specifically declared to support this project. A total of 933 large lobsters (140 – 220 mm CL; total biomass 2,386 kg, mean size 173 mm CL or 2.6 kg per individual), were translocated to widespread *C. rodgersii* barrens habitat and an adjacent kelp bed within the Elephant Rock Research Reserve (ERRR) in north east Tasmania in April and November 2008 (Figs. 3, 25 in main body of report; Table A5.1). In south east Tasmania, a total of 732 large lobsters (140 – 220 mm CL, total biomass 2,039 kg, mean size 178 mm CL or 2.8 kg per lobster) were translocated to kelp beds containing incipient *C. rodgersii* barrens patches within the North Bay Research Reserve (NBRR) in May 2009 and March 2010, (Figs. 3, 25 in main body of report; Table A5.1). Translocation of captured large lobsters involved maintain animals in flow-through holding tanks

onboard commercial fishing vessels, and / or in holding cages at sea, before transferral, following live export protocol, to aquarium facilities at fish processing plants where lobsters were tagged individually prior to transport to the research reserves in plastic bins covered with hessian soaked in sea water, and their release by divers on the sea floor. Translocated lobsters were individually tagged from the ventral surface with Passive Integrated Transponders (PIT) tags and/ or external T-bar tags. Carapace length and gender was recorded for each individual. Owing to the logistical constraints of obtaining large lobsters from disparate commercial fleet, translocated lobsters were tagged at different times, in different places and released across different dates, but broadly within the periods of autumn & spring in 2008 for ERRR; and autumn 2009 plus spring 2010 for NBRR (Table A5.1).

Patterns of habitat utilisation and dispersal

Reef habitat classification

Benthic reef habitats within the research reserves, plus adjacent fished reefs, were mapped using acoustic mapping in combination with towed underwater video transects for quantifying benthic habitats from swaths ~ 2.5 m wide sampled along aisles spaced at 60 m intervals across the reef surface. Detailed habitat maps of the study sites were created following the methods of Jordan et al. (2005). The spatial extent of rocky reef was defined at each site using variations in first and second echoes in the echogram collected by a single-beam sounder (Simrad EK60). Benthic habitats were simultaneously identified using geo-referenced benthic video towed within 5-8 m behind the vessel using a weighted low-drag towfish camera 'flown' over the benthos and maintained at approx. 2 m from the seafloor by a dedicated operator responding to an onboard monitor relaying video from the camera tow-fish. The camera and a GPS antenna were linked to AcrPad v6.0 (Environmental Systems Research Institute, ESRI) recording the track-log and overlaying coordinates on the video footage. Reef habitats were characterised as either kelp beds (canopy forming kelp dominating approx. >30% cover), widespread *C. rodgersii* barrens (100% cover for patches exceeding 1,000 m²) or deeper sessile invertebrate 'sponge garden' habitat (Table A5.2). In depths too shallow to map using vessel-based acoustics (intertidal to ~6 m depth), reefs were visually assessed and recorded as being dominated by *Durvillea potatorum* (Durvillaeaceae) in the lower intertidal grading to dense monospecific stands of *Phyllospora comosa* (Seirococcaceae) from ~3 to ~ 6 m depth which became mixed with *Ecklonia radiata* (Laminariales) at ~6-8 m depth where widespread barrens became dominant at ERRR.

Given that kelp beds within NBRR and adjacent fished reef at this site manifest as continuous and largely intact stands, with occasional barrens patches scattered throughout (Fig. 25, main body of report), individual barrens patches (location and approximate dimensions) were mapped *in situ* by divers towing GPS units. Habitat features, logged in WGS84 format, were loaded into the geo-processing software Eonfusion v2.0 (Myriax Pty. Ltd) for projection and delineation of habitat polygons defining each benthic habitat map.

Acoustic tracking of translocated lobsters

To determine habitat utilisation of translocated lobsters and fine scale movement in relation to benthic habitats, 22 of the translocated lobsters at ERRR were fitted with V16 continuous acoustic transmitters and tracked for up to ~8 weeks across kelp beds and *C. rodgersii* urchin barrens during both winter (12 individuals tracked) and summer periods (10 individuals tracked) in 2008/09 using the VRAP telemetry system (VEMCO Radio-linked Acoustic Positioning, AMRIX, Vemco Division; see Table A5.3).

Table A5.1. Details of translocation of large predatory capable lobsters and concomitant protection of reefs from lobster fishing for (A.) widespread *Centrostephanus rodgersii* barrens in north-east Tasmania, Elephant Rock Research Reserve (declared 23rd April 2008); and (B.) incipient *C. rodgersii* barrens in south-east Tasmania, North Bay Research Reserve (declared 1st November 2008).

	Research Reserve	Habitat	Release date	No. lobsters translocated	
A.	Elephant Rock Research Reserve	Widespread barrens	April 2008	476	
			November 2008	116	
					592
		Adjacent kelp beds	April 2008	213	
			November 2008	128	
					341
			<i>Total</i>	933	
B.	North Bay Research Reserve	Kelp bed with incipient barrens	May 2009	543	
			March 2010	189	
					732
					<i>Total</i>
				<i>Grand total</i>	1,665

Table A5.2. Habitat distribution at Elephant Rock (characterised by widespread barrens, North East Tasmania) and North Bay (kelp beds with incipient patch barrens, South East Tasmania) research sites.

Site	Habitat	Research Reserve		Entire sampling area (trapping grid incl. adjacent fished zones)	
		Area (m ²)	% of reef	Area (m ²)	% of reef
ER	Kelp beds	183,318	40.0	550,337	47.6
	Barrens	197,867	43.2	365,872	31.7
	Sessile invertebrates	77,140	16.8	239,025	20.7
			458,325		1,155,235
NB	Kelp beds	173,592	98.9	506,338	~98.9
	Incipient barrens	1,931	1.1	5,632	~1.1
			175,523		511,970

At NBRR, 6 large predatory capable lobsters were tracked for ~7-8 weeks with VRAP technology across kelp beds and incipient *C. rodgersii* barrens in summer 2010 (Table A5.4). Each transmitter emits a unique frequency between 51 and 84 kHzs at 3 kHz intervals with a transmission period of 2 seconds once activated. Transmitters were attached to the carapace of translocated and resident individuals using quick setting (5 min) epoxy resin. The VRAP system was deployed forming an equilateral triangle spanning 180 m on each side, above the rocky reef at each research site. The VRAP system successfully tracked the movement of the translocated lobsters tagged with transmitters with a positional accuracy of 1 to 2 meters when occurring inside the buoy triangle. If the transmitter moves outside the buoy triangle the accuracy decreases. To maintain positional accuracy, the system was recalibrated against known buoy positions every 60 mins.

Acoustic data processing

Location estimates were calculated from raw acoustic data collected by the VRAP receivers using VRAP v5.1.2 software (AMRIX, Vemco Division) and the default 'Position Average' algorithm. Location estimates for each acoustic transmitter were exported from the VRAP5.1.2 software program in standard geodetic format (using the WGS84) and batch loaded into the geo-processing software Eonfusion v2.0 (Myriax Pty. Ltd) for re-projection, processing and error removal. Location estimates were re-projected using the Universal Transverse Mercator (UTM) system and the Geocentric Datum of Australia 1994 (GDA94/MGA Zone55) to allow accurate distance and velocity calculations. Erroneous location estimates were removed by constructing a line feature between consecutive location estimates for each transmitter and examining each segment of each line feature. Location estimates were removed from the data if they resulted in line feature segments where the average velocity exceeded $3\text{m}\cdot\text{min}^{-1}$, and the difference in heading from the previous line segment formed an acute angle $<30^\circ$. Following the removal of each erroneous location estimate, line features were reconstructed and the process reiterated until no further erroneous location estimates were observed (two iterations were required).

Acoustic Data Analysis

Lobster Home Ranges (HR95, defined by polygons containing 95% of all positional estimates, i.e. 95% fixed kernel density, after Worton, 1989) were generated using the least-square cross validation method (LSCV), as fixed kernel estimates were least biased in the outer contours (Seaman et al., 1999). The proportions of different habitat types occurring within the HR were then derivable, as was estimation of time-spent residing on each habitat type. The velocity of movement for lobsters residing in kelp bed and barrens habitat were also calculated. Total displacement of lobsters by habitat type (classified by the habitat in which a lobster was first detected by VRAP) was calculated as the distance between initial and final positional estimates (up to ~ 8 weeks apart; see Tables A5.3, A5.4). The proportions of different habitat types within each HR95, time spent on sea urchin barrens vs. kelp beds, velocity; and displacement (i.e. total net distance moved divided by tracked duration in days) were examined with 2-way ANOVA testing the effects of 'Habitat' (fixed; kelp beds vs. urchin barrens), and 'Season' (fixed; winter vs. summer). All statistical analyses were conducted using *R* (v2.15.1). All analyses of variance were conducted following appropriate tests of assumptions and data were transformed to stabilise variance where necessary, as determined using the Box-Cox procedure.

Table A5.3. Habitat composition of Home Range (95%) and Activity Centre (defined as inner 50% of data around the HR centroid) of large acoustically tracked lobsters released in the Elephant Rock Research Reserve during (a.) Winter (Aug) 2008, and (b.) Summer (Dec) 2008; “Number of clean positional estimates” is that obtained following data filtering of erroneous positional estimates (see *Materials & Methods*); “Total Displacement (m)” is the distance moved from the initial to final positional estimate at conclusion of the study, or when tag was last locatable; “Displacement Rate” is “Total Displacement” divided by the number of days tracked.

Season	Lobster	No. clean positional estimates	Days tracked	Habitat composition (m ²) of Home Range						Total Displacement (m)	Displacement (m day ⁻¹)
				Home Range area (m ²)	Activity Centre area (m ²)	Kelp	Barrens	Invert	Sand		
Winter 8/07 - 15/09/2008	1	851	51	12,015	2,627	0	8,625	796	2,595	16	0.23
	2	84	26	10,226	1,121	3,704	6,071	0	451	77	1.11
	3	237	17	14,415	2,984	0	7,065	1,134	6,216	141	2.04
	4	2089	55	9,139	893	346	8,336	0	457	63	0.91
	5	94	17	19,219	1,641	11,243	7,151	0	825	141	2.04
	6	4152	55	8,177	1,031	7,931	0	0	246	3	0.04
	7	183	15	5,681	602	5,416	0	0	265	64	0.93
	8	417	19	3,837	718	0	3,615	0	221	38	0.55
	9	1759	57	11,736	1,782	93	8,146	1,003	2,494	189	2.73
	10	268	20	3,781	1,095	0	164	2,988	630	181	2.62
	11	876	29	5,090	893	0	4,422	163	505	309	4.48
	12	265	38	7,642	1,985	354	7,089	0	200	191	2.77
		average	940	33	9,247	1,448	2,424	5,057	507	1,259	118
Summer 7/12 - 30/12/2008	1	127	21	39,150	7,706	10,534	4,182	14,206	10,228	212	9.22
	2	84	12	84,222	12,220	38,030	33,253	10,313	2,626	166	7.20
	3	58	5	61,555	4,555	14,318	41,265	3,672	1,858	301	13.07
	4	121	13	17,218	1,279	2,166	14,329	523	199	237	10.28
	5	15	4	378,660	68,334	125,671	137,548	17,872	26,829	202	8.79
	6	11	3	26,046	4,426	6,377	19,669	0	0	53	2.30
	7	29	8	18,178	2,098	12,752	5,426	0	0	171	7.45
	8	132	15	23,758	2,640	0	3,515	7,300	12,943	493	21.41
	9	508	21	3,407	464	3,358	50	0	0	21	0.90
	10	185	19	17,136	1,802	1,553	5,545	4,680	5,358	20	0.87
	average	127	12	66,933	10,552	21,476	26,478	5,857	6,004	187	8.15

Table A5.4. (A.) Home Range (95%) and Activity Centre (defined as inner 50% of data around the HR centroid) areas of large lobsters acoustically tracked within kelp beds in the North Bay Research Reserve during Summer 2010/2011; “Number of clean positional estimates” is that obtained following data filtering of erroneous positional estimates (see *Materials & Methods*); “Total Displacement (m)” is the distance moved from the initial to final positional estimate at conclusion of the study, or when tag was last locatable; “Displacement Rate” is “Total Displacement” divided by the number of days tracked. (B.) Proportion of acoustically tracked time spent by large lobsters within incipient *Centrostephanus rodgersii* barrens patches and kelp beds at NBRR; “Expect. inside barrens” / “Expect. outside barrens” is the time expected to be spent inside/ outside barrens patches based on a strict 1:1 usage of habitats in proportion to availability; “Forage Ratio” is the ratio of time spent inside barrens patches relative to that spent in kelp beds, i.e. values >1.0 indicate more time within barrens patches based on availability of this habitat.; <1.0 indicates more time spent in kelp beds proper.

(A.) Summary of tracking details for large lobsters in North Bay Research Reserve:

Season	Lobster	No. clean positional estimates	Days tracked	HR Home Range area (m ²)	Activity Centre area (m ²)	Total Displacement (m)	Displacement Rate (m ^{-day})
Summer 17/12/2010 - 09/02/2011	1	1996	54	3,992	736	24	0.44
	2	1745	54	2,406	683	18	0.33
	3	2049	53	1,895	519	143	2.70
	4	5342	48	1,443	554	7	0.15
	5	5586	54	1,746	629	31	0.57
	6	23	53	7,990	2,837	59	1.11

(B.) Time spent within barrens patches:

Lobster	Time tracked (minutes)	Time Barrens (minutes)	Time Kelp beds (minutes)	% time barrens	% reef barrens	Expect. inside barrens	Expect. outside barrens	Forage Ratio
1	78,697	1,196	77,501	1.54%	1.03%	811	77,887	1.48
2	77,895	1,903	75,992	2.50%	1.03%	802	77,092	2.37
3	76,442	872	75,570	1.15%	1.03%	787	75,654	1.11
4	69,633	443	69,191	0.64%	1.03%	717	68,916	0.62
5	78,685	147	78,538	0.19%	1.03%	810	77,875	0.18
6	67,309	785	66,524	1.18%	1.03%	693	66,615	1.13
All	448,661	5,345	443,317	1.21%	1.03%	4,621	444,040	1.16

Patterns of diel activity for translocated lobsters were obtained from the velocity of successive moves in time steps of 0.1 fractions of the day (i.e. 2.4 hr periods). Frequency distributions of movement between day and night (using mean dawn and dusk periods across each monitoring session) were compared using non-parametric Kolmogorov-Smirnov tests conducted in R version 2.15.1.

Lobster catch-rates and abundance estimates across reef habitats and status

To estimate lobster abundance across kelp beds and sea urchin barrens, to examine dispersal of translocated lobsters, and to assess the effectiveness of reserve protection on lobster size and abundance, baited trap sampling of lobsters was performed at ~6 monthly intervals at each site. Constructed from welded steel frames covered with 25 by 25 mm string mesh, lobster traps were set evenly across the available reef area inside the research reserves, and on adjacent reefs which remained open to lobster fishing, by trapping intersecting points of a regular spaced 60 by 60 m virtual grid (see Fig. 25, main report). For each trap position, benthic habitat type was assessed during habitat mapping as described above (see Table A5.5). Approximately 70 traps were randomly deployed across each gridded trapping array on 4 consecutive nights in each trapping period, ensuring that no grid location was sampled twice in any one trapping period (Table A5.5). As is standard practice in commercial fishing operations, traps were baited with whole jack mackerel (*Trachurus declivis*) and couta (*Thyrsites atun*) heads, which were deployed on the reef in depths of ~ 3-45 m. Traps were effective at sampling lobsters to a minimum size of approximately 50 mm CL (~60 g) while lobsters below this size, while present at the sites, were likely to escape through the mesh. Traps were serviced from approx. 45 mins post-dawn to midday and were freshly rebaited before each deployment. Each captured lobster was measured for carapace length (CL, to nearest mm) with knife-edge callipers, and assigned to size categories of small (≤ 110 mm CL, i.e. legally undersized lobsters); medium (>110 & <140 mm CL); and large (≥ 140 mm CL, inclusive of large residents and large translocated individuals). Lobsters were sexed and, if untagged, tagged with a unique T-bar tag (as described above).

Table A5.5. Details of all trap sampling and lobster catches inside and outside research reserves at Elephant Rock (north east Tasmania) and North Bay (kelp beds with small incipient barrens present, south east Tasmania) 2008 – 2011.

Site	Status	Session	Date	No. traps			Lobster catch		Resident	
				Total	Kelp beds	Barrens	Kelp beds	Barrens	Kelp beds	Barrens
Elephant Rock	Reserve	1	27-31/05/2008	113	54	59	5	9	3	7
		2	12-15/8/2008	105	45	60	8	14	11	9
		3	9-12/12/2008	105	45	60	7	10	33	55
		4	21-24/04/2009	105	45	60	4	8	8	17
		5	8-11/12/2009	101	41	60	1	6	49	57
		6	3-6/8/2010	104	44	60	2	7	14	24
		7	30/11 - 3/12/2010	105	45	60	4	9	67	61
	Fished	1	27-31/05/2008	140	95	45	5	1	8	2
		2	12-15/8/2008	122	77	45	5	1	34	11
		3	9-12/12/2008	123	78	45	6	5	61	29
		4	21-24/04/2009	123	78	45	3	4	10	9
		5	8-11/12/2009	114	51	63	NA	NA	29	26
		6	3-6/8/2010	122	77	45	3	4	19	15
		7	30/11 - 3/12/2010	121	76	45	2	3	25	23
North Bay	Reserve	1	02-04/07/2009	125	125		14		35	
		2	15/07/2009	32	32		11		21	
		3	10-12/02/2010	127	127		1		62	
		4	02-04/06/2010	126	126		6		30	
		5	21-22/07/2010	60	60		11		53	
		6	18/11/2010	32	32		5		63	
		7	01-03/02/2011	127	127		7		12	5
	Fished	1	02-04/07/2009	82	82		3		78	
		2	10-12/02/2010	83	83		3		12	4
		3	02-04/06/2010	83	83		0		24	
		4	01-03/02/2011	73	73		1		55	

Analysis of catch-rate data

Patterns of variability in lobster catch rate (i.e. abundance of lobsters per pot) were analysed using Generalised Linear Models fitted to the Poisson distribution (i.e. catch data was heavily left-skewed, ranging from 0 to 5 lobsters per pot) using *R* version 2.15.1. Analysis of deviance of fully-saturated models (including all main and interactive effects), as per standard analysis of variance but substituting classical *F*-tests for maximum likelihood estimation, were performed separately to (1) test effects of sampling 'Period' (1-7) and 'Habitat' (kelp bed vs. widespread urchin barrens) on lobster abundance at ER using a factorial design; and (2) to a priori test the effect of reef 'Status' (reserve vs. fished) at the start and conclusion of the study using a 1-way design comparing lobster catch rates. For the first test, the effects of 'Period' (1-7) and 'Habitat' (kelp beds vs. urchin barrens) on the abundance of different lobster size-classes was examined inside the research reserve only given effects of fishing outside the reserve. In examining habitat distributions for small under-legal sized lobsters (<110 mm CL), which are not affected by harvesting, data were pooled across the reserve and adjacent fished reef. Secondly, the effect of reef 'Status' at the start and conclusion of the study was examined separately for each of the north east (i.e. ERRR) and south east (NBRR) regions. Parameters estimating the magnitude of difference in catch rates were obtained using the log link function and are expressed as multipliers of lobster abundance in kelp beds relative to urchin barrens, and reserve relative to fished reef, as appropriate.

As patterns in lobster catch may be influenced by depth as well as reef habitat type at ERRR (see Fig. 25, main body of report), the distribution of sampling effort across depths for kelp and barrens habitats was examined using the non-parametric Kolmogorov-Smirnov (KS) test. Depth distributions of each lobster size-class (Fig. A5.1) were also compared by a series of pair-wise KS tests. Note that while kelp beds were more frequent on shallower reef (~5-15 m depth) than barrens (~15-30 m depth) (see Fig. 25, main report; Fig. A5.1a), there was no difference in depth frequency distributions between size-classes of lobster, although depth distributions between large and medium size-classes of lobster were different (Table A5.6). To further explore the potential effect of depth on interpretation of habitat-specific patterns in lobster catch at ERRR, catch rates for each lobster size-class were examined across depth using linear regression (in *R* version 2.15.1). Data were pooled across all sampling occasions and binned by 2 m depth intervals to ensure that catch rates used in linear regressions were calculated from a minimum effort of 10 trap samples per depth.

In situ diver counts of lobsters: kelp bed vs. urchin barrens

Lobster abundance within kelp beds and adjacent sea urchin barrens was assessed *in situ* by divers counting all lobsters occurring within 50 x 4 m (= 200 m²) belt transects. Six replicate belt transects were positioned randomly within each of kelp bed and adjacent widespread *C. rodgersii* sea urchin barrens at ERRR and at two external fished reefs without added lobsters (Sloop Rock, -41°12'32, 148°17'36; and St. Helens Island, -41°20'38, 148°20'23). Transects were fixed in space and re-surveyed at ~6 monthly intervals on 5 occasions between 21/04/2008 to 23/12/2010. Due to low overall counts, data from pre-translocation at ERRR were also included. Lobsters were small, medium or large as described above, but for analysis were pooled into a count of total lobsters given low counts. Count data were analysed with GLM using the same approach and statistical distribution and link function as described above in analysing the data from trapping surveys.

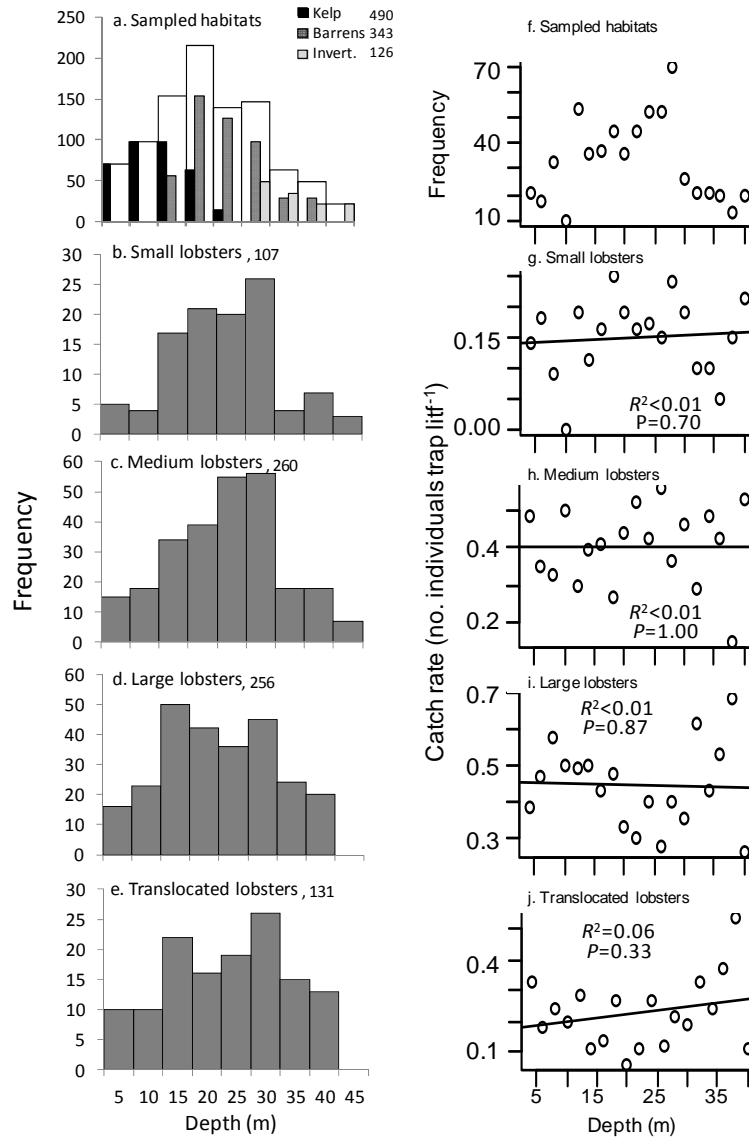


Figure A5.1. (a.) Frequency distribution of sampling (trap lifts) across depths at ERRR (open bars); narrow shaded bars show depth distributions across different habitats (total trap lifts per habitat depth combination shown in legend; significant differences were apparent between all pair-wise habitat comparisons, Kolmogorov-Smirnov (KS) tests, $P < 0.001$ in all cases). (b.-e.) Depth distributions of lobster catch by size-class; pair-wise tests revealed statistically similar depth distributions across size-classes for all but medium vs. large lobsters (see 6 pair-wise tests in Table A5.6); numbers at the top of each panel show samples sizes (n) in (a.) and the total number of trapped lobsters by size-class in (b.-e.). Right hand column shows scatter plots of the frequency distribution of trap lifts (f), and catch rate for each lobster size-class by 2 m depth intervals (g.-j.); R^2 and P values are shown for fitted lines.

Table A5.6. Pair-wise comparisons of depth distributions between different lobster size classes at (A.) ERRR, and (B.) NBRR. Kolmogorov-Smirnov tests, for 6 pair-wise tests. Table indicates D statistic and associated *P* value for each comparison. Significant difference is indicated by asterisk.

A.	Small	Medium	Large
Small	-	-	-
Medium	D = 0.05; 0.988	-	-
Large	D = 0.13; 0.169	D = 0.14; 0.015*	-
Large translocated	D = 0.11; 0.454	D = 0.10; 0.298	D = 0.08; 0.678

B.	Small	Medium	Large
Small	-	-	-
Medium	D = 0.12; 0.31	-	-
Large	D = 0.13; 0.91	D = 0.16; 0.78	-
Large translocated	D = 0.29; 0.13	D = 0.19; 0.60	D = 0.27; 0.48

Mark-recapture analysis: estimates of survival and catch-ability

While patterns in catch rate indicate relative abundances of lobsters in kelp beds and urchin barrens, and on fished and protected reef, mark-recapture modelling enables estimating survival and recapture probabilities, and absolute abundance. Because every translocated lobster and captured resident was uniquely tagged, individual captures and recaptures yielded 'encounter histories' for each tagged lobster across trapping sessions (Table A5.5; individuals were scored as either 'alive and present' = 1, or 'absent' = 0, at each re-sampling period). This enabled modelling individual survival estimates for translocated and resident lobsters using a Cormack-Jolly-Seber (CJS) framework modelling 'recaptures only' as available in the Program MARK[®] software (White and Burnham 1999). For CJS, the number of individuals re-sighted alive on subsequent sampling occasions is a function of the probability of survival (ϕ) and the probability that a surviving individual is encountered (ρ), referred to here as the recapture probability. Program MARK[®] uses Maximum Likelihood estimation to derive estimates of the parameters ϕ and ρ which maximize the likelihood of witnessing the observed frequency of individuals across different encounter history scenarios.

Modelling lobster survival and recapture probabilities commenced with testing the goodness-of-fit (GOF) of the most parameterized (saturated) model, which included factors of 'time', 'origin' (translocated or resident), 'gender' (male or female), and 'size' (small, medium or large). Following satisfactory GOF, program MARK uses maximum likelihood methods to estimate the conditional probabilities of apparent survival (ϕ) and recapture (ρ) (White and Burnham, 1999). The modelling procedure enables comparison of a series of reduced *a priori* models and thus to identify the best supported model given the variability in the data (Lebreton et al., 1992). Models are selected through an iterative process of pairwise comparisons between the parsimony of a starting model and that of related but simplified models from the candidate set. The minimum value of the quasi-likelihood form of the Akaike Information Criterion, QAICc, is used to select the most parsimonious model of the hierarchy of possible models. Candidate models were ranked in order of most parsimonious based on the lowest QAICc (Burnham and Anderson, 1998).

While CJS enables estimating survival and recapture probabilities, the Jolly-Seber framework (offered as the POPAN model in program Mark[®] - which is noted as a particularly robust parameterisation of the Jolly-Seber model) enables estimation of total population size, *N*. Because benthic habitat maps provided accurate polygons of planar reef area, lobster densities (no. individuals m⁻²) were estimable. Because this approach to mark-recapture analysis requires multiple re-surveys to ensure robust encounter histories, *N* is best estimated by inclusion of the full temporal extent of all encounters, and thus here we report on *N* at final sampling only. Furthermore, because over parameterisation is

problematic, we provide a total N as opposed to providing mark-recapture model estimates of N within each size-class of lobster (let alone for each size-class of lobster within each habitat within either fished or reserve reefs). Thus, our approach was to estimate total N and subsequently estimate abundance within each size-class by factoring for the proportion of lobsters across size-classes as observed during the final sampling period (this was achievable given that recapture probabilities were not size-dependent for lobsters within or outside research reserves). POPAN models the four parameters φ (apparent survival); p (recapture probability, assuming the animal is alive and within the study area), $Pent$ (probability of entry into the population for the current occasion), and N (super-population size). For t occasions, there are $t-1$ estimates of φ , t estimates of p , $t-1$ estimates of $Pent$, and 1 estimate of N . The $t-1$ $Pent$ estimates correspond to the probability of entry for occasions 2, 3, ..., t . The probability of being in the population on the first occasion is equal to $Pent(0) = 1 - \sum(Pent(i))$. The *MLogit* link function provides a constraint that makes the sum of the $Pent$ parameters ≤ 1 , with the probability of occurring in the population on the first occasion as $1 - \sum(Pent(t))$.

A constraint of both CJS and POPAN mark–recapture approaches that rely on tag-resighting data for survival estimates is that the estimates are confounded by events such as tag loss or emigration from the area defined by the trapping array that lead to a tag becoming unavailable for resighting. Thus, estimates of mortality will be inflated by tag loss and movement of lobsters away from the trapping area. The analysis allowed for unequal resighting probabilities (p) across surveys owing to differences in sampling effort (pot lifts) and seasonal variation in catch ability of rock lobsters (Lebreton et al., 1992; Zeigler et al. 2002, 2003, 2004). In addition to the standard assumptions of the CJS procedure, i.e. that (i) every marked animal in the population has the same probability of recapture, (ii) every marked animal has the same probability of surviving, (iii) marks are not lost or missed, and (iv) all samples are instantaneous and each release is immediately after sampling, several additional assumptions were necessary in this analysis, namely that (v) there was no effect of the identity of the person tagging on tag loss, (vi) tag loss was equivalent between translocated and resident animals, and (vii) that season and length of time ‘at large’ had no effect on tag loss.

The following figures and tables are presented as supplementary information. They are referred to in the main body of the report but are presented as a technical appendix so as not to detract from the readability of the main report.

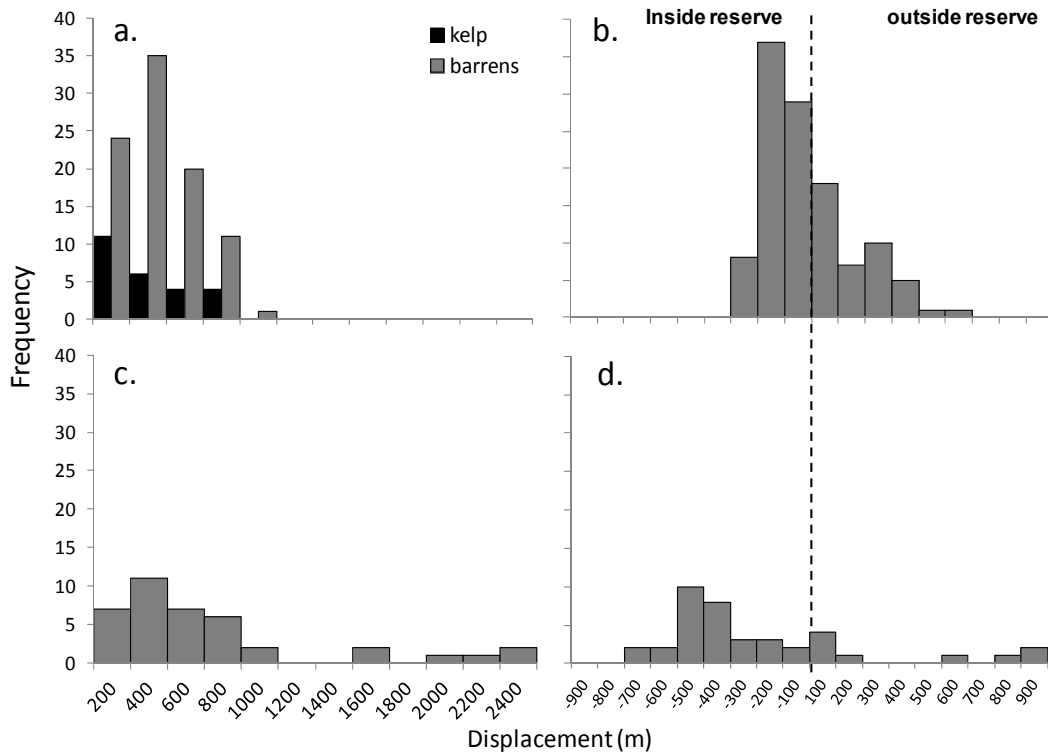


Figure A5.2. Displacement (between sites of release and first recapture) of translocated lobsters caught by traps; (a.) by kelp bed and barrens habitat at ERRR (Kolmogorov Smirnov test; $D = 0.263$, $P = 0.132$); with displacement distances averaging 358 m ($\pm 21SE$, $n=91$) and 308 m ($\pm 44SE$, $n=25$) for lobsters inhabiting barrens and kelp beds respectively; overall mean = 346.9m ($\pm 19SE$, $n=116$) overall. (b.) Displacement of lobsters from release and reserve boundary by kelp bed and barrens habitat at ERRR; kelp = $-109.3 \pm 35.9SE$, $n= 25$; barrens $-52.73 \text{ m} \pm 24.11 \text{ SE}$, $n= 79$; [pooled data is shown as no diff. between kelp vs. barrens, $D=0.1949$; $P=0.4661$]; overall mean across habitats at ERRR (mean $-66.32\text{m} \pm 20.30SE$, $n=104$), i.e. occurring within reserve (negative); (c.) Displacement of translocated lobsters caught by traps at NBRR (based on first recapture events only across 4 sampling sessions), mean $627.62\text{m} \pm 98.32SE$, $n=39$; KS test, NBRR vs. ERRR, $D=0.2807$; $P=0.0201$); but ERK vs. NBRR revealed non-sig. Diff. $D=0.3323$, $P=0.07$. (d.) Displacement of translocated lobsters relative to the reserve boundary at NBRR; mean $-277.39 \text{ m} \pm 70.00SE$, $n=39$.

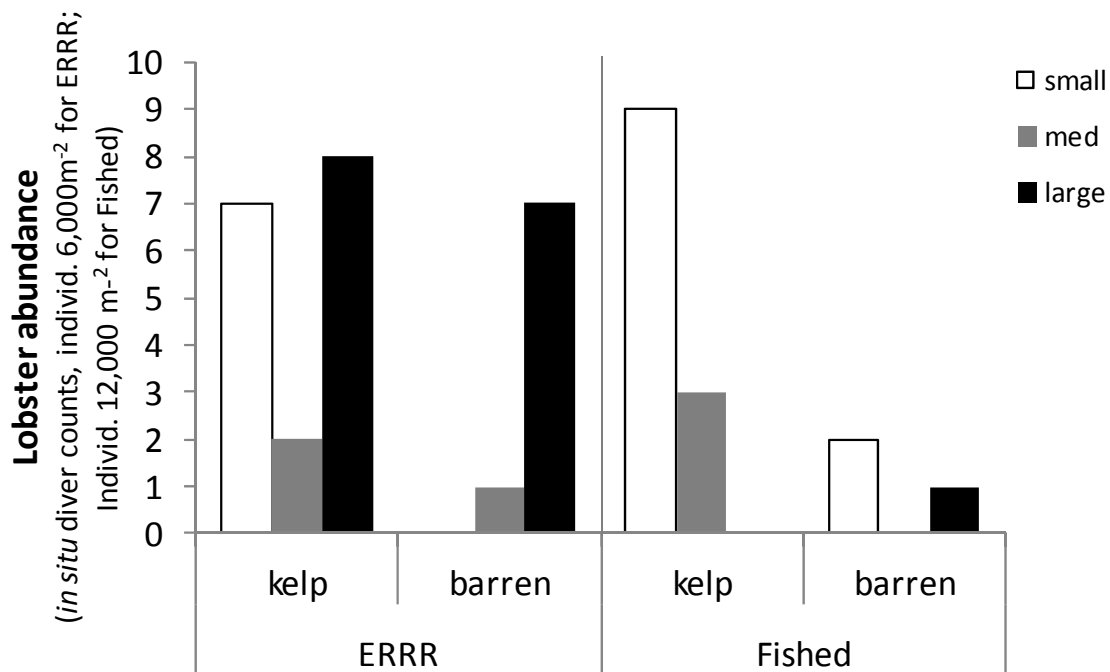


Figure A5.3. Lobster abundance by habitat type inside and outside ERRR as assessed *in situ* by divers ranging ~12 to 18 m depth. Fished sites are pooled for Sloop Rock and St. Helens Is (these are control sites without added lobsters and open to fishing, and are nearby to but not juxtaposed with the translocation area at ERRR. Data pooled over 5 sampling periods Autumn 2008 to Summer 2011, n=30, 200 m² belt transects per habitat at ERRR (6 fixed belt transects * 5 sampling periods, 6,000 m² in total); and n=60 transects per habitat (6 transects * 5 sampling periods * 2 sites) across the two fished sites (12,000 m² surveyed in total).

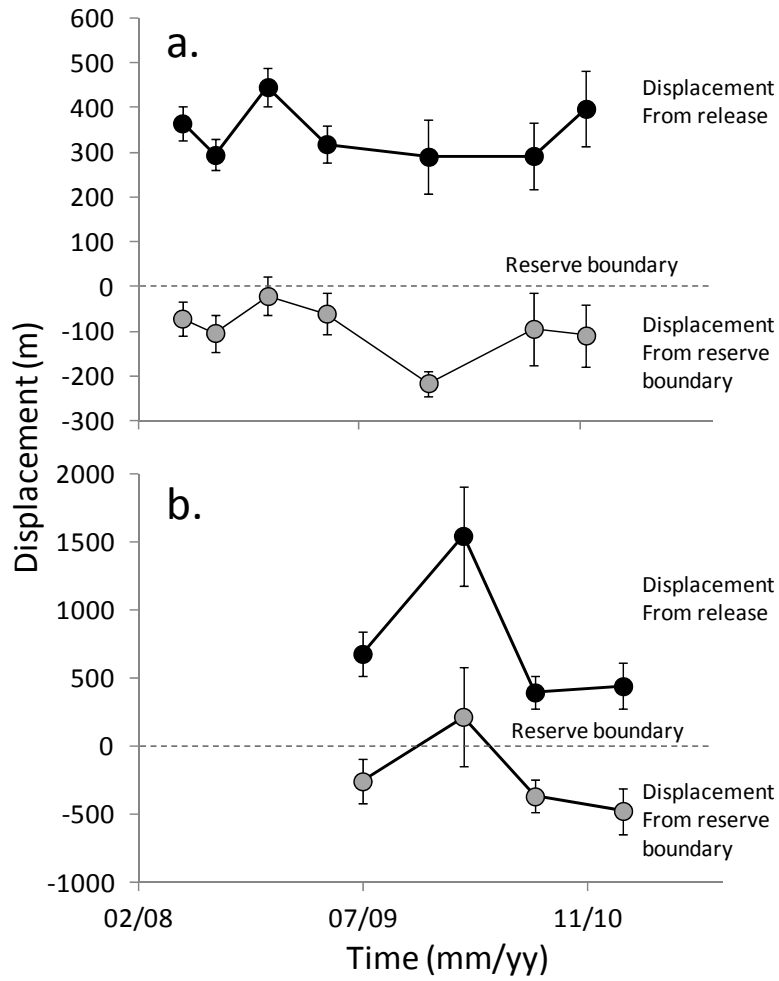


Figure A5.4. Temporal trends of displacement of large translocated lobsters from release positions and distance to nearest reserve boundary at ERRR (a.) and NBRR (b.), 2008-2011. For distance to nearest reserve boundaries (lower portion of each panel), negative values occur within research reserve boundaries while positive values occur on fished reef beyond reserve boundaries.

Table A5.7. Analysis of deviance table [Model: poisson, link = log; response = *in situ* lobster counts, size-classes pooled due to low overall counts in some size-classes; terms added sequentially (first to last)] examining the effect of habitat (kelp vs. barrens) and sampling period on the abundance of lobsters (a.) on reef inside ERRR; (b.) reefs subject to lobster fishing; and (c.) overall analysis examining reef status (reserve vs. fished (2 fished sites post-hoc pooled, as inclusion of site not important, LR-test $P=0.33$)), habitat and period effects. Factor indicates the multiplicative effect of kelp habitat on lobster abundance (including 95% confidence intervals shown in parentheses); and multiplicative effect of the reserve on lobster abundance in (c.).

		df	Deviance Resid.	df	Resid. Dev	Pr(>Chi)		Factor (lower – upper 95%CI)
a. ERRR	NULL			59	87.41			
	Habitat	1	3.6515	58	83.76	0.0560		2.13 (0.98-4.90)
	Period	1	1.4546	57	82.30	0.2278		
	Habitat*Period	1	0.3017	56	82.00	0.5828		
b. Fished	NULL			119	91.52			
	Habitat	1	8.7331	118	82.79	0.0031	**	2.18 (0.20-35.36)
	Period	1	2.2814	117	80.51	0.1309		
	Habitat*Period	1	0.5217	116	79.99	0.4701		
c. All	NULL			179	193.47			
	Status	1	14.5409	178	178.93	0.0001	***	1.25 (0.08-24.10)
	Habitat	1	10.9648	177	167.97	0.0009	***	2.18 (0.20-35.36)
	Period	1	0	176	167.97	1.0000		
	Status*Habitat	1	1.4198	175	166.55	0.2334		
	Status*Period	1	3.736	174	162.81	0.0533		
	Habitat*Period	1	0.7049	173	162.11	0.4011		
	Status*Habitat*Period	1	0.1185	172	161.99	0.7307		

TableA5.8. Analysis of deviance table [Model: poisson, link = log; response = *in situ* lobster counts; size-classes pooled due to low overall counts in some size-classes; terms added sequentially (first to last)] examining the effect of reef status (reserve vs. fished), for (a) ER Initial; (b) ER Final; (c) NB Initial; and (d.) NB Final. For significant effects, parameter estimates are shown as a multiplier of the abundance of lobsters on fished reef (including 95% confidence intervals shown in parentheses), thus values >1.00 indicate higher lobster abundance within reserves relative to fished reef.

Elephant Rock - <i>Initial</i>							
Lobster class		df	Deviance	Resid. df	Resid. Dev	P P(> Chi)	Parameter estimate
Large translocated	<i>null</i>			272	187.06		
	status	1	5.07	271	181.99	0.02	*
Large	<i>null</i>			272	246.37		
	status	1	5.63	271	240.74	0.02	*
Medium	<i>null</i>			272	265.99		
	status	1	0.27	271	265.71	0.60	ns
Small	<i>null</i>			272	261.11		
	status	1	1E-05	271	261.11	1.00	ns
All large	<i>null</i>			272	399.66		
	status	1	10.59	271	389.07	0.001	**
Legal-size residents	<i>null</i>			272	351.02		
	status	1	3.83	271	347.19	0.05	.

Elephant Rock - <i>Final</i>							
Large translocated	<i>null</i>			249	75.65		
	status	1	18.22	248	57.427	2E-05	***
Large	<i>null</i>			249	167.45		
	status	1	41.52	248	125.93	1E-10	***
Medium	<i>null</i>			249	306.43		
	status	1	23.07	248	283.36	2E-06	***
Small	<i>null</i>			249	188.14		
	status	1	0.06	248	188.08	0.81	ns
All large	<i>null</i>			249	222.81		
	status	1	58.62	248	164.19	2E-14	***
Legal-size residents	<i>null</i>			249	361.68		
	status	1	52.27	248	309.41	5E-13	***

Table A5.8 (con't...)

North Bay -Initial								
Lobster class		df	Deviance	Resid. df	Resid. Dev	P P(> C hi)		Parameter estimate
Large translocated	<i>null</i>			208	16.60			
	status	1	2.11	207	31.65	0.15	ns	
Large	<i>null</i>			208	18.60			
	status	1	1.99	207	16.60	0.16	ns	
Medium	<i>null</i>			208	16.60			
	status	1	0.00	207	0	1.00	ns	
Small	<i>null</i>			208	6E-10			
	status	1	41.94	207	259.60	9E-11	***	0.25 (0.16-0.39)
All large	<i>null</i>			208	29.54			
	status	1	0.28	207	42.61	0.59	ns	
Legal-size residents	<i>null</i>			208	217.66			
	status	1	1.99	207	18.60	0.16	ns	
North Bay - Final								
Large translocated	<i>null</i>			199	51.50			
	status	1	2.35	198	49.16	0.13	ns*	4.02 (0.72-75.21)
Large	<i>null</i>			199	115.65			
	status	1	6.89	198	108.75	<0.01	**	3.45 (1.33-11.74)
Medium	<i>null</i>			199	201.04			
	status	1	1.54	198	199.50	0.21	ns	
Small	<i>null</i>			199	212.93			
	status	1	0.71	198	212.22	0.40	ns	
All large	<i>null</i>			199	137.33			
	status	1	9.22	198	128.11	<0.01	**	3.56 (1.51-10.44)
Legal-size residents	<i>null</i>			199	243.23			
	status	1	6.00	198	237.23	0.01	*	1.78 (1.12-2.94)

Table A5.9. Mark-recapture summaries for resident and translocated lobsters on reefs inside and outside ERRR and NBRR.

Site	Origin of lobsters	Number tagged	Number of occasions re-sighted				Re-sighted at least once
			0	1	2	3	
ERRR	Resident	447	408	34	4	1	39
	Translocated	784	683	89	10	2	101
NBRR	Resident	361	337	23	1	0	24
	Translocated	785	736	49	3	0	52
ERRR plus adjacent fished	Resident	791	733	51	6	1	58
	Translocated	784	620	136	25	3	164
NBRR plus adjacent fished	Resident	636	604	30	2	-	32
	Translocated	785	726	56	3	-	59

Table A5.10. Model reduction summary of CJS estimates for ERRR (see methods). Satisfactory fit of saturated model, GOF, $P=0.093$.

Rank	Model description	Hypothesis	AICc	Delta AICc	AICc Weights	Model likelihood	Num . Par	Deviance
1	$\phi(O_{1-2}^T; O_{3-7}^T; O_{1-7}^R) p(t)$	Translocated lobster survival is different immediately after release, then constant with period and same as residents thereafter; recapture varies through time	493.81	0.00	0.32	1.00	8	158.67
2	$\phi(.) p(t)$	Survival does not vary, recapture varies through time	494.25	0.44	0.26	0.80	7	161.19
3	$\phi(O_{1-2}^T; O_{3-7}^T; O_{1-7}^R) p(t)$	Translocated lobster survival is different immediately after release, then constant with period and different to residents thereafter; recapture varies through time	495.41	1.60	0.14	0.45	9	158.19
4	$\phi(t) p(t)$	Survival and recapture varies through time	495.65	1.84	0.13	0.40	11	154.25
5	$\phi(O) p(t)$	Translocated lobster survival is different to residents; recapture varies through time	496.32	2.51	0.09	0.29	8	161.18
6	$\phi(S*G*O; O_{1-2}^T; O_{3-7}^T) p(t)$	Translocated lobster survival is different immediately after release, then constant with period and different to residents which varies with size and gender; recapture varies	498.96	5.16	0.02	0.08	13	153.34
7	$\phi(S*G*O) p(t)$	Survival varies with size, gender, and origin	499.99	6.19	0.01	0.05	12	156.48
8	$\phi(t) p(.)$	Survival varies through time, while recapture not dependent on time	500.27	6.46	0.01	0.04	7	167.20
9	$\phi(.) p(.)$	Survival and recapture not dependent on group or time	501.23	7.42	0.01	0.02	2	178.39
10	$\phi(O_{1-2}^T; O_{3-7}^T; O_{1-7}^R) p(O_{1-7}^T; O_{1-7}^R)$	Translocated lobster survival is different immediately after release, then constant with period and different to residents thereafter; recapture not dependent on time for	503.42	9.61	0.00	0.01	10	164.12
11	$\phi(O_{1-2}^T; O_{3-7}^T; O_{1-7}^R) p(O_{1-7}^T; O_{1-7}^R; S_{1-7}^L; G_{1-7}^M; O_{1-7}^R)$	Translocated lobster survival is different immediately after release, then constant with period, recapture not dependent on time for translocated or large resident males	503.49	9.68	0.00	0.01	10	164.18
12	$\phi(O_{1-2}^T; O_{3-7}^T; O_{1-7}^R) p(O_{1-7}^T; O_{1-7}^R; S_{1-7}^L; G_{1-7}^M; O_{1-7}^R)$	Translocated lobster survival is different immediately after release, then constant with period, recapture not dependent on time for translocated or large residents	504.12	10.31	0.00	0.01	10	164.82
13	$\phi(S*G*O) p(.)$	Survival varies with size, gender and origin	507.19	13.38	0.00	0.00	7	174.13
14	$\phi(t) p(S*G*O)$	Survival varies with time and recapture varies with size, gender, and origin	510.54	16.73	0.00	0.00	13	164.91
15	$\phi(.) p(S*G*O)$	Survival constant and recapture varies with size, gender, and origin	510.68	16.88	0.00	0.00	8	175.55
16	$\phi(S*G*O) p(S*G*O)$	Both survival and recapture varies with size, gender, and origin	512.94	19.14	0.00	0.00	12	169.43
17	$\phi(S*G*O*t) p(t)$	Survival varies with size, gender, origin, and time; recapture varies with time	522.57	28.77	0.00	0.00	34	130.18
18	$\phi(S*G*O*t) p(.)$	Survival varies with size, gender, origin, and time	527.76	33.96	0.00	0.00	30	144.63
19	$\phi(.) p(S*G*O*t)$	Survival constant and recapture varies with size, gender, origin, and time	529.50	35.69	0.00	0.00	39	125.29
20	$\phi(O_{1-2}^T; O_{3-7}^T; O_{1-7}^R) p(S*G*O*t)$	Translocated lobster survival is different immediately after release, then constant with period and same as residents thereafter; recapture is dependent on group and varies	530.06	36.26	0.00	0.00	40	123.46
21	$\phi(S*G*O) p(S*G*O*t)$	Survival varies with size, gender, and origin; recapture also varies time	530.70	36.89	0.00	0.00	40	124.09
22	$\phi(t) p(S*G*O*t)$	Survival varies with time and recapture varies with size, gender, origin, and time	531.71	37.90	0.00	0.00	43	117.84
23	$\phi(S*G*O*t) p(S*G*O)$	Survival varies with size, gender, origin and time; recapture varies with size, gender, origin	535.13	41.32	0.00	0.00	35	140.40
24	$\phi(S*G*O*t) p(S*G*O*t)$	Saturated model	978.32	484.51	0.00	0.00	62	104.10

Survival (ϕ) and resighting (p) probabilities may be a function of group (size, S; gender, G; origin, O), or time (t). Subscripts refer to sampling periods (1–7); Superscripts refer to resident (R), translocated (T), female (F), or male (M). A semi-colon separates the survival parameters in each model. Model QAICc, a measure of the parsimony of each model; Model weight, a measure of the relative weight of evidence in support of a model and used for model averaging; #Par, the number of parameters in the model. Model terminology follows Lebreton et al. (1992) and Besnard et al. (2007).

Table A5.11. Model reduction summary of CJS estimates for NBRR. Satisfactory fit of saturated model, GOF, $P=0.939$.

Rank	Model description	Hypothesis	AICc	Delta AICc	AICc Weights	Model Likelihood	Num. Par	Deviance
1	$\emptyset(.) p(t)$	Survival not dependent on size, gender or origin, recapture dependent on time	243.23	0.00	0.14	1.00	7	94.18
2	$\emptyset(O_{1-2}^T O_{3-7}^T O_{1-7}^R) p(O_{1&4}^T O_{2-3,5-7}^T O_{1-7}^R)$	Translocated lobster survival and recapture is different immediately after release, then constant with period and same as residents thereafter	243.26	0.03	0.13	0.98	8	92.10
3	$\emptyset(S^*G^*O) p(t)$	Survival dependent on group, recapture dependent on time	243.47	0.24	0.12	0.89	12	83.73
4	$\emptyset(O_{1-2}^T O_{3-7}^T O_{1-7}^R) p(t)$	Translocated lobster survival is different immediately after release, then constant with period and same as residents thereafter, recapture dependent on time	244.20	0.97	0.08	0.62	8	93.04
5	$\emptyset(S^*G^*O; O^T O^R S^L) p(t)$	Lobster survival dependent on size, gender and origin with large residents the same as translocated, recapture dependent on time	244.41	1.19	0.07	0.55	11	86.84
6	$\emptyset(S^*G^*O; O_{1-2}^T O_{3-7}^T O^R S^L) p(t)$	Translocated lobster survival is different immediately after release, then constant with period and same as large residents thereafter, recapture dependent on time	244.69	1.46	0.07	0.48	12	84.96
7	$\emptyset(S^*G^*O; O^T O^R S^L) p(t)$	Translocated lobster survival is the same as large residents, recapture dependent on	244.86	1.64	0.06	0.44	8	93.70
8	$\emptyset(.) p(S^*G^*O)$	Recapture dependent on size, gender and origin	244.95	1.72	0.06	0.42	7	95.90
9	$\emptyset(O_{1,4}^T O_{2-3,5-7}^T O_{1-7}^R) p(t)$	Translocated lobster survival is different immediately after release, then constant with period and same as residents thereafter, recapture dependent on time	244.99	1.77	0.06	0.41	8	93.83
10	$\emptyset(O_{1-2}^T O_{2-7}^T O_{1-7}^R) p(t)$	Translocated lobster survival is different immediately after initial release, then constant with period and same as residents thereafter, recapture dependent on time	245.26	2.04	0.05	0.36	8	94.11
11	$\emptyset(S^*G^*O; O_{1,4}^T O_{2-3,5-7}^T) p(t)$	Lobster survival dependent on size, gender and origin with translocated lobsters different survival post release, recapture dependent on time	245.57	2.35	0.04	0.31	13	83.66
12	$\emptyset(S^*G^*O; O_{1-2}^T O_{2-7}^T) p(t)$	Lobster survival dependent on size, gender and origin with translocated lobsters different survival post initial release, recapture dependent on time	245.62	2.40	0.04	0.30	13	83.71
13	$\emptyset(t) p(O_{1&4}^T O_{2-3,5-7}^T O_{1-7}^R)$	Capture of translocated lobsters different immediately after release	245.62	2.40	0.04	0.30	7	96.57
14	$\emptyset(S^*G^*O; O_{1-2}^T O_{3-7}^T O^R S^L) p(t)$	Translocated lobster survival is different after release then same as large residents, recapture dependent on time	246.09	2.86	0.03	0.24	12	86.35
15	$\emptyset(t) p(t)$	Survival and recapture dependent on time	249.68	6.45	0.01	0.04	11	92.11
16	$\emptyset(t) p(S^*G^*O)$	Survival dependent on time, recapture dependent on size, gender and origin	250.84	7.61	0.00	0.02	12	91.10
17	$\emptyset(S^*G^*O) p(S^*G^*O)$	Survival and recapture dependent on size, gender and origin	254.11	10.89	0.00	0.00	12	94.38
18	$\emptyset(.) p(.)$	Survival and recapture not dependent on group or time	258.74	15.51	0.00	0.00	2	120.02
19	$\emptyset(S^*G^*O) p(.)$	Survival dependent on size, gender, and origin	261.33	18.10	0.00	0.00	7	112.28
20	$\emptyset(t) p(.)$	Survival, but not recapture, dependent on time	265.25	22.02	0.00	0.00	7	116.20
21	$\emptyset(S^*G^*O^*t) p(t)$	Survival dependent on size, recapture dependent on time	265.50	22.28	0.00	0.00	33	56.64
22	$\emptyset(.) p(S^*G^*O^*t)$	Recapture dependent on size, gender, origin and time	271.79	28.57	0.00	0.00	37	52.70
23	$\emptyset(t) p(S^*G^*O^*t)$	Survival dependent on time, recapture dependent on size, gender, origin and time	281.29	38.06	0.00	0.00	41	51.66
24	$\emptyset(S^*G^*O) p(S^*G^*O^*t)$	Survival dependent on size, gender, and origin; recapture also dependent on time	281.70	38.48	0.00	0.00	42	49.40
25	$\emptyset(S^*G^*O^*t) p(S^*G^*O)$	Survival dependent on size, gender, origin and time; recapture dependent on size, gender,	281.76	38.53	0.00	0.00	33	72.89
26	$\emptyset(S^*G^*O^*t) p(S^*G^*O^*t)$	Saturated model	292.10	48.87	0.00	0.00	49	40.43
27	$\emptyset(S^*G^*O^*t) p(.)$	Survival dependent on size, gender, origin and time	293.12	49.90	0.00	0.00	29	94.19

Survival (ϕ) and resighting (p) probabilities may be a function of group (size, S ; gender, G ; origin, O), or time (t). Subscripts refer to sampling periods (1–7); Superscripts refer to resident (R), translocated (T), female (F), or male (M). A semi-colon separates the survival parameters in each model. Model QAICc, a measure of the parsimony of each model; Model weight, a measure of the relative weight of evidence in support of a model and used for model averaging; #Par, the number of parameters in the model. Model terminology follows Lebreton et al. (1992) and Besnard et al. (2007).

Table A5.12. Best estimate of large predatory capable lobster abundance within ERRR based on parameters derived using survival determined from best supported CJS model (Table A5.9 above). Shown are survival (ϕ , fixed according to CJS model as two estimates; ϕ_1 for translocated lobsters immediately post-translocation, and ϕ_2 for resident lobsters and translocated lobster post the immediate release period); recapture (p) probabilities as a function of sampling period (1-7); probability of entry into population (pent) split by residents (all lobster size-classes the same) and translocated lobsters.

Parameter	Estimate	Standard Error	95% Confidence Interval		
			Lower	Upper	
1: ϕ_1	0.9776	0.0000	0.9776	0.9776	*Fixed
2: ϕ_2	0.9998	0.0000	0.9998	0.9998	*Fixed
3:p 1	0.0305	0.0067	0.0198	0.0468	
4:p 2	0.0526	0.0105	0.0355	0.0774	
5:p 3	0.1189	0.0204	0.0844	0.1650	
6:p 4	0.0475	0.0098	0.0316	0.0708	
7:p 5	0.0508	0.0079	0.0374	0.0686	
8:p 6	0.0217	0.0040	0.0150	0.0312	
9:p 7	0.0662	0.0100	0.0491	0.0886	
10:pent 1(residents)	1.04E-01	6.15E-02	3.06E-02	2.98E-01	
11:pent 2 (residents)	8.10E-09	0.00E+00	8.10E-09	8.10E-09	
12:pent 3 (residents)	1.99E-09	0.00E+00	1.99E-09	1.99E-09	
13:pent 4 (residents)	6.94E-01	5.31E-02	5.82E-01	7.88E-01	
14:pent 5 (residents)	2.64E-09	3.06E-06	-5.99E-06	6.00E-06	
15:pent 6 (residents)	1.85E-13	2.11E-11	-4.12E-11	4.16E-11	
16:pent 1 (trans)	2.02E-01	4.78E-02	1.24E-01	3.12E-01	
17:pent 2 (trans)	1.13E-08	0.00E+00	1.13E-08	1.13E-08	
18:pent 3 (trans)	4.34E-07	0.00E+00	4.34E-07	4.34E-07	
19:pent 4 (trans)	1.53E-09	0.00E+00	1.53E-09	1.53E-09	
20:pent 5 (trans)	5.78E-06	1.33E-03	3.36E-201	1.00E+00	
21:pent 6 (trans)	4.64E-08	1.20E-05	3.30E-225	1.00E+00	
22:N small residents	560	87	419	765	
23:N medium residents	1,230	173	943	1630	
24:N large residents	642	98	483	870	
25:N trans	697	108	520	949	
N trans**	209				
N large residents + trans	851				

* Survival estimates from best supported CJS model, i.e. rank 1 model in Table A5.9.

**2 stage survival rate applied to exact known number of large lobsters initially translocated

Table A5.13. Best estimate of large predatory capable lobster abundance within NBRR based on real function parameters derived using survival determined from best supported CJS model (Table A5.10 above). Shown are survival (ϕ , fixed according to CJS model as two estimates; ϕ_1 for translocated lobsters immediately post-translocation, and ϕ_2 for resident lobsters and translocated lobster post the immediate release period); recapture (p) probabilities as a function of sampling period (1-7); probability of entry into population (pent) split by residents (each lobster size-classes different) and translocated lobsters.

Parameter	Estimate	Standard Error	95% CI		
			Lower	Upper	
1: ϕ_1	0.9965	0.0000	0.9965	0.9965	*Fixed
2: ϕ_2	0.9997	0.0000	0.9997	0.9997	*Fixed
3:p1	0.0201	0.0046	0.0128	0.0313	
4:p2	0.0130	0.0033	0.0079	0.0213	
5:p3	0.0282	0.0063	0.0181	0.0437	
6:p4	0.0153	0.0041	0.0091	0.0257	
7:p5	0.0305	0.0068	0.0196	0.0472	
8:p6	0.0280	0.0061	0.0182	0.0429	
9:p7	0.0540	0.0108	0.0364	0.0795	
10:pent 1 (small residents)	1.2E-07	5.1E-05	8.3E-225	1.0E+00	
11:pent 2 (small residents)	1.1E-01	1.7E-01	4.3E-03	7.8E-01	
12:pent 3 (small residents)	3.2E-07	0.0E+00	3.2E-07	3.2E-07	
13:pent 4 (small residents)	1.7E-11	0.0E+00	1.7E-11	1.7E-11	
14:pent 5 (small residents)	2.1E-01	1.4E-01	4.7E-02	5.7E-01	
15:pent 6 (small residents)	3.2E-15	2.0E-11	-3.9E-11	3.9E-11	
16:pent 1 (medium)	7.7E-08	3.4E-05	5.5E-225	1.0E+00	
17:pent 2 (medium)	6.0E-07	3.2E-04	4.3E-224	1.0E+00	
18:pent 3 (medium)	2.2E-11	0.0E+00	2.2E-11	2.2E-11	
19:pent 4 (medium)	6.0E-13	1.1E-09	-2.2E-09	2.2E-09	
20:pent 5 (medium)	6.4E-14	2.1E-10	-4.2E-10	4.2E-10	
21:pent 6 (medium)	2.6E-12	6.6E-10	-1.3E-09	1.3E-09	
22:pent 1(large residents)	6.9E-08	3.3E-05	4.9E-225	1.0E+00	
23:pent 2(large residents)	6.9E-08	3.2E-05	4.9E-225	1.0E+00	
24:pent 3(large residents)	3.6E-14	0.0E+00	3.6E-14	3.6E-14	
25:pent 4(large residents)	1.9E-08	7.8E-06	1.4E-225	1.0E+00	
26:pent 5(large residents)	2.8E-01	2.6E-01	2.9E-02	8.3E-01	
27:pent 6(large residents)	4.1E-01	2.7E-01	7.1E-02	8.6E-01	
28:pent 1(translocated)	3.1E-09	1.1E-06	-2.2E-06	2.2E-06	
29:pent 2 (translocated)	2.0E-08	0.0E+00	2.0E-08	2.0E-08	
30:pent 3 (translocated)	7.4E-07	3.5E-04	5.3E-224	1.0E+00	
31:pent 4 (translocated)	1.6E-09	3.1E-07	-6.1E-07	6.1E-07	
32:pent 5 (translocated)	1.6E-12	0.0E+00	1.6E-12	1.6E-12	
33:pent 6 (translocated)	1.3E-13	0.0E+00	1.3E-13	1.3E-13	
34:N small residents	1,161	225	808	1,707	
35:N med residents	1,052	195	745	1,522	
36:N large residents	341	96	203	591	
37:N trans residents	546	120	361	842	
N trans*	317				
N large residents + trans	661				

* Survival estimates from best supported CJS model, i.e. rank 1 model in Table A5.10.

**2 stage survival rate applied to known number of large lobsters initially translocated

Table A5.14. CJS model reduction summary examining effects of habitat (kelp bed vs. urchin barrens) on the survival and recapture probabilities of lobsters (legal-sized) through time inside the ERRR. Satisfactory fit of saturated model, GOF, $P=0.656$. Parameter estimates averaging across top 10 models: kelp 0.99971 ± 0.00024 , barrens 0.99965 ± 0.00021 , kelp $4.4\% \pm 0.17$, barrens $4.9\% \pm 0.00171$.

Rank	Model description	Hypothesis	AICc	Delta AICc	AICc Weights	Model Likelihood	Num. Par	Deviance
1	$\emptyset(.) p(.)$	Survival & recapture independent of habitat or time	197.36	0.00	0.33	1.00	2	45.78
2	$\emptyset(t) p(.)$	Survival dependent on time	198.56	1.20	0.18	0.55	6	38.62
3	$\emptyset(.) p(h)$	Recapture dependent on habitat	198.80	1.44	0.16	0.49	3	45.16
4	$\emptyset(h) p(.)$	Survival dependent on habitat	199.42	2.06	0.12	0.36	3	45.78
5	$\emptyset(t) p(h)$	Survival dependent on time, recapture dependent on habitat	200.30	2.94	0.08	0.23	7	38.22
6	$\emptyset(h) p(h)$	Survival & recapture dependent on habitat	200.51	3.15	0.07	0.21	4	44.79
7	$\emptyset(t) p(t)$	Survival & recapture dependent on time	202.43	5.07	0.03	0.08	9	36.01
8	$\emptyset(.) p(t)$	Recapture dependent on time	202.54	5.19	0.02	0.07	7	40.46
9	$\emptyset(h) p(t)$	Survival dependent on habitat, recapture dependent on time	204.70	7.35	0.01	0.03	8	40.46
10	$\emptyset(t) p(h*t)$	Survival dependent on time, recapture dependent on habitat & time	208.64	11.29	0.00	0.00	14	30.97
11	$\emptyset(h*t) p(.)$	Survival dependent on habitat & time	209.05	11.69	0.00	0.00	11	38.19
12	$\emptyset(h*t) p(h)$	Survival dependent on habitat & time, recapture dependent on habitat	210.24	12.89	0.00	0.00	12	37.14
13	$\emptyset(.) p(h*t)$	Recapture dependent on habitat & time	210.72	13.37	0.00	0.00	13	35.34
14	$\emptyset(h*t) p(t)$	Survival dependent on habitat & time, recapture dependent on time	211.27	13.92	0.00	0.00	14	33.60
15	$\emptyset(h) p(h*t)$	Survival dependent on habitat, recapture dependent on habitat & time	212.50	15.14	0.00	0.00	14	34.82
16	$\emptyset(h*t) p(h*t)$	Saturated model	216.80	19.44	0.00	0.00	18	29.69

Survival (\emptyset) and resighting (p) probabilities may be a function of habitat (h), or time (t).

Table A5.15. POPAN estimates for total lobster population size inside and outside ERRR as estimated from mark-recapture across 7 sampling occasions (6 sampling intervals).

Site	Parameter	Estimate	SE	95% Confidence Interval	
				Lower	Upper
ERRR	1: ϕ 1	0.984	0.010	0.948	0.995
	2: ϕ 2	1.000	0.0E+00	1.000	1.000
	3: ϕ 3	0.995	0.002	0.988	0.998
	4: ϕ 4	1.000	1.3E-05	5.4E-67	1.000
	5: ϕ 5	1.000	1.3E-05	2.8E-126	1.000
	6: ϕ 6	0.977	0.002	0.973	0.980
	7:p1	0.971	2.044	1.2E-61	1.000
	8:p2	0.042	0.013	0.024	0.075
	9:p3	0.082	0.023	0.046	0.140
	10:p4	0.057	0.022	0.026	0.121
	11:p5	0.071	0.013	0.049	0.102
	12:p6	0.030	0.006	0.020	0.046
	13:p7	1.000	0.0E+00	1.000	1.000
	14:pent1	0.585	0.128	0.333	0.799
	15:pent2	2.5E-07	0.0E+00	2.5E-07	2.5E-07
	16:pent3	3.4E-10	2.9E-07	-5.6E-07	5.7E-07
	17:pent4	0.402	0.127	0.193	0.653
	18:pent5	9.2E-09	0.0E+00	9.2E-09	9.2E-09
	19:pent6	3.7E-13	0.0E+00	3.7E-13	3.7E-13
	20:N	2,595	323	2,054	3,333
ER fished	1: ϕ 1	0.5000	0.0E+00	0.5000	0.5000
	2: ϕ 2	0.9982	0.0084	0.0564	1.0000
	3: ϕ 3	0.9936	0.0065	0.9540	0.9991
	4: ϕ 4	1.0000	1.2E-05	0.0005	1.0000
	5: ϕ 5	1.0000	0.0E+00	1.0000	1.0000
	6: ϕ 6	0.9694	0.0053	0.9570	0.9783
	7:p1	1.0000	0.0175	3.7E-07	1.0000
	8:p2	1.0000	0.0E+00	1.0000	1.0000
	9:p3	0.0939	0.0821	0.0154	0.4073
	10:p4	0.0290	0.0290	0.0040	0.1834
	11:p5	0.0021	0.0015	0.0005	0.0089
	12:p6	0.0180	0.0105	0.0057	0.0553
	13:p7	1.0000	0.0E+00	1.0000	1.0000
	14:pent1	0.0250	0.0106	0.0108	0.0569
	15:pent2	0.3936	0.2885	0.0573	0.8740
	16:pent3	0.1195	0.2677	0.0009	0.9522
	17:pent4	0.4560	0.2780	0.0853	0.8828
	18:pent5	3.5E-05	0.0071	4.8E-16	1.0000
	19:pent6	1.2E-09	9.0E-07	-1.8E-06	1.8E-06
	20:N	2,517	1,022	1,239	5,544

Phi = survival; *p* = recapture probability; *pent* = probability of entry into population; *N* = total lobster population estimate.

Table A5.16. POPAN estimates for total lobster population size inside and outside NBRR as estimated from mark-recapture across 7 sampling occasions (6 sampling intervals).

Site	Parameter	Estimate	SE	95% Confidence Interval	
				Lower	Upper
NBRR	1: ϕ 1	1.000	0.0E+00	1.000	1.000
	2: ϕ 2	1.000	0.0E+00	1.000	1.000
	3: ϕ 3	0.998	0.005	0.774	1.000
	4: ϕ 4	0.990	0.012	0.895	0.999
	5: ϕ 5	1.000	2.7E-05	2.0E-72	1.000
	6: ϕ 6	1.000	0.019	1.8E-213	1.000
	7:p1	0.813	22.487	4.5E-126	1.000
	8:p2	0.009	0.003	0.005	0.016
	9:p3	0.018	0.005	0.010	0.030
	10:p4	0.012	0.007	0.004	0.037
	11:p5	0.036	0.011	0.020	0.064
	12:p6	0.037	0.011	0.021	0.066
	13:p7	0.077	0.112	0.004	0.647
	14:pent1	0.983	0.474	0.000	1.000
	15:pent2	1.2E-16	3.3E-15	-6.3E-15	6.5E-15
	16:pent3	1.5E-18	4.2E-17	-8.0E-17	8.3E-17
	17:pent4	5.6E-18	1.6E-16	-3.0E-16	3.1E-16
	18:pent5	6.0E-17	1.7E-15	-3.2E-15	3.3E-15
	19:pent6	4.5E-19	1.2E-17	-2.4E-17	2.5E-17
	20:N	3,588	908	2,246	5,914
NB Fished	1: ϕ 1	1.000	0.0E+00	1.000	1.000
	2: ϕ 2	0.999	0.005	0.001	1.000
	3: ϕ 3	1.000	0.001	1.2E-06	1.000
	4: ϕ 4	1.000	0.0E+00	1.000	1.000
	5: ϕ 5	0.957	0.166	0.008	1.000
	6: ϕ 6	1.000	0.000	1.000	1.000
	7:p1	0.588	10.181	2.0E-11	1.000
	8:p2	2.4E-09	2.4E-06	-4.8E-06	4.8E-06
	9:p3	0.075	0.090	0.006	0.512
	10:p4	0.011	0.009	0.002	0.056
	11:p5	1.4E-11	0.0E+00	1.4E-11	0.000
	12:p6	4.3E-08	2.9E-05	6.0E-19	1.000
	13:p7	0.971	22.814	4.7E-10	1.000
	14:pent1	0.001	0.213	1.4E-14	1.000
	15:pent2	0.749	1.396	1.4E-06	1.000
	16:pent3	0.162	0.841	1.1E-06	1.000
	17:pent4	4.3E-06	0.003	5.9E-17	1.000
	18:pent5	0.018	0.525	2.6E-13	1.000
	19:pent6	0.004	0.266	5.1E-14	1.000
	20:N	2,013	1,888	576	10,056

Phi = survival; *p* = recapture probability; *pent* = probability of entry into population; *N* = total lobster population estimate.

Table A5.17. Lobster abundance and density estimates at ERRR and NBRR generated from mark recapture analysis (POPAN). Estimates are based on total lobster population size for each reserve factored by the proportion of catch within each size-class at final sampling (where mark-recapture estimates were based on all lobster recaptures naïve to translocation having occurred, i.e. all lobsters were pooled as one group blind to translocation). Estimates by habitat at ERRR were factored by relative catch rates of each size-class across kelp beds vs. sea urchin barrens (see parameter estimates in Table 14, main report). For large lobsters in the fished zone, the relative habitat-specific estimates of catch rate obtained for barrens and kelp habitats from within ERRR were used to factor abundance across habitats (kelp beds vs. urchin barrens; see Table 14, main body of report).

Site	Status	Habitat	Area (m ²)	% of reef	Lobster abundance				Lobster density (individ. m ⁻²)			
					Total	Large	Medium	Small	Total	Large	Medium	Small
ER	Research Reserve	Kelp beds	183,318	40.0	988	354	447	187	0.0054	0.0019	0.0024	0.0010
		Barrens	197,867	43.2	1,187	590	483	115	0.0060	0.0030	0.0024	0.0006
		Total	458,325	100	2,595	1130	1,118	347	0.0057	0.0025	0.0024	0.0008
	Fished	Kelp beds	367,019	47.6	1,321	289	404	628	0.0036	0.0008	0.0011	0.0017
		Barrens	168,005	31.7	590	204	185	202	0.0035	0.0012	0.0011	0.0012
		Total	696,909	100	2,517	683	768	1,067	0.0036	0.0010	0.0011	0.0015
NB	Research Reserve	Kelp beds	175,523	100*	3,588	897	1,187	1,504	0.02044	0.00511	0.00676	0.00857
	Fished	Kelp beds	336,447	100*	2,013	161	886	1,127	0.00605	0.00050	0.00215	0.00340

(*1.1% incip. barrens)

Table A5.18. Estimates of lobster density (A) and lobster biomass density (B) by size-class inside and outside the research reserves.

A.		Lobster density (individ. 100 m⁻²)					legal resid.
Site	Status	Total	All large	large	medium	small	
ER	Research Reserve	0.57	0.25	0.19	0.24	0.08	0.43
	Fished	0.36	0.10	0.10	0.11	0.15	0.21
	<i>Reserve Factor</i>	1.57	2.52	1.92	2.21	0.49	2.07
NB	Research Reserve	2.04	0.47	0.37	0.49	0.90	0.85
	Fished	0.60	0.05	0.05	0.22	0.34	0.27
	<i>Reserve Factor</i>	3.42	9.40	7.32	2.25	2.65	3.21
B.		Lobster biomass density (kg hectare⁻¹)					legal resid.
Site	Status	Total	All large	large	medium	small	
ER	Research Reserve	79.27	53.82	35.90	21.70	3.74	57.60
	Fished	36.10	18.73	18.73	9.80	7.57	28.53
	<i>Reserve Factor</i>	2.20	2.87	1.92	2.21	0.49	2.02
NB	Research Reserve	131.93	90.37	59.96	41.55	37.57	101.51
	Fished	40.82	8.19	8.19	18.44	14.19	26.62
	<i>Reserve Factor</i>	3.23	11.04	7.32	2.25	2.65	3.81

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APPENDIX 6: Monitoring the impact of populations of large lobsters on sea urchins and benthic community structure

This work is being prepared for publication in a peer-reviewed journal. Here is presented the abstract of the paper, broad context of the work, an outline of the approach to analysis of the data, and other information in support of the outline given in the main body of the report.

Abstract

Wholesale shifts in ecological landscapes can be exceedingly difficult to reverse if new configurations are reinforced with positive feedbacks. In response to a rapidly warming coastal ocean environment, the habitat-modifying sea urchin *Centrostephanus rodgersii* (Diadematidae) has extended range south to eastern Tasmania where it has commenced grazing of productive kelp beds causing phase-shift to widespread sea urchin barrens habitat. Ecological overfishing of large predatory lobsters *Jasus edwardsii* (Palinuridae) has functionally reduced an important benthic predator of barrens-forming sea urchins. Here we explicitly test the effect of re-building populations of predatory-capable lobsters on sea urchin populations and benthic community structure (seaweed and macro-invertebrates) in largely intact kelp beds supporting scattered incipient barrens patches, and on extensive sea urchin barrens. We used large-scale controlled reversal-of-fishing experiments in which large predatory-capable lobsters were translocated to two research reserves, protected from fishing and established for the purpose, in south east (incipient barrens) and north east (extensive barrens) Tasmania. In the north east, there was no sign of recovery of seaweeds on extensive barrens at the research reserve or on nearby control reefs remaining open to fishing and without added lobsters, although predator-driven declines in urchin abundance were observed in seaweed beds within the reserve, after 2.5 years of monitoring. In the south east, sea urchin abundances declined significantly at the reserve site with added lobsters, but not at control sites. Moreover, in the reserve site incipient barrens patches decreased in size but increased in size at the control sites open to fishing, with greatest proportional change in size evident in smaller patches. This result showed that barrens patches are more easily 'reversed' when small in size – and likewise can expand rapidly when small – but become more difficult to reduce once larger barrens are formed. Collectively the results suggest that rebuilding resilience of desirable kelp beds by reinstating trophic relationships in the food web will be more effective in preventing overgrazing in the first instance than promoting recovery of kelp beds once extensive urchin barrens have formed. Management for local-scale resilience of desirable ecosystem states will be most tractable and cost effective as a proactive measure, while reactive management in response to phase shift to an alternative state (after the fact) will likely require more drastic intervention and be exceedingly costly by comparison.

Context

While living systems are by their very nature renewable, there are increasing local and regional examples of altered ecosystems that have been pushed beyond regenerative limits to no longer meet societal requirements for goods and services depended upon (Scheffer et al. 2012). Worldwide many systems are deemed collapsed, with many more nearing or at theoretical maximum exploitative capacity (Halpern et al 2008; Steffen et al. 2011). Superimposed on increasing demand on natural resources is climate change which in marine systems in Australia is already impacting key biological processes and redefining the distribution of species, key resources and entire ecosystem structure and functioning (e.g. Johnson et al. 2011).

Ecosystems show innate resilience and constantly tolerate fluctuating abiotic and biotic conditions, however major shifts in ecosystem dynamics – to new 'basins of attraction' – can occur if critical tipping

points are exceeded (Scheffer et al. 2001, 2012). Of particular concern for natural resource management are non-linear, or 'catastrophic', phase shifts, whereby wholesale change in the underlying ecosystem dynamic occurs once a critical stress threshold is passed. Return to the former (and usually more desirable) ecosystem state can be exceedingly difficult, requiring an altogether different dynamic and path of recovery (the 'reverse' phase-shift) for the system to return to its former state (e.g. Lewontin 1969; May 1977; Holling 1973; Sutherland 1974; Scheffer et al. 2001). Each state is often reinforced by different positive feedbacks (e.g. Marzloff et al. 2011) that enhance its' own persistence or resilience (*sensu* Holling 1973). It follows that defining mechanisms of resilience operating within different ecosystem configurations is pivotal to identifying management 'levers' most able to maintain resilience of a desirable, or erode the resilience of an undesirable, ecosystem state.

As a result of a rapidly warming coastal environment, the habitat-modifying sea urchin *Centrostephanus rodgersii* (Diadematidae) has extended its range southwards to establish populations in eastern Tasmania where in some areas it has overgrazed productive seaweed beds causing phase-shift to extensive and impoverished sea urchin barrens habitat (Johnson et al. 2005, 2011; Ling 2008; Ling et al. 2008, 2009a,b). In north east mainland Tasmania where the urchin was first observed in 1978, *C. rodgersii* barrens occur at scales of 10^5 m² (Johnson et al. 2005, 2011; Ling et al. 2009b), but more southerly populations are more recent and grazing impacts are less severe (Ling et al. 2009b; Johnson et al. 2011). In south east Tasmania most barrens manifest as incipient patches at scales of 10^0 - 10^1 m² within otherwise intact kelp beds. *C. rodgersii* barrens in Tasmania realise a massive loss of local biodiversity (Ling 2008) and biomass on reefs, and detract significantly from the 'goods and services' provided by rocky reefs because lucrative reef-based fisheries for abalone (*Haliotis rubra*) and rock lobster (*Jasus edwardsii*) do not occur at commercial levels on extensive barrens habitat (Strain & Johnson 2009; Johnson et al. 2005, 2011).

While climate change is responsible for the incursion of *C. rodgersii* into Tasmanian waters, building of its populations to the point where extensive destructive grazing can occur is ostensibly due to intensive fishing of rock lobster, its main predator (Ling et al. 2009a; Ling & Johnson 2012). Field and laboratory experiments show that supra-legal rock lobsters (≥ 140 mm carapace length) are the principal predators of emergent *C. rodgersii* (i.e. sea urchins >70 mm test diameter), but these large predatory capable lobsters are currently rare on shallow eastern reefs due to intense fishing (Ling et al. 2009a; Ling & Johnson 2012).

Here we use large-scale manipulations of predatory lobsters to assess the resilience of the alternative seaweed bed and barrens habitat states. This was achieved by translocating large predatory capable lobsters to research reserves protected from fishing and declared specifically for the project. One reserve (in north east Tasmania) contained extensive *C. rodgersii* barrens (~ 20 ha in extent), while the reserve in south east Tasmania supported well developed kelp beds with scattered incipient barrens patches (10^0 - 10^1 m²). We report on responses to these manipulations, relative to nearby similar 'control' reefs without added lobsters and open to fishing, of sea urchin populations, other macro invertebrates and seaweeds over ~ 2.5 years.

Methods

Statistical analyses

Response of benthic invertebrates and macroalgae

Data were analyzed using a combination of univariate (2-way ANCOVA) and multivariate (2-way PERMANOVA, PERMDISP and Canonical Analysis of Principal components) statistical approaches. Univariate analyses were conducted in R v2.12.2, and multivariate analyses were conducted using PRIMER v6 (Clarke and Gorley 2006). All multivariate analyses were conducted using square root transformed data and Bray Curtis similarities. Data from belt transects were aggregated at the transect level (i.e. mean covers and densities from data recorded in 5 m × 1 m blocks), with percentage covers for algal groups and barrens corrected for sand cover (i.e. algal and barrens cover is assumed to be a percentage of available reef habitat, not the total area surveyed). Cover of sand habitat on the fixed transects was generally low (mean < 5% across all transects).

For analysis of sea urchin densities, trends at each site were examined using analysis of covariance (ANCOVA), with 'Days' since the initial survey as the covariate, to separate the independent effects of changes in time (the trend of interest) from spatial variability among transects. Tests for the effect of the 'lobster enhancement' treatment (i.e. protection within the research reserve plus translocation of large lobsters) was examined only if significant differences were detectable for the site level analysis (i.e. where there was a significant 'Site * Days' interaction), and if differences between the two controls sites (C1 and C2) were not different at a *P*-value of >0.25 (effectively amounting to post hoc pooling of control treatments, after Winer et al. 1991). Analyses were conducted separately for kelp and barrens habitats at north-eastern sites, and for incipient barrens (i.e. kelp-dominated) habitat in south east (the only habitat type occurring in this region).

Examination of algal and invertebrate community level responses to lobster enhancements were performed with multivariate PERMANOVA conducted using a 2-way analysis of variance design including the factors 'Period' and 'Site' (both as fixed factors) for the beginning and end survey periods only. Analyses were conducted separately for kelp and barrens habitats at north-eastern sites. A significant interaction between 'Period' and 'Site' is expected if the lobster translocation treatment has an effect on dynamics of particular groups (univariate case) or at the community level (multivariate case). Since significant PERMANOVA can reflect either differences in multivariate location or dispersion, PERMDISP was used to test for differences in dispersion where significant PERMANOVA effects were detected. Multivariate differences in algal and invertebrate communities were visualized using Canonical Analysis of Principal components (CAP; Anderson et al. 2008), constrained to maximize separation between levels of the factor 'Period * Site' (where 'Period' considered initial and final surveys only).

Fine-scale habitat changes

Dynamics of the kelp bed / barrens interface was analyzed using 2-way ANOVA for 'Period' by 'Site', using data from the beginning and end survey periods only, and at two different intervals (0–5 m and 5–10 m) from the kelp/barrens interface marker. Due to the unbalanced design in this analysis (which arises because markers for two transects from Sloop Rock could not be relocated during subsequent surveys), Type III sums of squares were used to test for the significance of main effects where interaction effects were non-significant (which was the case for all analyses, *P*>0.25).

For sites in the south east, dynamics of incipient *C. rogersii* barrens patches (i.e. abundance and size-frequency) at the NBRR and associated controls sites (as assessed by timed diver swims) were analysed using mixed model 2-way asymmetric ANOVAs assessing the effect of large lobster enhancement at the first monitoring period 'Before' lobster translocation versus last monitoring period ('After') across

NBRR and control sites. To assess the treatment level effect of lobster enhancement, control sites were considered together in an asymmetrical contrast (i.e. of NBRR vs. (C1,C2 together)) or were pooled where appropriate (i.e. $P > 0.25$) to provide a more robust comparison with lobster enhancement research reserves.

For marked barrens patches monitored through time, because patches were fixed in space (i.e. the same patches were assessed through time), dynamics of patches across SE sites was examined using asymmetrical ANOVA on the change in patch size across the period 'Before - After' the lobster enhancement treatment (i.e. patch size at first sampling minus patch size at final sampling). The effect of lobster translocation was assessed using an asymmetrical contrast of 'treatment' versus 'control' treatments (i.e. NBRR vs. (C1,C2 together)) .

A list of algal species encountered on belt transects at the study sites in south east and north east Tasmania is given in the following table.

Table A6.1. Algal groups recorded for belt transects in north- and south-east Tasmania.

Name	Canopy forming macroalgae	Understorey
<i>Acrocarpia paniculata</i>	✓	
<i>Carpoglossum confluens</i>		✓
<i>Carpomitra costata</i>		✓
<i>Caulerpa brownii</i>		✓
<i>Caulerpa flexilis</i>		✓
<i>Caulerpa geminata</i>		✓
<i>Caulerpa obscura</i>		✓
<i>Caulerpa trifaria</i>		✓
<i>Chaetomorpha coliformis</i>		✓
<i>Cladophora feredayi</i>		✓
<i>Codium spp.</i> ⁽¹⁾		✓
<i>Colpomenia peregrina</i>		✓
<i>Cystophora monoliformis</i>	✓	
<i>Cystophora platylobium</i>	✓	
<i>Cystophora retroflexa</i>	✓	
<i>Dictyopteris mulleri</i>		✓
<i>Dictyota dichotoma</i>		✓
<i>Durvillaea potatorum</i>	✓	
<i>Ecklonia radiata</i>	✓	
Encrusting coralline algae		
Encrusting/erect invertebrates ⁽²⁾		
Erect coralline algae		
Red filamentous algae		✓
Red foliose algae		✓
Green filamentous algae		✓
<i>Halopteris paniculata</i>		✓
<i>Lessonia corrugata</i>	✓	
<i>Macrocystis pyrifera</i>	✓	
<i>Perithalia caudate</i>		✓
<i>Phyllospora comosa</i>	✓	
<i>Sargassum spp.</i> ⁽³⁾	✓	
<i>Sporocnus comosus</i>		✓
<i>Ulva spp.</i> ⁽⁴⁾		✓
<i>Undaria pinatifida</i>	✓	
<i>Xiphophora gladiata</i>		✓
<i>Zonaria spp.</i> ⁽⁵⁾		✓

⁽¹⁾ *Codium spp.* = *C. fragile* and *C. pomoides*⁽²⁾ Encrusting/erect invertebrates = a generic grouping for encrusting and erect sponges and byozoans⁽³⁾ *Sargassum spp.* = *S. verruculosum*, *S. varians*, *S. fallax*, *S. decipiens*, *S. paradoxum*⁽⁴⁾ *Ulva spp.* = *U. australis* and *U. taeniata*⁽⁵⁾ *Zonaria spp.* = *Z. turneriana*, *Z. angustata*, *Z. spiralis*, *Lobophora variegata*, *Distromium flabellatum*, *Exallosorus olseni*

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APPENDIX 7: Estimating lobster rates of lobster predation on *Centrostephanus rodgersii* in the field – methods based on DNA detection in lobster faeces and modelling changes in urchin density

This work has been developed as a paper for submission to *Molecular Ecology*.

Title: Using molecular prey detection to quantify rock lobster predation on barrens-forming sea urchins.

Authors: K. S. Redd, S. D. Ling, S. D. Frusher, S. Jarman & C. R. Johnson

Presented here is the abstract of the paper, an outline of the broader context of the work, and additional details of the methodology used to augment the simpler and more general outline given in the main body of the report.

Abstract

We apply 'quantitative' PCR (qPCR) molecular techniques to detect *in situ* rates of consumption of sea urchins by the southern rock lobster (*Jasus edwardsii*, Palinuridae). An efficient and non-lethal method was used to source and screen lobster faecal samples for the presence of DNA from the ecologically important 'barrens-forming' sea urchins *Centrostephanus rodgersii* (Diadematidae) and *Heliocidaris erythrogramma* (Echinometridae). Lobster faecal samples were collected from trap caught specimens sourced in winter and summer seasons over two years within two no-take research reserves. The reserves were declared for the purpose of rebuilding large predatory-capable lobsters to assess the potential for predator-driven remediation of kelp beds on rocky reefs either (1) extensively overgrazed by sea urchins (north eastern Tasmania), or (2) at an incipient stage of barrens development showing initial signs of overgrazing (south eastern Tasmania). Molecular assays showed high variability in the proportion of lobsters testing positive to sea urchins, with significant variability detected across different years and seasons dependent on lobster size. Independently derived estimates of lobster predation rate on sea urchins (determined from observed declines in sea urchin abundances within the reserve boundaries over ~2.5 years) suggest that rates of molecular prey detection generally overestimated rates of sea urchin predation by lobsters. Furthermore, smaller size-classes of lobster previously shown to be incapable of directly preying on emergent sized sea urchins showed relatively high rates of positive tests to assays. This result indicates that some lobsters ingest non-predatory sources of sea urchin DNA, which possibly emanate from any of several sources: (1) uptake of *C. rodgersii* DNA material accumulated on the benthos (we show that urchin DNA is detectable in benthic sediments and sea urchin faecal material, and which is sometimes subsequently detectable in faeces – albeit at low rates – when lobsters are fed fresh urchin faecal material and sediment in the laboratory); (2) scavenging events (we routinely observed multiple small lobsters to feed on fresh carcasses of large urchins killed by large lobsters on which they are incapable of preying directly); and (3) predation by rock lobsters on small pre-emergent urchins that live cryptically within the reef matrix (although this possibility could not be assessed). While both the DNA-based approach and direct monitoring of urchin populations both indicate high absolute predation rates of large lobsters on emergent urchins, the study has shown clearly that in some cases absolute predation rates and inferences of predator-prey interactions cannot be reliably estimated from molecular signals obtained from the faeces of benthic predators. At a broad semi-quantitative level, the approach is useful to identify relative magnitudes of predation and temporal and spatial variability in predation.

Context

Understanding the composition of the diet of individual species is fundamental in defining trophic interactions and relating trophic structure to the functioning of marine communities. Estimating the rate at which particular prey are consumed and thus quantifying overall *per capita* effects of predators on prey populations is particularly important when interactions involve species capable of exerting overwhelming influence on ecosystem dynamics, such as between kelp grazing sea urchins and their predators on temperate rocky reefs (e.g. sea otters, Estes & Palmisano 1974; clawed lobsters, Breen & Mann 1976; fish, Cowen 1983; and spiny lobsters, Tegner and Levin 1983, Ling et al. 2009a). Marine ecologists have usually identified predator-prey interactions and inferred the effects of consumption either by opportunistic observations (e.g. Estes & Palmisano 1974; Estes et al. 1998), visual examination of gut contents (e.g. Estes et al. 1978; Cowen 1983) or scats (Estes & Duggins 1995), by running laboratory trials over days (e.g. Tegner & Levin 1983; Ling et al. 2009a), conducting trials *in situ* over several months (Ling et al. 2009a) to tracking abundances of predators and their prey in nature over decades (e.g. reviewed by Babcock et al. 2010; Watson & Estes 2011). However, given inherent difficulty in directly observing predator-prey interactions, and the possibility of large spatial and temporal variability in these dynamics, determining interaction strengths between species in nature remains a fundamental and challenging task for marine ecologists.

In recent decades, advances in molecular biology have shown that prey DNA recovered from predator faecal material can be used to identify the prey consumed (Symondson 2002; Pompanon, 2012). High resolution molecular tools represent an emerging potential to define and quantify species interactions. As a non-lethal and largely non-intrusive dietary sampling technique, DNA testing of predator faecal material also resolves conservation and ethical issues posed by more traditional approaches to dietary studies that require sacrificing large numbers of animals (Jarman and Wilson 2004; Redd et al. 2008). Furthermore, large numbers of samples can be processed quickly and efficiently allowing more quantitatively robust description of food-web structure and thus better inferences of community dynamics. This meets an increasingly urgent need as rapidly changing ocean climates and other human-derived stressors progressively alter marine food webs and lead to major shifts in ecosystem structure and function (e.g. Johnson et al. 2011; Wernberg et al. 2011).

On the warming temperate coast of eastern Tasmania (south east Australia), climate-driven range extension of the habitat-modifying sea urchin *Centrostephanus rodgersii* (Diadematidae) poses a considerable ecological threat given this species' capacity to overgraze productive seaweed beds and effect a wholesale shift in reef state and ecology to impoverished sea urchin dominated 'barrens' habitat (Johnson et al. 2005, 2011; Ling 2008; Ling et al. 2008, 2009b). Owing to grazing by this single species, ~50% of all near-shore rocky reef is maintained as barrens habitat within the sea urchins' native range in New South Wales (Andrew & O'Neill 2000; reviewed by Andrew & Byrne 2007) and in northeast Tasmania where the urchin first established in Tasmanian waters (Johnson et al. 2005, 2011). Thus, the threat of overgrazing in Tasmania is significant, with major implications given that these kelp beds support south east Australia's most valuable fisheries – for southern rock lobster (*Jasus edwardsii*) and black lip abalone (*Haliotis rubra*) – which are not commercially viable on urchin barrens (Johnson et al. 2005, 2011; Ling et al. in prep.). This large ecological shift, associated with ocean warming and range-extension of this habitat-modifying sea urchin, is also influenced by the effects of intensive fishing of the key predator of the sea urchins (Ling et al. 2009a; Ling & Johnson 2012). In eastern Tasmania, field and laboratory experiments show that supra-legal rock lobsters (≥ 140 mm carapace length, i.e. 30-35 mm CL above the minimum legal size) are the principal predators of emergent sizes of *C. rodgersii* (i.e. of individuals >70 mm test diameter), but that these large predatory capable lobsters are currently rare due to intense fishing pressure (Ling et al. 2009a).

The impact of fishing on the abundance of large predatory capable lobsters in eastern Tasmania is

demonstrated clearly by long-term monitoring comparing reefs inside marine protected areas with nearby reefs open to intensive fishing (Edgar et al. 2009; Ling et al. 2009a). Evidence of cascading trophic effects as a result of rebuilding abundances of large predatory lobsters (*Jasus edwardsii*) within protected areas is evident where native sea urchin species capable of overgrazing in New Zealand (*Evechinus chloriticus*, Shears & Babcock 2002) and Tasmania (*Heliocidaris erythrogramma*, Johnson et al. 2004; Pederson & Johnson 2006; Ling et al. 2010), occur at relatively low densities in areas where predatory capable lobsters are abundant (reviewed by Babcock et al. 2010). In New Zealand, ongoing predator-driven recovery of kelp beds on extensive barrens habitat has been observed to occur over several decades post cessation of fishing (Shears & Babcock 2003; reviewed by Babcock et al 2010).

In an attempt to determine whether management practices to increase the number of large predatory lobsters would be an efficient means of remediating extensive established *C. rodgersii* barrens, and/or prevent further barrens formation at sites where the urchin is established but barrens formation is at an incipient stage, two no-take research reserves were declared in eastern Tasmania to facilitate rebuilding populations of large predatory lobsters. To accelerate the rebuilding, large predation-capable lobsters captured in remote areas by the commercial fishery were translocated to each of the research reserves. Here we evaluate the capacity of qPCR molecular techniques to quantify absolute rates of ingestion of sea urchins by large lobsters within these reserves in an attempt to better understand trophic dynamics in this rapidly changing rocky reef system.

Methods

This section provides greater detail of the work to estimate rates of predation by rock lobsters on sea urchin populations conducted at the research reserves described earlier (i.e. at the sites of translocation of rock lobsters). The experimental sites were those at Elephant Rock in the north east (ERRR; 41.25°S 148.35°E; with an extensive *Centrostephanus rodgersii* barrens of ~200,000 m² within the reserved area covering ~50% of the reef at the site) and at North Bay in south east Tasmania (NBRR; 42.84°S, 147.92°E; where incipient barrens' patches totalled ~1% of the reef area (see Table A7.1).

There were two components to this work. The primary aim was to use 'quantitative' PCR (qPCR) to detect species-specific sea urchin DNA in faecal pellets obtained from lobsters as a measure of instantaneous predation rate. This estimate was then compared with an independent estimate of predation rate determined from the change in urchin densities at the reserve sites (relative to control areas without added lobsters) related to mean lobster density over the study period at each site.

Sampling rock lobsters

Faecal samples from individual lobsters were obtained by trapping lobsters within the research reserves during winter and summer seasons over two years post translocation of lobsters (see Fig. A7.1A). Traps were set across the available reef area within the reserves on a regular spaced virtual grid (60 m between grid points). For ERRR, each trap position was assigned to either kelp or sea urchin barrens habitat following intensive video mapping of the benthos at each grid point. As per commercial operations, traps were baited with whole jack mackerel (*Trachurus declivis*) and cuta (*Thyrsites atun*) heads, which were deployed on reef in depths of ~3-45 m. Traps were effective at sampling lobsters to a minimum size of approximately 50 mm carapace length (CL; ~60 g fresh weight) while lobsters below this size, while present at the sites, were likely to escape through the mesh of the trap (25 by 25 mm). Each captured lobster was measured for carapace length to the nearest mm with knife-edge callipers and assigned to size categories of small (≤ 110 mm CL, i.e. undersized lobsters); medium (>110 & <140 mm CL); and large (≥ 140 mm CL), inclusive of large residents and large translocated individuals. Captured lobsters were then sampled for faecal material, tagged (if they were

untagged residents), and released at the site of capture.

Faecal material collection

Lobster faeces were collected using a 100-1,000 μL pipette with disposable tips. For each faecal sample a new sterile tip was used to prevent contamination between samples. The tip was inserted directly into the anal pore of the lobster to remove faeces from the hindgut. The collected material was immediately pipetted into a 1.5 mL micro centrifuge tube containing 500 μL of MilliQ water, stored on ice and frozen at -20°C as soon as could be arranged. The volume collected varied from approximately 10 μL to 1 mL depending on the size of lobster and fullness of the hindgut. Rock lobsters which failed to yield a faecal sample were recorded as 'non-feeding' (for proportions of lobster catch deemed to be feeding, refer to Fig. A7.1B). Water was removed from samples before DNA extraction by centrifuging at 10,000 g for 30 s. Excess water was poured off and the sample tubes centrifuged again. Any remaining water was then removed by pipette prior to DNA extraction.

DNA extraction

The Ultra Clean™ Faecal DNA Kit (Mo Bio Laboratories, Inc.) was used for DNA extractions on rock lobster faecal samples following the manufacturer's protocols with the supplied proprietary buffers and reagents. Due to the large number of samples processed in this way, the 96-well format was chosen for time efficiency. All DNA extracted from faecal samples using this kit was ready for PCR and the manufacturer's protocol appeared to remove any potential PCR inhibitors.

PCR amplification

Precautions were taken during preparation of PCR reactions to minimize the possibility of contamination by extraneous DNA. Aerosol-resistant barrier pipette tips were used for preparing all PCR reactions and pipette tips were either sterile and pre-packaged or autoclaved prior to use. All PCR reactions were prepared in a dedicated hood where PCR tubes, pipettes and pipette tips were subjected to UV light for a minimum of 10 minutes prior to setting up each PCR reaction.

The components of the 14 μL PCRs were as follows: 10 μL SYBRgreen (Sensimix, Quantace, Biorline), 1.25 μL each primer (Geneworks), 1.5 μL 50mM MgCl_2 (Quantace, Biorline), and 2 μL (~ 50 ng) template DNA. Both positive and negative controls were run with each batch of PCRs. For negative controls 2 μL MilliQ H_2O was used as template and for positive controls ~ 40 ng template DNA from *Centrostephanus rodgersii* and *Heliocidaris erythrogramma* was used to confirm reaction success. For internal standards, plasmids with the 650bp 16s amplicons from *C. rodgersii* and *H. erythrogramma* insertions were used and serial dilutions of 1:10, 1:100, 1:1,000, 1:10,000 and 1:100,000 obtained using a CAS-1200N robotic liquid handling system (Corbett Research) provided standard curves for each qPCR reaction.

The PCR primer sets used in this experiment (Table A7.2) were obtained from GeneWorks Pty. Ltd. Custom Oligonucleotide service, and diluted to 10 μM for use in setting up PCR reactions. Real-time PCR reactions were set up with a CAS-1200N robotic liquid handling system (Corbett Research) and run for 50 cycles in a RotorGene RG 3000 (Corbett Research) with an annealing temperature at 54°C .

Table A7.1. Habitat distribution and mean abundance of (i) sea urchins, and (ii) lobsters retained on reefs inside (A.) Elephant Rock Research Reserve (ERRR) and (B.) North Bay Research Reserve (NBRR). The ERRR experiment commenced with declaration of the protected area on 21/04/2008, while the NBRR experiment started on 30/09/2008. Based on reef area and observed patterns in sea urchin abundance within the ERRR, the population of *Centrostephanus rodgersii* (*C.r.*) on widespread barrens declined from a density of 2.31 to 1.93 individuals m⁻² and in kelp bed habitat (*Ecklonia radiata*) from 1.77 to 1.32 m⁻², while *Heliocidaris erythrogramma* (*H.e.*) declined from 1.77 to 1.32 m⁻² and from 0.25 to 0.20 m⁻² on barrens and kelp habitat respectively over the 955 day study period. Within NBRR, the *C. r.* population declined from 0.12 to 0.02 m⁻² and *H.e.* from 1.26 to 0.55 m⁻² over the 840 day study period. Note that the remaining 17% of reef at ERRR was classified as deep invertebrate community / sediment matrix occurring along the sand edge of the reef at ~35-45 m depth for which we had no diver-based information on sea urchin densities at either the start or end of monitoring. For (ii), population estimates for are based on mark-recapture ratios of large lobsters CL≥140 mm and total legal lobsters CL ≥110 mm and are averaged over the duration of the study period.

				<i>Abundance</i>							
				<i>Sea urchin</i>						<i>Lobster</i>	
				Start		End		loss		<i>Time Integrated</i>	
<i>Site</i>	<i>Habitat</i>	<i>Area (m²)</i>	<i>% reef</i>	<i>C.r</i>	<i>H.e</i>	<i>C.r</i>	<i>H.e</i>	<i>C.r</i>	<i>H.e</i>	<i>Large</i>	<i>Total Legal</i>
ERRR	Seaweed bed	183,318	40	324,473	45,830	241,980	36,664	82,493	9,166	340	832
	Widespread Barrens	197,867	43	457,073	31,659	381,883	15,829	75,190	15,830	367	898
B. NBRR	Seaweed bed with incipient barrens	175,523	100	21,589	221,159	3,558	96,538	18,031	124,621	661	1,713

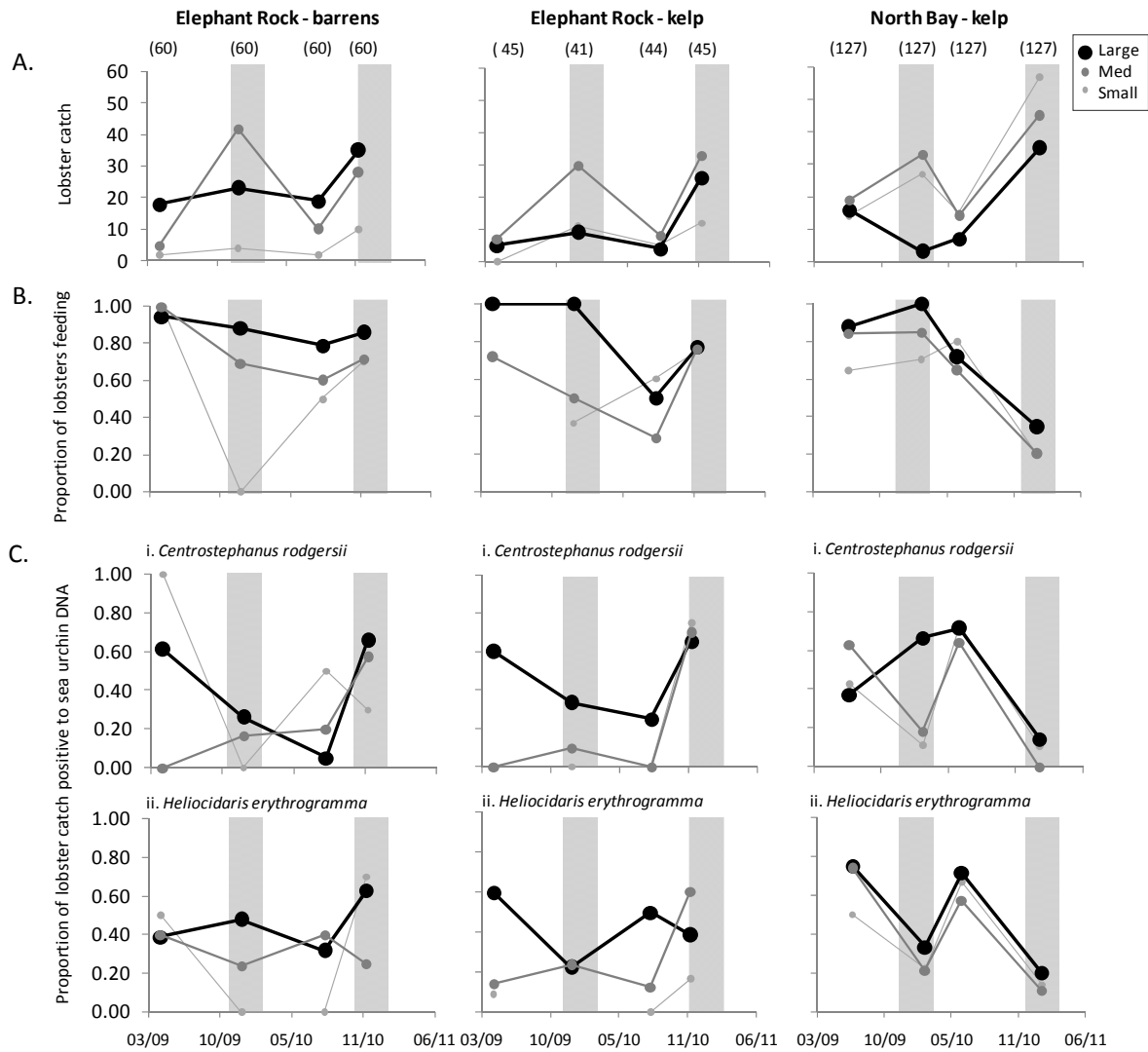


Figure A7.1. (A.) Catch of lobsters by size-class (see legend); number of trap lifts to attain catch is shown in parentheses above each sampling occasion. (B.) Proportion of trap-caught lobsters by size-class deemed to be feeding; i.e. those for which a faecal sample was obtainable. (C.) Proportion of trap-caught lobsters by size-class testing positive to DNA assay for sea urchins (i) *Centrostephanus rodgersii* and (ii) *Heliocidaris erythrogramma* in lobster faecal material sourced from research reserves at Elephant Rock (barrens & seaweed habitats; LHS & middle columns respectively) and North Bay (seaweed / incipient barrens only; RHS column) during winter and summer sampling 2009-2011. Note that lobster size classes are: Large, ≥ 140 mm carapace length (CL); medium, ≥ 110 mm & < 140 mm CL; small, < 110 mm CL. Filled grey regions represent summer periods where feeding rates of lobsters and catch-ability reach an annual high (see Ziegler et al. 2002, 2003, 2004).

Table A7.2. PCR primers used including sequence of each primer, target organism or group, and DNA region amplified. DNA regions are mitochondrial nuclear large subunit ribosomal RNA gene (16s rDNA).

Primer	Sequence (5'-3')	Target Species/Group	DNA	Region
Centro16sf	GGAACAGCAAACATGGAGAGTCCTGC	<i>Centrostephanus rodgersii</i>	16s	rDNA
Centro16sr	CCGTCTTGCCATTCATGCCAGTCTCTA	<i>Centrostephanus rodgersii</i>	16s	rDNA
Helio16sf1	TCAAAGGAAGTTACCG	<i>Heliocidaris erythrogramma</i>	16s	rDNA
Helio16sr1	CCCTTAAAAGCTTCTGCACCCT	<i>Heliocidaris erythrogramma</i>	16s	rDNA

Filtering PCR amplifications: determining presence of sea urchin DNA

PCR amplification curves were screened for (1) non-normal amplification curves, including a minimum threshold for fluorescence (threshold values of relative fluorescent units (RFU) were set at 0.1 RFU for *C. rodgersii* and 0.6 RFU for *H. erythrogramma* such that curves that appeared otherwise normal but that did not exceed this threshold were considered abnormal and were also removed); and (2) lower and upper *Ct* thresholds to minimise effects of false positives as a result of primer dimerization (i.e. reactions that developed unrealistically quickly indicated by *Ct* values of < 8 cycles; and reactions manifest as normal curves but that took too many cycles to amplify, consistent with primer dimerization, were excluded from consideration). Thus, positive tests for assays of *C. rodgersii* were considered as those $8 < Ct \text{ value} < 40$; and for *H. erythrogramma* as $8 < Ct \text{ value} < 45$ (see Fig. A7.2 for *Ct* frequency distributions for (a) each urchin species obtained from analysis of faecal material of trap caught lobsters at the reserve sites field; (b) of lobsters used in aquarium feeding trials (see below), and (c) of sediment samples obtained from the two translocation sites (see below, and Table 22, main body of report).

Recent advances in molecular biology have shown that in some cases prey DNA recovered from predator faecal material can be used not only to identify the prey consumed (Symondson 2002) but also to quantify the amount ingested (Deagle & Tollit 2006). However for field based samples, quantifying exact or even relative dietary intake is difficult because the amount of prey DNA in faeces is influenced not only by the amount ingested but also by other confounding factors including varying rates of digestion among individuals, the time between ingestion and defecation, the freshness of the recovered faecal material, and the condition of the ingested prey in circumstances where consumption is through scavenging of prey remains. Studies of marine birds and mammals in captivity show that the ratios of prey DNA detected loosely match the ratio of fish species fed during trials (Deagle & Tollit 2006; Deagle et al. 2010). But where prior feeding regimes are unknown (such is the case for wild-caught animals) it is currently not feasible to estimate even relative quantities of prey consumed using sensitive molecular techniques, so we adopted binary scoring (0,1). Thus, instantaneous predation rates of lobsters on sea urchins were scored as the number of individual lobsters in a given catch testing positive to sea urchin DNA, which we assumed could arise from ingestion of urchin DNA at any time over the previous 3-days (earlier work established that *C. rodgersii* DNA is detectable in lobster faecal samples for 7-60 hours after ingestion, so the assumption of 3 days errs on the conservative; Redd et al. 2008).

Analysis of variability in lobster feeding on sea urchins based on assays from field samples

Patterns of variability in the proportion of lobsters positive for sea urchin DNA (as defined by Ct thresholds outlined above) were assessed with binomial Generalised Linear Models (GLMs) with Logit link functions fitted using *R* (Ver. 2.15.1). GLMs relax the restrictions imposed by standard regression models on both the distribution of the response (here binomial) and the functional relationship between the response and predictors (here logit). Analysis of the deviance of fully-saturated models (including all main and interactive effects), as per standard analysis of variance but substituting classical *F*-tests for maximum likelihood estimation, were performed separately for each site. For ERRR, a 4-way model was assessed (*Year*Season*Size*Habitat*) in which there were 2 levels of *Year*, 2009 vs. 2010; *Season*, winter vs. summer; *Habitat*, seaweed bed vs. barren; and 3 levels of *Size*, small lobsters (≤ 110 mm CL) vs. medium lobsters (>110 & <140 mm CL) vs. large lobsters (≥ 140 mm CL). For NBRR, where habitat consisted entirely of seaweed bed (albeit supporting small incipient barrens patches), the 3-way model consisting of *Year*Season*Size* was examined.

Potential passive sources of sea urchin DNA: benthic sediments and excreted sea urchin faeces

Direct observations of large rock lobsters during daylight hours indicate that they sometimes appear to 'taste' and / or consume sedimentary material; a feature also noted occasionally for resident individuals (S. D. Ling *pers. obs.*). It was therefore necessary to assay for the presence of sea urchin DNA in benthic sediments, and to assess the potential for qPCR to detect sea urchin DNA in lobster faeces following ingestion of sediment or cast urchin faeces by rock lobsters. Benthic sediment samples were collected by SCUBA divers at both the ERRR and NBRR sites using 25 mL HSW sterile syringes (Henke Sass Wolf, GmbH) to obtain ~20 ml samples across a range of water depths and habitats. Distinct habitats at ERRR included both sea urchin barrens and adjacent seaweed dominated areas which were sampled at 10 m (seaweed habitat), and 15, 20 and 25 m (barrens habitat) depth, while at NBRR samples were from the seaweed bed and incipient barrens patches within it at a depth of ~8 m.

Feeding lobsters benthic sediment/ sea urchin faecal material

Rock lobsters used in feeding trials were captured by trapping in the Crayfish Point Marine Reserve at Tarooma, Tasmania (42.95 °S, 147.34 °E) in April 2010. Lobsters were collected opportunistically ensuring an even distribution of sexes and a wide range of sizes. The size (carapace length = CL) of all captured lobsters was measured to the nearest mm. Captured lobsters were immediately taken to the laboratory and kept in aerated, flow-through seawater tanks. For the duration of the feeding trials, lobsters were maintained under ambient light conditions and water temperatures in outdoor aquaria at the Institute for Marine and Antarctic Studies Marine Research Laboratories, Tarooma, Tasmania.

For each trial individual lobsters were placed in one section of a 450 l tank separated into three sections with plastic mesh and dividers. Each lobster was provided with a 400 mm x 200 mm concrete block as a shelter. All lobsters were starved for > 3-days prior to each feeding trial to facilitate gut evacuation and to remove any remaining prey DNA from the digestive tract (Redd *et al.* 2008). For each trial, fresh sea urchin faecal material was obtained from both species by allowing individuals of *H. erythrogramma* and *C. rodgersii* to defecate overnight in aquaria. To prepare gelatine 'food parcels' based on both the sea urchin faecal material and the benthic sediment samples, filtered seawater was heated to 100° C and mixed with gelatine (Davis, New Zealand), stirred and then poured into 30 ml

plastic moulds to which the component of each diet formula (i.e. sediment, or fresh sea urchin faecal pellets, or fresh sea urchin gonad tissue) was added and stirred in once the mixture had cooled to ~25°C using a new pipette tip to prevent contamination between diet formulas. The mix was then allowed to solidify in a standard refrigerator.

A gelatine 'food parcel' (with appropriate dietary element) was introduced to each lobster at 1700 h and individual lobsters were monitored for feeding activity. Only lobsters that fed actively and consumed the entire food sample within the first hour were used in the feeding trials. No additional food was provided to lobsters for the duration of the trial and each lobster was sampled only once in each trial. Lobsters were selected for faecal collection over the next two days at times (hours after commencement of feeding) based upon results of previous experiments to determine the longevity of dietary signals in lobster faeces (Redd *et al.* 2008). Lobsters were allocated diets randomly to eliminate any systematic 'tank' effect. For each sampling time, attempts were made to collect faecal material from at least three lobsters. For each of the individual faecal samples, qPCR assays were performed twice to guarantee the consistency of the result.

Lobster predation rates estimated from decline in sea urchin populations

Independent estimates of lobster predation rates on *C. rodgersii* were obtained by monitoring urchin and lobster populations.

Estimating change in sea urchin abundance

Diver-based counts of abundances of emergent sea urchins (*Centrostephanus rodgersii* and *Heliocidaris erythrogramma*) were performed at both the ERRR and NBRR sites using fixed belt-transects (50 m length by 2 m width) to monitor changes in their density. To distinguish changes in sea urchin density that might be attributable to dynamics unrelated to the addition of lobsters and declaration of the reserves, sea urchin densities were also monitored in the same way at nearby control sites (matched by similar reef types, with one to the north and one to the south of each research reserve). For north east sites where rocky reef habitat exists as seaweed bed or widespread sea urchin barrens, a total of 12 independent fixed belt transects were surveyed to assess change in urchin populations within ERRR and at both control sites, with transects established on both seaweed-dominated ($n=6$) and sea urchin barrens habitats ($n=6$) at each site (Fig. 22, main report). In the south east, 6 independent fixed belt transects were established within the seaweed bed supporting incipient barrens inside the reserve (NBRR) and outside at both control sites (Fig. 22, main report). In both regions, surveys were conducted on 5 occasions (approximately equally spaced) between 2008 and 2011, with one survey before and four after translocation of large lobsters. However, to quantify change in the populations of both sea urchin species at experimental and control sites in both regions, we compared only the first (pre-translocation of lobsters = 'before') and last (= 'after') surveys in the study (see explanation below; these two surveys were ~2.5 years apart).

Two approaches were used to assess change in urchin populations at the two experimental sites relative to the appropriate control sites (referred to as C1 and C2 in each region). First we compared the change in urchin density (= 'B-A' = 'density before' – 'density after', given fixed transects) between control and experimental sites. To minimise risk of Type II error, the 'B-A' metric was compared among control sites (C1 and C2 in each region) using 1-way ANOVA to assess the possibility of 'post-hoc pooling' of control sites based on the usual criterion $P>0.25$ in the comparison C1 vs. C2. For *C. rodgersii* in both the NE and SE regions, $P>0.25$ for this comparison ($P = 0.448$ and 0.284 respectively), so control sites were pooled

and compared with the experimental site in each region. For *H. erythrogramma* changes in density at C1 and C2 were similar in the NE ($P = 0.673$) and so control sites were pooled for this region, but in the SE the change in density was different at the two control sites ($P = 0.032$; at one site there was a decline, at the other an increase, in density – see Table 23, main body of report), so the control sites were not pooled. After pooling (or not), for both urchin species and for both the NE and SE regions, the change in density ('B-A') in the experimental sites and adjacent control sites was compared by 1-way ANOVA.

In the second and complementary approach, which addressed a related but distinctly different null hypothesis, because transects were fixed in space it was possible to separate the independent effects of change in urchin density and spatial variability using paired t-tests to determine whether the change in urchin density ('B-A') at each site differed significantly from zero. In these tests we controlled overall experiment-wise Type I error rates using the Dunn-Sidak adjustment to α for $n = 3$ tests within each region (i.e. reserve and two control sites were examined separately in each region). For the NE, because predatory lobsters were observed to move freely between adjacent habitats and urchins in both habitats were equally accessible to lobsters, benthic transects were pooled across habitats to give an overall trend of urchin population dynamics at the site level (i.e. $n = 12$ replicate transects for reserve and control sites).

Estimating large lobster abundance

Every translocated and captured resident lobster caught within both ERRR and NBRR was uniquely tagged for individual identification. Trap sampling was performed ~6 monthly at both NBRR and ERRR over the ~2.5 year study, yielding individual "encounter histories" for each lobster (individuals were scored as either, 'present and alive' or 'absent' at each re-sampling period). This enabled modelling individual survival estimates for translocated (group 1) and resident lobsters (group 2) using the Cormack-Jolly-Seber (CJS) 'recaptures only' mark-recapture routine available in the Program MARK® software (White and Burnham 1999). For CJS, the number of individuals re-sighted alive on subsequent sampling occasions is a function of 2 probabilities: the probability of survival (ϕ), and the probability that a surviving individual is encountered (ρ). Program MARK® uses Maximum Likelihood estimation to derive estimates of the parameters ϕ and ρ which maximize the likelihood of witnessing the observed frequency of individuals across different encounter history scenarios.

Following goodness-of-fit testing of the saturated model [i.e. where ϕ and ρ depend on both lobster group and time, formally denoted ϕ (group*time) and ρ (group*time)], the most parsimonious CJS model (based on Akaike's Information Criterion) was then used to inform estimates of the lobster populations using the POPAN routine in MARK®. For translocated lobsters, the estimated apparent 'survival' rate (which reflects both survival and emigration of lobsters out of the reserve site) was low immediately post-release of translocated lobsters, as evidenced by the best supported CJS model in which translocated lobsters showed lower survival than resident lobsters, but thereafter translocated lobsters demonstrated survival rates similar to resident animals. For translocated lobsters, the best estimate of the number retained the reserve sites was obtained by projecting daily survival rates (obtained by the best supported CJS model) upon the known number of lobsters released over the duration of the study.

Where the starting abundance was unknown, i.e. for resident lobsters, the POPAN model was used to estimate abundances of resident lobsters by size-class (large, 140mm CL; medium ≥ 110 & < 140 mm CL; small, < 110 mm CL) within each reserve at the time of final

sampling. The total abundance of large lobsters ≥ 140 mm CL (translocated plus resident lobsters) capable of preying on emergent size-classes of *C. rodgersii* (Ling and Johnson 2009), and of medium- and large-sized lobsters (translocated plus residents) ≥ 110 mm CL capable of consuming emergent *H. erythrogramma* (Pederson and Johnson 2006), were estimated for each reserve.

Estimating predation rates

Independent estimates of mortality rates of emergent sea urchins (i.e. excluding the smallest size classes of sea urchins, approx. <70 mm test diameter, that are restricted to “cryptic habitats” within the interstices of the reef and not visible or accessible to divers without them rolling boulders) were determined for comparison with rates of ingestion of sea urchin DNA obtained from molecular analysis of lobster faecal material. Given consistent and statistically significant declines in sea urchin populations at both reserve sites over the duration of the study (significant declines were observed for both *C. rodgersii* and *H. erythrogramma* at NBRR, and *C. rodgersii* within ERRR; see footnotes in Table 23, main body of report), but relatively small and non-significant changes, and lack of an overall trend, in urchin populations at adjacent control sites, we assumed that urchin population declines at the reserve sites were solely the result of predation by lobsters.

For each reserve site and for each species of sea urchin, we estimated the mean number of sea urchins to which each lobster had access, and fitted an exponential decay model based on a three day time step to preserve the observed density of urchins at the beginning and end of the experimental period (observation periods were 955 days at ERRR and 840 days at NBRR). Exponential decay was fitted on the basis of the pattern of mortality observed in four populations of tagged *C. rodgersii* subject to predation by lobsters inside and outside of two marine reserves (Ling *et al.* 2009b) and to patterns of urchin decline at the reserve sites themselves. This is ecologically sensible since it captures declining absolute predation by lobsters as sea urchin densities, and thus encounter rates, decline. We also ran a similar exercise but where the initial and final urchin densities at ERRR and NBRR over the experimental periods were taken as the mean densities estimated by fitting an exponential decay through all data from every sampling period (note that in this exercise, for NBRR the exponential fit was significantly better than a linear fit, while for ERRR the exponential fit did not provide a better description than a linear fit). Since the estimated predation rates were within 1% across the two methods, here we report on calculations based only on the observed sea urchin densities at the beginning and end of the study inside the research reserves.

Extensive data on movement of individual lobsters provided by VRAP acoustic tagging technology provided robust estimates of the home range area of individual lobsters (Ling *et al. in prep.*) and indicated that lobster densities were sufficiently high that home ranges were overlapping at both study sites. On this basis the mean number of sea urchins to which each lobster had access was estimated as the total number of sea urchins in each reserve divided by the number of predatory-capable lobsters in the reserves. As outlined earlier, based on extensive empirical and experimental observation of size-specific predation on sea urchins by lobsters, predatory-capable lobsters for *Centrostephanus rodgersii* were deemed as those >140 mm CL (Ling *et al.* 2009b) while lobsters >110 mm CL were considered capable of predating *Heliocidaris erythrogramma* (Pederson & Johnson 2006).

Cross-checking two independent estimates of predation rates

Representing the best integrated DNA-based estimate of sea urchin predation within the reserves over the duration of our study, rates of DNA-based predation by each lobster size-

class were averaged across seasons and years, with mean values and confidence intervals generated from 10,000 bootstrap simulations of the observed variability between different years and seasons. For purposes of cross-checking DNA based predation estimates within the research reserves, the rate of instantaneous lobster predation was calculated from the observed decline in urchin abundance using an exponential decay function with 3-day time step from which we calculated the mean number (over the entire study period) of urchins consumed per lobster per 3-day period to account for the observed decline in sea urchins. Mean values and CIs for instantaneous '3-day predation rates' were estimated from 10,000 bootstrap simulations of the variability in predicted large lobster abundance and variability in the change in urchin abundance across replicate fixed transects surveyed at the start and conclusion of the study within the reserves. Estimating predation rates on urchins based on both the DNA assays and observed declines in urchin densities at the reserve sites assumes that each lobster would not consume more than 1 urchin within any 3-day period. While this assumption may be conservative (deliberately), it is supported by *in situ* remote video surveys of lobsters consuming sea urchins within marine reserves (see Ling et al. 2009b) where, particularly for large urchins, on average no more than a single urchin was observed to be consumed by large individually identifiable lobsters within a 3-day period. In addition, as was the case in deriving overall mean-field estimates of predation rate based on DNA assays pooled across years and seasons, in deriving estimates of predation to explain declines in sea urchins we calculated an average across the entire study period.

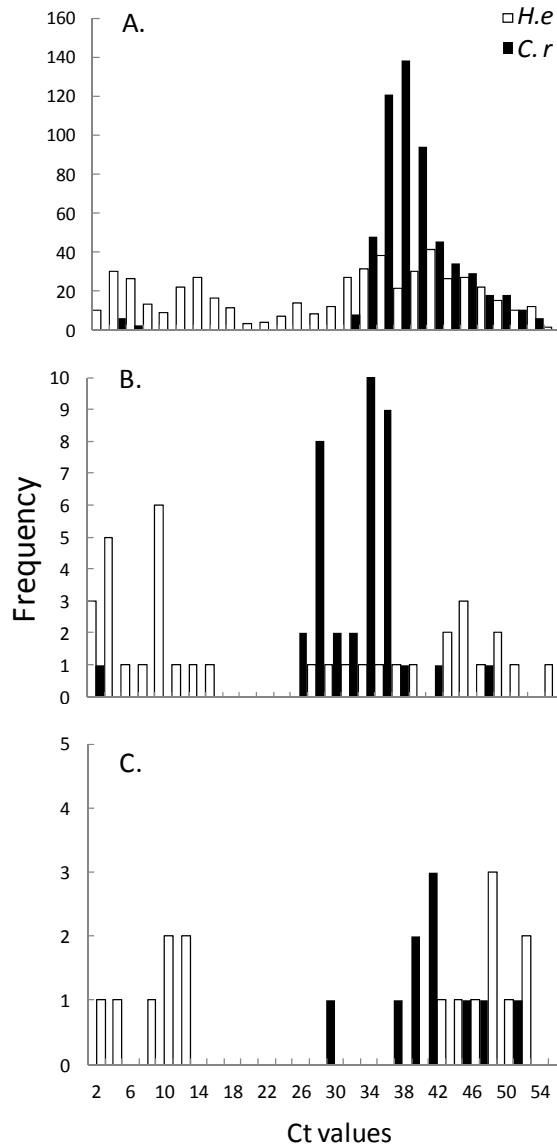


Figure 7.2. Distribution of Ct values obtained from PCR amplifications detecting DNA primers for the sea urchins *Centrostephanus rodgersii* (*C.r*) and *Heliocidaris erythrogramma* (*H.e*) across all sampling of: (A.) lobster faecal pellets from the research reserves in eastern Tasmania [total lobsters collected=1,331; total faecal samples yielded & analysed = 619; samples yielding Ct values=587 (*C.r*) & 513 (*H.e*)]; (B.) benthic sediments from both research reserves [total sediment samples=38; samples yielding Ct values=38 (*C.r*) & 36 (*H.e*)]; and (C.) urchin faeces and lobster faeces examined during laboratory feeding trials [total samples=19; samples yielding Ct values=10 (*C.r*), 16 (*H.e*)].

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APPENDIX 8: Development, calibration, validation and sensitivity analysis of the TRITON ecosystem model

Elements of this work have been submitted for publication in *Ecological Applications*. Here is provided the abstract from the submitted paper, the broader context in which the work can be considered, and a more detailed and technical outline of the methods and results than is presented in the main body of the report.

Title: Sensitivity analysis and pattern-oriented validation of a model with alternative community states: TRITON, a simulation model of ecological dynamics of temperate rocky reefs in Tasmania

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Abstract

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

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

Context

Models of ecological dynamics can be helpful to inform decision-making and improve the management of human activities that rely on natural resources (Clark et al., 2001; Smith et al., 2011). More specifically, simulation models can be useful decision-support tools to assess the effects of different management scenarios in ecosystems with alternative community states, where anthropogenic effects can lead to dramatic and possibly irreversible changes in structure and function across entire landscapes (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). However, building reliable simulation models requires a comprehensive understanding of key processes and drivers of system dynamics, and the accuracy of simulations will depend on the robustness of model parameterisation. Ecological processes, especially trophic interactions, are by essence variable and the dynamics of systems can be sensitive to this variation. However, ecological processes are usually difficult to measure precisely (Novak, 2010). It follows that, even in well-studied ecosystems, a complete and precise understanding and quantification of ecological processes is rarely possible. Thus, uncertainty arises as a major feature of ecological models, stemming from the variable nature of ecological processes, from imperfect understanding of the mechanisms underpinning ecosystem dynamics, and limited ability to quantify complex natural processes with precision (Saltelli et al., 2000).

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

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

- (i) structural uncertainty, which refers to model structure and its resolution, e.g. the extent to which species are aggregated, or the nature of functional groups;

the number and certainty of trophic and other ecological interactions considered; and the spatial and temporal scales of relevant physical and ecological processes (Laskey, 1996; Hosack et al., 2008; Marzloff et al., 2011);

- (ii) choice of model formulation, which includes programming choices (e.g. discrete versus continuous time (Deng et al., 2008), the timing of processes operating at different scales, and whether the model is spatially explicit) as well as the particular representation of ecological processes in the model (e.g. alternative ways to account for density-dependence in functional responses; Skalski and Gilliam, 2001);
- (iii) uncertainty in model parameterisation; uncertainty in individual parameter estimates, which can rapidly compound depending on interactions in the model, contributes directly to uncertainty in model outputs (Saltelli et al., 2000; Cariboni et al., 2007).

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

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

states. Structural uncertainty has been comprehensively tested in this model (Marzloff et al., 2011) and hence this paper focuses on sensitivity to uncertainty in model formulation and parameterisation. Using Monte-Carlo simulations, we explore the effects of parameter uncertainty on the behaviour of the model.

Our work comprises three steps: First, we quantify model sensitivity to alternative formulations and input parameters using the extended Fourier amplitude sensitivity test (FAST), a quantitative model-independent sensitivity analysis technique for complex simulation models (Saltelli et al., 1999). The extended FAST assesses the contribution to model output variance of each input parameter, including through interactions with other factors. We analyse model global behaviour as well as specific components of its dynamics; by decomposing overall model dynamics into ‘forward’ shift (from seaweed bed to barren) and ‘backward’ shift (from barren back to seaweed bed) components, the sensitivity tests overcome problems inherent to sensitivity analysis of models with hysteresis (van Nes and Scheffer, 2003). Second, we use sensitivity analysis to identify sources of model uncertainty and select an adequate ‘minimum realistic’ model form that can adequately tackle key management questions, i.e. estimate thresholds in community dynamics and assess community-level effects of alternative management scenarios. We compare the dynamics of Monte-Carlo simulations against large-scale patterns observed on Tasmanian reefs to validate model behaviour, and calibrate the propensity of the simulated community to shift from the seaweed bed to the sea urchin barren state against the known probability of barrens formation in south eastern Australia. Finally, the sensitivity analysis helps to both identify key ecological processes that drive Tasmanian reef community dynamics, and highlight gaps in knowledge about processes of high influence on community dynamics. In this context the sensitivity analysis provides a valuable tool to guide and prioritise future data collection and urge for critical further manipulative experiments about Tasmanian reef dynamics.

Methods

We developed a simulation model of Tasmanian reef communities, which we have called TRITON (Temperate Reefs In Tasmania with IObsters and urchiNs), to test the ecological consequences of different management scenarios applied to rocky reef systems in eastern Tasmania. If simulation modelling is to assist management of formation of barrens habitat by overgrazing by the urchins, the ability of TRITON to realistically capture the potential for discontinuous shifts between the two alternative states (seaweed bed versus sea urchin barren) is essential. The following subsections describe the structure of the TRITON model, its parameterisation and the empirical data available to calibrate model dynamics. We then outline the extended Fourier amplitude analysis test (FAST; Saltelli et al., 1999) used to test model sensitivity to parameter values, before specifying both the simulation characteristics and the important output metrics screened for the sensitivity tests.

TRITON: local dynamics of Tasmanian rocky reef communities

TRITON represents the mean community dynamics of an individual patch of rocky reef (area 100 m² - 10 ha; depth 8 - 35 m on open exposed reef habitat where *C. rodgersii* barrens occur in Tasmania). The dynamics of three functional groups or species are captured explicitly (Fig. 8.1), representing the dynamics of the seaweed bed (SW) (Equ. 1), the sea urchin *Centrostephanus rodgersii* (CR) (Equ. 2) and rock lobsters (RL) (Equ. 3). Size-structured dynamics for both sea urchin and rock lobster populations are key for TRITON to realistically capture both the effects of size-related fishing regulations (e.g., legal size), and the size-

structured nature of lobster predation on the urchin (Ling et al., 2009a) (cf. Equ. 2). Each is introduced in turn:

(i) The **seaweed bed (SW)** includes understory algal assemblages and all canopy-forming macroalgae dominated by *Ecklonia radiata* at depth > 6 m, or *Phyllospora comosa* on shallow reef (but generally include small contribution < 5% covers of other large phaeophytes, including representatives of the genera *Cystophora*, *Sargassum*, *Sierococcus*, *Carpoglossum*, *Acrocarpia*). The understanding of both the dynamics of the different guilds of algae that constitute the seaweed bed, and the details of overgrazing of these different algal species and groups by *C. rodgersii* is incomplete. Thus, in the model, the seaweed bed compartment corresponds to the current minimum realistic representation of temperate algal communities. Seaweed assemblage dynamics follow logistic growth (Equ. 1), with parameters derived from monitoring macroalgal recovery from a barren state over two years after experimental removal of the urchins (Figs. AT8.1 and AT8.2; Appendix AT8; Ling, 2008). Propagule supply is assumed to be constant and independent of the local state of the seaweed bed, as external supply from adjacent macroalgal beds is not limiting (CR Johnson, personal observation). Although a range of herbivorous species rely on macroalgae as part of their diet, only *C. rodgersii* has demonstrated the ability to overgraze Tasmanian seaweed beds on exposed rocky reefs on the open coast. The native purple sea urchin (*Heliocidaris erythrogramma*) also forms barrens habitat (but on a smaller scale than *C. rodgersii*) in relatively sheltered bays in eastern Tasmania (Valentine and Johnson, 2005), but TRITON focuses exclusively on the dynamics of exposed inshore reefs where the effect of *H. erythrogramma* is marginal. Thus, grazing by the long-spined sea urchin is the only explicit source of seaweed biomass loss in the model. Urchin grazing rate is assumed to be constant, dissimilar to northern hemisphere stronglylocentroid urchins that destructively graze seaweeds by forming a grazing front once critical density and behavioural thresholds are reached (Lauzon-Guay et al., 2009). In Tasmania there is no evidence of density-dependence of *Centrostephanus rodgersii* grazing rate, and the effects of individual grazers are additive. Across incipient and extensive barrens habitat, sea urchin destructive grazing shows a remarkably consistent ratio of ~0.6 m² of grazed area per individual urchin irrespective of the size of the barrens patch (Flukes et al., 2012). Although all size classes of emergent urchins consume seaweed at the same rate for a given biomass of urchins (the last term in Eq. 1), larger urchin individuals have a higher per capita destructive impact on standing macroalgae in the model since urchin population dynamics (see Eq. 2) capture biomass gain from one size class to the next due to individual growth. The equation for the seaweed assemblage is given as:

$$SW_{t+1} = \max \left(0, \underbrace{r_{SW}}_{\text{Recruitment}} + SW_t \times \left(\underbrace{1 + \alpha_{SW} \times \frac{(K_{SW} - SW_t)}{K_{SW}}}_{\text{Logistic population dynamics}} - \underbrace{\beta_{SW,CR} \times \sum_{s=1}^{N_{CR}} CR_{s,t}}_{\text{Urchin grazing}} \right) \right) \quad \dots \text{(Equ. 1)}$$

where SW_t is seaweed biomass at time t (g. 200 m⁻²); r_{SW} , seaweed recruitment rate (g. year⁻¹. 200 m⁻²); α_{SW} , seaweed intrinsic growth rate (year⁻¹); K_{SW} , seaweed carrying capacity (g. 200 m⁻²); $\beta_{SW,CR}$, sea urchin grazing rate (g of SW. g of CR⁻¹. year⁻¹. 200 m⁻²); $CR_{s,t}$, biomass density of sea urchins in size class s at time t (g. 200 m⁻²).

(ii) **Population growth of *C. rodgersii*** is size-structured (Eq. 2) and fitted against data from large-scale population surveys on the east coast of Tasmania (Fig. AT8.3; Appendix AT8; Ling et al., 2009b; Johnson et al., 2011). Despite its destructive grazing of seaweed beds, sea

urchin population dynamics is independent of seaweed consumption because sea urchins forage on drift material, ephemeral filamentous algae and microalgae to subsist on barrens habitat in the absence of attached canopy macroalgae (Ling and Johnson, 2009). In TRITON, the size structure of sea urchin individuals is distributed across 21 size classes ranging from 40 to 120 mm test diameter using 4.12 mm increments (Fig. AT8.6; Appendix AT8). The effect of habitat complexity on survival of juveniles (provision of crevices to shelter from predation) is implicitly modelled in the Monte-Carlo simulations through changes in mean recruitment rate. Only adult animals of test diameter >70 mm are fully emergent in Tasmania and smaller individuals largely stay cryptic in crevices, with virtually no effect on standing macroalgae through grazing and likely very limited interactions with rock lobster (Ling et al., 2009a; Ling and Johnson, 2012; SD Ling, unpublished data). Hence, only these larger animals affect seaweed material and are exposed to lobster predation in the model. Recruitment is stochastic and independent of local population size given that *C. rodgersii* has a planktotrophic larval stage of ca. 3 months duration that disperses with currents at scales of 10^2 - 10^3 km (Huggett et al., 2005; Banks et al., 2007). The southern rock lobster is the only effective predator of *C. rodgersii* in Tasmanian waters. Because a lobster's ability to handle a given size of sea urchin is determined by the size of its front pair of walking legs (Ling et al., 2009a), predation of *C. rodgersii* by rock lobster is constrained by the relative size of prey and predator (Equ. 2). Hence, size-structured predation by lobsters (third term of Equ. 2) is the only explicit source of natural mortality on sea urchins in the model. The predation rate $\beta_{CR,RL}$ accounts for density-dependence of *C. rodgersii* predation following any of Holling's Type I, II or III functional responses (Holling, 1966; cf. Fig. AT8.11 and Tables AT8.7 and AT8.8 in Appendix AT8 for further details about the definition and parameterisation of Holling's functional responses in TRITON). The equation for urchin dynamics is given as:

$$\begin{aligned}
 CR_{s,t+1} = \max & \left(0, \underbrace{r_{CR}}_{\substack{\text{Recruitment to the first size class} \\ \text{(only if } s=1)}} + \underbrace{CR_{s,t} \times \exp(-\beta_{CR_s})}_{\substack{\text{Biomass at time } t \text{ affected} \\ \text{by natural mortality}}} \right) \\
 & + \underbrace{\sum_{j=1}^{j < s} (\delta'_{s,j} \times CR_{j,t})}_{\substack{\text{Growth between different size classes accounts} \\ \text{for individual weight gain}}} - \underbrace{\left(\sum_{i>s}^{N_{CR}} \delta_{i,s} \right) \times CR_{s,t}}_{\substack{\text{Size-structured predation}}} - \underbrace{\beta_{CR,RL} \sum_{i=\text{minCL}}^{N_{RL}} RL_{i,t}}_{\substack{\text{Size-structured predation}}} - \underbrace{CR_{s,t} \times (1 - \exp(-F_{CR_s}))}_{\substack{\text{Culling mortality}}} \right) \quad \dots \text{ (Equ. 2)}
 \end{aligned}$$

where $CR_{s,t}$ is biomass of sea urchin in size class i ($\text{g} \cdot 200 \text{ m}^{-2}$); r_{CR} , urchin recruitment rate to the first size class $s = 1$ ($\text{g} \cdot \text{year}^{-1} \cdot 200 \text{ m}^{-2}$), and where the mean recruitment rate μ_{CR} varies stochastically (see below); β_{CR} , urchin natural mortality (year^{-1}); F_{CR} , urchin harvesting mortality (year^{-1}); $\delta_{i,j}$, abundance-based growth transition probability from size class j to i (year^{-1}); $\delta'_{i,j}$, biomass-based growth transition probability from size class j to i (year^{-1}); $\beta_{CR,RL}$, size-structured lobster predation rate on sea urchins of size class s ($\text{g of CR} \cdot \text{g of RL}^{-1} \cdot \text{year}^{-1} \cdot 200 \text{ m}^{-2}$), which follows any of Holling's Type I, II or III functional responses. Only lobsters from size classes larger than CL_{min} can prey on urchins of class s ; the minimum carapace length (CL_{min} , in mm) for rock lobster to predate upon sea urchin individuals of a given test diameter (TD, in mm) can be expressed after Ling et al (2009a) as $CL_{\text{min}} = \alpha_1 \log(\text{TD}) - \alpha_2$ where α_1 and α_2 are scalars defining the allometry of the size-structured interaction (cf. Appendix AT8, section 3.2.2).

Recruitment to the smallest emergent size class of urchins in a given year is determined in part by a binomial term which determines whether a recruitment event will occur at all in any given year, which acknowledges that water temperatures in some years are not sufficiently warm to support larval development (Ling et al. 2008). When recruitment does occur, its magnitude is determined with a parameter μ from a uniform distribution ranging between minimum and maximum absolute values (and which reflects variability between reefs, with some reefs consistently receiving more recruits than others on average) modified by a lognormal scaling quantity (with mean γ_{CR} and standard deviation σ_{CR}) to capture annual stochastic variation (cf. Equation AT8.4 and Fig. AT8.5 in Appendix AT8 for details).

(iii) The size-structured **rock lobster (RL) population** component is derived from the Tasmanian rock lobster fishery stock assessment model (see Punt and Kennedy, 1997; McGarvey and Feenstra, 2001), and so TRITON represents the lobster population across 31 size classes ranging from 65 to 215 mm of carapace length by 5 mm increments. This enables a realistic representation of the effects of size-related fishing regulations (e.g. minimum legal sizes are 105 and 110 mm carapace length for females and males, respectively). The lobster size-structured population model was closely fitted against observed population recovery following protection from fishing (Figs. AT8.4 and AT8.8 in Appendix AT8; Barrett et al., 2007). The natural mortality term accounts for sources of mortality that are not explicitly captured elsewhere in the equation, e.g. through predation by sharks or cephalopods (Pecl et al., 2009).

The lobster population in the model relies on the local state of the seaweed bed as an essential source of habitat and food. More specifically, abundances of juveniles are lower on barrens habitat than in adjacent kelp beds, while observations associated with experimental manipulation of large lobsters suggest that abundances of large supra-legal predatory-capable lobsters are largely unaffected by barrens habitat (Fig. AT8.10; Johnson et al., unpublished data). Canopy-forming macroalgae can facilitate both, settlement of lobster puerulus by providing a complex three-dimensional structure and development of juvenile lobsters by supporting a broad diversity of invertebrate prey species (Ling, 2008). Therefore, a constant coefficient, ranging from 0 (for no recruitment on barren habitat) to 1 (for no effect of barrens on recruitment), scales lobster recruitment as a function of the state of the seaweed bed (cf. first term of Equ. 3; Table AT8.5). Lobster recruitment rate r_{RL} is (i) stochastic following a lognormal stochastic function and (ii) independent of the local lobster population given that lobsters have an 18-24 month pelagic larval stage, implying large-scale dispersal (Bruce et al., 2007). The equation for rock lobster dynamics is given as:

$$\begin{aligned}
 RL_{s,t+1} = \max & \left(0, \underbrace{r_{RL} \left[1 - (1 - \beta_{RL,SW}) \left(1 - \frac{SW_t}{K_{SW}} \right) \right]}_{\text{Recruitment to the first size class (only if } s=1 \text{) gets reduced as barren habitat expands.}} + \underbrace{RL_{s,t} \times \exp(-\beta_{RL})}_{\text{Biomass at } t \text{ affected by natural mortality}} \right) \\
 & + \underbrace{\left(\sum_{j=1}^{j < s} (\delta_{s,j}^y \times RL_{s,t}) - \left(\sum_{i>s}^{N_{RL}} \delta_{i,s} \right) \times RL_{s,t} \right)}_{\text{Growth between different size classes accounts for individual weight gain}} \underbrace{\left(1 - \exp(-F_{RL_s}) \right) \times RL_{s,t}}_{\text{Fishing mortality}} \right) \quad \dots \text{ (Equ. 3)}
 \end{aligned}$$

where $RL_{s,t}$ is the biomass of rock lobsters in size class s at time t ($g. 200 m^{-2}$); r_{RL} , lobster

recruitment rate ($\text{g} \cdot \text{year}^{-1} \cdot 200 \text{ m}^{-2}$), which derives from a mean recruitment rate μ_{RL} varied stochastically with a lognormal stochastic function of mean γ_{RL} and standard deviation σ_{RL} (Fig. AT8.7); $\beta_{\text{RL,SW}}$ is a scalar, ranging from 0 for no lobster recruitment on barren grounds to 1 for no effect of barrens habitat on lobster mean recruitment; β_{RL} , lobster natural mortality (year^{-1}); $\delta'_{s,j}$, biomass-based transition probability from size class j to s , or element of the s^{th} row, j^{th} column of the transition probability matrix (year^{-1} or $\text{g} \cdot \text{g}^{-1} \cdot \text{year}^{-1}$); $\delta_{i,s}$, abundance-based transition probability from size class s to i (year^{-1} or $\text{individual} \cdot \text{individual}^{-1} \cdot \text{year}^{-1}$); SW_t , seaweed biomass density at time t ($\text{g} \cdot 200 \text{ m}^{-2}$); $F_{\text{RLS},t}$, fishing mortality for lobster of class s (year^{-1}).

Recruitment rates vary stochastically for both lobster and sea urchin populations (See Equ. 2 and 3), while propagule supply is assumed constant for the seaweed bed (Equ. 1). Recruitment is independent of local spawning population densities: indeed, for all three modelled groups, larval or propagule settlement occurs over much larger spatial scales than individual reefs (Banks et al., 2007; Banks et al., 2010; Johnson, unpublished data; Linnane et al., 2010; Coleman et al., 2011).

Parameterisation

Variables are expressed as fresh weight biomass density with a default parameterisation for a reef area of 200 m^2 (variables in $\text{g} \cdot 200 \text{ m}^{-2}$). Biomass density allows for weight-based (rather than abundance-based) trophic interactions and was derived from experimental or other empirical observation (Table A8.1; see Appendix AT8 for details). All modelled processes were parameterised from *in situ* observations or measurements (Ling, 2008; Redd et al., 2008; Barrett et al., 2009; Ling and Johnson, 2009; Ling et al., 2009b), field- or laboratory-based experiments (Hill et al., 2003; Ling et al., 2009a), or well-validated models (Punt and Kennedy, 1997; Punt et al., 1997; McGarvey and Feenstra, 2001). For each parameter, Table A8.1 summarises data sources and the estimated distribution of each parameter (i.e. mean and standard deviation for normal distributions; minimum and maximum bounds for uniform distributions). For normally distributed parameters, values within the 90% confidence interval (bounded by the 5 and 95% quantiles) were explored during the sensitivity analyses. As well as enveloping uncertainty in modelled processes, these ranges implicitly encompass the span of environmental conditions (e.g. habitat, depth) and anthropogenic forcing (e.g. fishing pressure) encountered on Tasmanian rocky reefs. Appendix AT8 comprehensively describes all data sources and the estimation of model parameters.

Global sensitivity analysis with the extended Fourier amplitude sensitivity test (FAST)
The extended Fourier amplitude sensitivity test (extended FAST) does not assume linearity or monotony between model inputs and outputs, and hence provides a robust quantitative and model-independent sensitivity analysis method for models of complex systems dynamics (Saltelli et al., 1999). In the absence of sufficient empirical data to derive distributions, we assumed uniform distributions for input parameters within the bounds given in Table A8.1. The extended FAST assigns a unique frequency to each input parameter. These frequencies define the cyclic exploration of each parameter's range through successive Monte-Carlo simulations. Thus, using multidimensional frequency decomposition, the contribution of each input to the variance of the output is expressed as a total sensitivity index including both the main effect attributable to that parameter, and higher degree effects from interactions with other parameters (Saltelli et al., 1999). Following preliminary tests, each parameter range was divided into 500 levels. This sampling resolution brought the total number of Monte-Carlo simulations per test to $500n$ (where n refers to the

number of input parameters screened).

Types of simulations and key outputs screened for sensitivity analysis

We used FAST sensitivity analysis tests to dissect the influence of model formulation and input parameters on TRITON's general behaviour and, more specifically, on its ability to shift from seaweed bed to sea urchin barren and back (see following subsections). Model outputs were saved monthly for each 50-year-long simulation, and the extended FAST applied to several output metrics. The first of these was the mean simulated biomass of each model group over the last 10 years of simulation. Note that the relative biomass of the seaweed bed is directly convertible to percentage cover of seaweed. We also used the first axis of a Principal Component Analysis on the three normalised biomass densities as a one-dimensional summary of community state (accounting for 73% of the total variance).

Sensitivity to the formulation of rock lobster predation on sea urchins

We specifically tested for sensitivity of TRITON's general behaviour to alternative formulations of the lobster predation rate (simulations with random initial condition; see Table A8.2). Density-dependence of lobster predation rate on urchin density was represented as a Holling Type I, II or III functional response (Fig. A8T.11; Holling, 1966), and the effects on overall model behaviour compared using the FAST sensitivity analysis (Fig. A8.2). The effects of alternative formulations of lobster predation rate were also examined by comparing the scores on the first two axes of the PCA of simulation outcomes with each of the Holling Type I, II or III functional responses (Fig. A8.3). The comparison of the projection of simulation outcomes with each functional response on the first two PCs was both qualitative (based on the visual inspection; Fig. A8.3), and statistical (using a MANOVA with the type of functional response as a factor).

Global sensitivity and pattern-oriented model validation

We investigated the influence of input factors on the general behaviour of TRITON with a global sensitivity test (Figs. A8.2c and A8.4) in which all parameters varied and initial conditions were unconstrained (Table A8.2). Monthly outputs from these simulations were used to investigate both model community composition and the dynamics of the TRITON model (Fig. A8.5a), and to assess the model's ability to mimic observed patterns (Fig. A8.5b) of seaweed percentage cover and sea urchin density from large surveys of reef habitat and reef species abundance around Tasmania during the period 2000-2011 (Johnson et al., 2005; Johnson et al., 2011; this study), which we converted to biomass densities directly comparable to model outputs. The frequency of occurrence of community states along the Tasmanian coastline, which encompasses a gradient of local contexts in terms of fishing pressure, habitat complexity and urchin invasion history, could then be compared to the patterns emerging from Monte-Carlo simulations with TRITON (Fig. A8.5).

Sensitivity analysis of the forward and backward shifts

We also focused on the effect of input parameters on the 'forward' (kelp bed to urchin barren state) and 'backward' (seaweed recovery from the barren state) shifts. In each of these cases, initial conditions were constrained to mimic either an urchin-free seaweed bed (for the forward shift) or a well-established sea urchin population on extensive barrens habitat (for the backward shift; see Table A8.2). For the sensitivity tests on the forward (Fig. A8.6) and backward (Fig. A8.7) shifts, we also measured the time for the community to shift to the alternative state as an important feature of model dynamics. A shift to the barren state was defined as seaweed bed cover dropping below 10%, while seaweed bed recovery corresponded to >50% seaweed cover (see Table A8.2).

Choice and calibration of a minimum-realistic model

In marine ecosystem models, recruitment rates are often the most uncertain parameters and are commonly used as calibration factors (e.g. Marzloff et al., 2009). In TRITON we adjusted *C. rodgersii* recruitment to ensure both that simulations could achieve realistic sea urchin biomass densities, and that across Monte-Carlo simulations the model's propensity to shift 'forward' (from the seaweed bed to the sea urchin barren state) agrees with large-scale surveys of barren habitat across reefs where *C. rodgersii* occurs.

No meaningful optimisation could be designed to calibrate the goodness-of-fit of the model against multiple quantitative criteria (e.g. Klepper, 1997; Duboz et al., 2010). In particular, because of the occurrence of alternative states, consideration of model mean dynamics to capture mean community composition is not meaningful. Also, because of the model complexity an interpretable analytical solution could not be derived to formally validate the occurrence of alternative stable states within the estimated parameter space as was achieved, for example, by Fung et al. (2011). Accordingly, we used pattern-oriented modelling, proposed as a means to calibrate agent-based models (Grimm et al., 2005), as an effective way to validate and calibrate the behaviour of TRITON against the data available for Tasmanian reef dynamics.

In the context of pattern-oriented modelling, we note that in regions where *C. rodgersii* has been present for several decades and where key reef predators have been depleted by fishing (e.g. New South Wales, the Furneaux group and north-eastern Tasmania), about 50% of coastal rocky reef habitat is reported as sea urchin barrens (Andrew and O'Neill, 2000; Johnson et al., 2011). Thus, we focused on the ability of TRITON to reproduce across a set of Monte-Carlo simulations initialised in the seaweed bed state (see Table A8.2) these large-scale patterns of barren formation emerging across reef habitat where *C. rodgersii* occurs. In these simulations, fishing mortality was set to mimic historical fishing mortalities derived from the rock lobster stock assessment model for eastern Tasmania (FRL within 1-1.8 year⁻¹; Klaas Hartmann, pers. comm.), and size-structured predation of lobsters on sea urchins, which notably influences TRITON's behaviour and its ability to shift to sea urchin barrens (Figs. A8.4, A8.6), was set based only on field observations and ignoring information from tank predation experiments in which lobster predation on sea urchin is artificially enhanced (Ling et al., 2009a) ($\alpha_2 = 49$ in: $CL_{min} = \alpha_1 \log(TD) - \alpha_2$; where CL_{min} is the minimum carapace length (in mm) for lobster to prey on sea urchins of test diameter TD (in mm); cf. section 3.2.2 in Appendix AT8). The proportion of simulations shifting 'forward' (from seaweed bed to sea urchin barren habitat) was specifically examined as a function of sea urchin mean recruitment rate (μ_{CR} ; Equ. 2) so as to calibrate the probability of sea urchin barrens formation across Monte-Carlo simulations with TRITON (Fig. A8.8).

Results

We first consider sensitivity of model behaviour to the various parameters before considering the calibration and validation of the model.

Sensitivity analysis and identifying parameters that most influence model behaviour*Functional response for lobster predation*

Checking that the particular formulation of density dependence in lobsters' predation on urchins has minor influence on model behaviour can be taken as a component of model validation. For each of Holling's Type I, II or III functional responses, the two parameters

defining the shape of the response had no more influence on model behaviour than did most of the other 14 input factors (cf. FAST sensitivity indices in Fig. A8.2). Indeed, the influence of these two parameters was relatively small compared to parameters with greatest influence on model behaviour (i.e. lobster fishing mortality, sea urchin recruitment, initial sea urchin population density, seaweed growth rate), and also smaller than the influence of the coefficient defining the allometry of rock lobster size-structured predation on sea urchins. The projection of simulation outcomes on the first two PCs also suggests that the nature of the functional response has little influence on model behaviour (Fig. A8.3) in that the pattern of scores on the first two PCs (capturing 87.4% of the total variability) are similar for all three functional responses. Although results from MANOVA suggest significantly different mean scores (P value $< 10^{-15}$; $F_{2,23997} = 67.5$ from MANOVA Pillai's Trace statistic) on the first two PCs for each type of functional response, this is likely to reflect the very large number of replications (8000 simulations, which ensures extremely small multivariate standard errors and large power) rather than ecologically meaningful differences. Given that overall model behaviour was not sensitive to either the choice of functional response or to its parameterisation, we adopted the Type III functional response, which is consistent with most models of predation behaviour in decapods based on field observations (see Table AT8.8 for complete list of references; Appendix AT8).

Global sensitivity analysis

The sensitivity to input parameters of final abundances (after 50 years of community development) of seaweed, sea urchins and lobsters, and of overall community structure, was examined across 8000 Monte-Carlo simulations with unconstrained initial conditions (Figs. A8.2c, A8.4). Total extended FAST sensitivity indices quantify input parameters' relative contribution to model output variance for a given sensitivity test (but their absolute values are not comparable across different extended FAST tests). Overall, the most influential variables were similar for each component of community structure we examined, namely fishing mortality of lobsters, sea urchin recruitment rate, sea urchin initial abundance and seaweed growth rate (although some other variables were moderately influential for some components). However, the rank order of influence differed depending on whether it was final densities of seaweed, sea urchins or lobsters that were examined. Final biomass density of seaweed is predominantly determined by, in order of importance: the initial density of sea urchins; urchin recruitment rates; seaweed growth rate; size-structured lobster predation on sea urchin; lobster fishing mortality and initial biomass (cover) of seaweed (Fig. A8.4a). The two most influential parameters on final sea urchin biomass densities are sea urchin recruitment rate and lobster fishing mortality (Fig. A8.4b). Not surprisingly, the final biomass density of lobsters is mostly determined by lobster fishing mortality and, to a lesser extent, lobster recruitment rate (Fig. A8.4c). In comparison, other input parameters defining lobster population dynamics (e.g. initial biomass, natural mortality, the extent of dependency on the state of the seaweed bed) have a marginal influence.

Given these results, it is not surprising that overall community structure described by the first principal component of the mean-centred normalised simulated biomasses of the three groups (and accounting for 73% of the total variance; Fig. A8.2c) is most influenced by, in order of importance: lobster fishing mortality; sea urchin recruitment rate; initial sea urchin abundance; seaweed growth rate; and finally the three parameters defining lobster predation on sea urchins. Across all four outputs considered in this sensitivity analysis, the carrying capacity and recruitment rate of the seaweed assemblage; sea urchin natural mortality and their grazing rate; initial abundance and natural mortality of lobsters; and the coefficient of lobster dependency on the state of the seaweed bed, have relatively marginal

influence on the end point community structure in the simulations. Fig. A8.5a depicts the general behaviour of TRITON, i.e. the range and frequency of model community composition and mean trajectory (fortnightly change in biomass) emerging from these 8000 Monte-Carlo simulations with random initial conditions.

The final two sets of sensitivity tests quantify the contribution of input parameters to two specific and important features of model behaviour, respectively, the ‘forward’ shift from the seaweed assemblage to sea urchin barren habitat (Fig. A8.6), and the ‘backward’ shift from extensive sea urchin barrens to recovery of dense seaweed cover (Fig. A8.7). We conducted these sensitivity analyses on the scores of the first principal component of the mean-centred normalised simulated biomasses of the three model groups, as a one-dimensional summary of final community state (which explained 73% of the total variance in final community composition). Sea urchin recruitment rate, lobster fishing mortality, seaweed growth rate and the three parameters defining lobster predation rate most influenced the tendency to shift from dense seaweed assemblage to sea urchin barrens (Fig. A8.6a). TRITON’s ability to shift from an established sea urchin barren state back to dense seaweed cover was essentially driven by the values of lobster fishing mortality and recruitment rate (Fig. A8.7a).

In considering only the subset of simulations that either shifted ‘forward’ (Fig. A8.6b) or ‘backward’ (Fig. A8.7b), we investigated the effects of the most influential parameters (i.e. lobster fishing mortality and the mean recruitment rates of sea urchins (Fig. A8.6b) and rock lobsters (Fig. A8.7b) on the time to transition from one state to the other. Formation of extensive sea urchin barrens becomes more likely and the time to destructive grazing of seaweed beds becomes shorter in an essentially linear manner with increasing lobster fishing mortality and sea urchin mean recruitment rate (Fig. A8.6b). Conversely, as fishing mortality on lobsters decreases and their recruitment rate increases, the time to recovery of a dense seaweed cover from the barren state decreases in an approximately linear fashion (Fig. A8.7b). Note, however, that the likelihood of seaweed bed recovery from extensive sea urchin ‘barrens’ is small (less than 10%), even as fishing mortality of lobsters is reduced and their recruitment increased.

A final important point to emerge for all sensitivity analyses (Figs. A8.2, A8.4, A8.6 and A8.7) is that interaction terms contribute consistently more - and in most cases very much more - to the variance of model outputs than first order ‘main’ effects due to single input parameters acting directly on their own. Across all input parameters and all output variables considered in global sensitivity analysis tests (Figs. A8.2, A8.4), interaction terms contribute to over 80% of variance in model outputs. The total influence on model output variance of all input parameters is greater than the sum of their direct individual influence. This highlights the dominant contribution of complex non-linear interactions between modelled processes to TRITON’s overall dynamics.

Pattern-oriented validation and calibration of TRITON

Sensitivity analyses proved useful to explore model behaviour, to assess sources of model uncertainty, and to define a parsimonious and reliable version of TRITON for application to management questions. To calibrate model behaviour to empirical observations, attention was paid to parameters influencing the ‘forward’ shift (i.e. lobster fishing mortality, sea urchin recruitment, seaweed growth rate, allometry of lobster size-structured predation on sea urchin; cf. Fig. A8.6). Lobster size-structured predation was based on field observations indicating that only large lobsters (>140 mm carapace length) can prey on emergent sea

urchins (Ling et al. 2009a), and the range of lobster fishing mortality for these calibration simulations corresponded to historical levels experienced in eastern Tasmania. Smaller lobsters may occasionally predate smaller urchins largely confined to the interstices of the reef matrix but this is likely to be offset by our assumption that any lobster >140 mm CL can predate any emergent sea urchin it encounters. The effects of other influential parameters, seaweed growth rate and sea urchin recruitment rate, on the risk of barren formation is non-linear (Fig. A8.8a), with the likelihood of barrens forming increasing dramatically, and becoming almost certain, when sea urchin recruitment rates exceed a threshold of about 7000 g. 200 m⁻². year⁻¹.

Monte-Carlo simulations with TRITON, in which combinations of input parameters are comprehensively tested, adequately encompass the diversity and spatial heterogeneity encountered on Tasmanian rocky reefs. For example, the patterns shown in Fig. A8.8a can be interpreted as some reefs being more prone to barrens formation than others depending on seaweed productivity and local recruitment of urchins. The proportion of simulations shifting to sea urchin barrens increases non-linearly from about 15% up to 80% as the maximum value of the range of sea urchin mean recruitment rate is increased from 2000 to 10000 g. 200m⁻². year⁻¹ (Fig. A8.8b). The two grey dashed horizontal lines (Fig. A8.8b) delimit the bulk range of sea urchin barrens habitat extent (~50% of reef area) in New South Wales (Andrew and O'Neill, 2000) and northeastern Tasmania (Johnson et al., 2005, 2011) where *C. rodgersii* is long established. Consequently, maximum sea urchin recruitment rate was set to 6000 g. 200 m⁻². year⁻¹ to ensure that the probability of the TRITON model shifting to barrens is in line with large-scale observations of the extent of sea urchin barrens in reef areas where *C. rodgersii* has been long established.

At a holistic level, the capacity of the model to demonstrate shifts (in either direction) between seaweed and sea urchin dominated reefs represents a validation of the observed dynamics. We aggregated monthly outputs from the 8000 Monte-Carlo simulations to compare patterns emerging from simulations with TRITON to patterns observed in large-scale surveys (Johnson et al., 2005; Johnson et al., 2011; this study) of Tasmanian temperate reef communities (Fig. A8.5). Fig. A8.5a describes the frequency of the different community states in terms of seaweed bed versus sea urchin biomass densities with overlaid arrows representing the model mean trajectory (i.e. fortnightly change in biomass density through simulations) at different points of reef state. In Fig. A8.5b, data from large-scale surveys (Johnson et al., 2005; Johnson et al., 2011; this study) describes the frequency of reef communities on the east coast of Tasmania in 2000-2011 being in any given state. Importantly, both the modelled and observed reef communities identify two persistent and dominant states representing (i) the seaweed bed state with a high cover of seaweed and a low density of sea urchin and (ii) the sea urchin barren state with virtually no algal cover and a high density of sea urchins. This indicates broad agreement of the behaviour of the model with observations of the occurrence of the two states in the field. Note that the volume of output from the TRITON model enables a much more continuous picture of the range of community states encountered on Tasmanian reefs than can be obtained by direct diver-based measurements. Moreover, the model can provide insight on aspects of reef dynamics that have not been able to be documented from field observations, in particular the point at which recovery from extensive sea urchin barrens commences as urchin density falls (bottom left region of Fig. A8.5a). The conspicuous 'hole' of low frequency of observations of this state – i.e. very low urchin density and seaweed biomass at ~10⁵ g.200 m⁻² – in eastern Tasmania (Fig. A8.5b) reflects that there is no evidence of recovery of seaweed cover on any of the extensive barrens monitored thus far.

Model limitations and guidance for future research

Derivation of all parameter estimates was based upon the best available information at time of model development (see Technical Appendix AT8 for further details). However, the results presented here are only as useful as the precision and accuracy of the parameter estimates, and so it is worthwhile to acknowledge areas where parameter definition or the relative coarseness in representing ecological processes may limit the realism of TRITON. Some of the ecological processes of seaweed-urchin-lobster dynamics on subtidal rocky reefs in eastern Tasmania are captured rather coarsely in TRITON and would benefit from further field-based research. In particular it may be useful to have quantitative estimates of the size-dependent vulnerability of macroalgae to grazers and the magnitude of any size-structured dynamics of seaweed beds; density-dependence in sea urchin grazing rates; importance of seaweed habitat to the recruitment, productivity and carrying capacity of lobster population; lobster predation rates at medium and high sea urchin densities (i.e. density dependence in predation impact); the strength of predatory interactions between small cryptic sea urchins living in the reef matrix and rock lobsters; and effects of habitat, depth and reef profile on all of the modelled processes. Storms and wave action can abrade seaweed cover (e.g. Reed et al., 2011) but these effects are likely to be marginal on *E. radiata* beds in eastern Tasmania (CR Johnson, pers. obs.); Current evidence and observation suggests that none of these effects is large relative to the important parameters identified in the model, but if any of these effects did prove to be large, then the detail of model dynamics may be different to that presented here. Nonetheless, given current knowledge, we are comfortable to suggest that it is unlikely that any of these effects would materially influence the qualitative dynamics of the phase shifts and hysteresis in broad terms.

Table A8.1. Parameter estimates and confidence intervals used in Monte-Carlo simulations with TRITON. Data sources used to define (a) seaweed bed logistic growth, (b) sea urchin size-structure dynamics, (c) rock lobster size-structured dynamics, (d) lobster dependency on the seaweed bed, (e) urchin grazing rate, (f) rock lobster predation and (g) allometric relationships are also specified.

a) Seaweed bed logistic growth with α , intrinsic growth rate; K, carrying capacity; μ , mean annual recruitment rate. (Fitted against observations of seaweed bed recovery following the removal of grazers; Ling, 2008)

Parameter	Units	Estimate	Std. error	Conf. interval
α_{SW}	year ⁻¹	4.43	1.65	1.72-7.14
K_{SW}	g SW.200 m ⁻²	3.4e+05	3.6e+04	2.8e+05-4e+05
μ_{SW}	g SW.200 m ⁻² year ⁻¹	5000		2500 - 10000

b) Sea urchin size-structured population growth with a growth transition matrix derived from an inverse logistic growth function (Ling et al., 2009b); β_{CR} , annual natural mortality; μ_{CR} , mean annual recruitment rate. The annual stochastic recruitment function follows a binomial distribution with a 0.4 probability of success, which is combined with a lognormal distribution of mean $\gamma_{CR} = -0.15$ and standard deviation $\sigma_{CR} = 0.5$. (Fitted against large-scale population surveys; Johnson et al., 2005; Ling et al., 2009b)

Parameter	Units	Estimate	Conf. interval
β_{CR}	year ⁻¹	0.11	0.1-0.15
μ_{CR}	g CR.200 m ⁻² . year ⁻¹	4100	2500-10000

c) Lobster size-structured population growth with a growth transition matrix derived from polynomial growth functions (McGarvey and Feenstra, 2001); β_{RL} , annual natural mortality; μ_{RL} , mean annual recruitment rate. The annual stochastic recruitment function follows a lognormal distribution of mean $\gamma_{RL} = 0.15$ and standard deviation $\sigma_{RL} = 0.6$.

(Fitted against observation of population recovery following protection from fishing; Barrett et al., 2009)

Parameter	Units	Estimate	Conf. interval
β_{RL}	year ⁻¹	0.23	0.20-0.26
μ_{CR}	g CR.200 m ⁻² . year ⁻¹	350	200-800

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

(Johnson and Ling, unpublished data)

Parameter	Units	Estimate	Std. error	Conf. interval
$\beta_{SW,RL}$	constant	0.64	0.11	0.46 - 0.83

e) Urchin grazing rate

(After in situ experiments by Hill et al., 2003)

Parameter	Units	Estimate	Std. error	Conf. interval
$\beta_{SW,CR}$	g SW.g CR ⁻¹ . year ⁻¹	5.94	1.10	4.13-7.75

f) Functional responses of lobster predation on urchin with B_{CR} , urchin biomass density (g. 200 m⁻²)

(Fitted against predation estimates from Ling et al., 2009a and this study)

- Holling Type I as $\beta_{CR,RL} = \min(\beta N, \beta')$

Parameter	Units	Estimate	Std. error	Conf. interval
β	g RL ⁻¹ .year ⁻¹	6.68e-04	2.27e-05	6.31e-04 - 7.05e-04
β'	g CR. g RL ⁻¹ .year ⁻¹	9.40	3.00	4.46 - 14.33

- Holling Type II as $\beta_{CR,RL} = \beta N / (1 + \beta' N)$

Parameter	Units	Estimate	Std. error	Conf. interval
β	g RL ⁻¹ .year ⁻¹	11.09e-04	1.68e-04	8.34e-04 - 13.85e-04
β'	g CR ⁻¹	1.10e-04	0.20e-04	7.76e-05 - 14.19e-05

- Holling Type III as $\beta_{CR,RL} = \beta N^2 / (1 + \beta' N^2)$

Parameter	Units	Estimate	Std. error	Conf. interval
β	g CR ⁻¹ . g RL ⁻¹ .year ⁻¹	2.35e-07	0.55e-07	1.46e-07 - 3.25e-07
β'	g CR ⁻¹ .g CR ⁻¹	2.50e-08	0.60e-08	1.47e-08 - 3.60e-08

g) Allometric and other size-based relationships

Length-weight relationship for the long-spined sea urchin (Ling, unpublished data)

$B = 0.00267 \times TD^{2.534}$ with B, urchin individual weight (g); TD, urchin test diameter (mm).

Length-weight relationship for the southern rock lobster (Punt and Kennedy, 1997)

$B = 0.000271 \times CL^{3.135}$ with B, lobster individual weight (g); CL, lobster carapace length (mm).

Size-structured predation of lobster on urchin (after Ling et al., 2009a): $TD_{\max} = \alpha \exp(0.023 \text{ CL})$ with $\alpha \in [3.08:5.12]$ or

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

Table A8.2. Initial conditions for the different sets of Monte-Carlo simulations, where the modelled community can be initialised in either the seaweed bed or in the sea urchin barren state (biomass densities in g. 200 m⁻²). Unconstrained initial conditions are used for global sensitivity test. The values of seaweed biomass densities associated with 10% and 50% of canopy cover are also used to define presence (1) or absence (0) of a shift to the alternative state at the end of a simulation: a persistent shift to sea urchin barrens is assumed if the seaweed bed cover drops below 10%, while recovery of seaweeds from the barren state corresponds to the seaweed bed re-growing above a 50% of cover.

Initial State:	Dense seaweed cover	Sea urchin barrens	Unconstrained
Seaweed assemblage	$2 \times 10^5 - 4 \times 10^5$ (more than 50% cover)	$0 - 4 \times 10^4$ (less than 10% cover)	$0 - 4 \times 10^5$
Sea urchins	0 – 4000	$7 \times 10^4 - 1.4 \times 10^5$	0 – 1.4×10^5
Rock lobsters	0 – 1.4×10^4	0 – 1.4×10^4	0 – 1.4×10^4

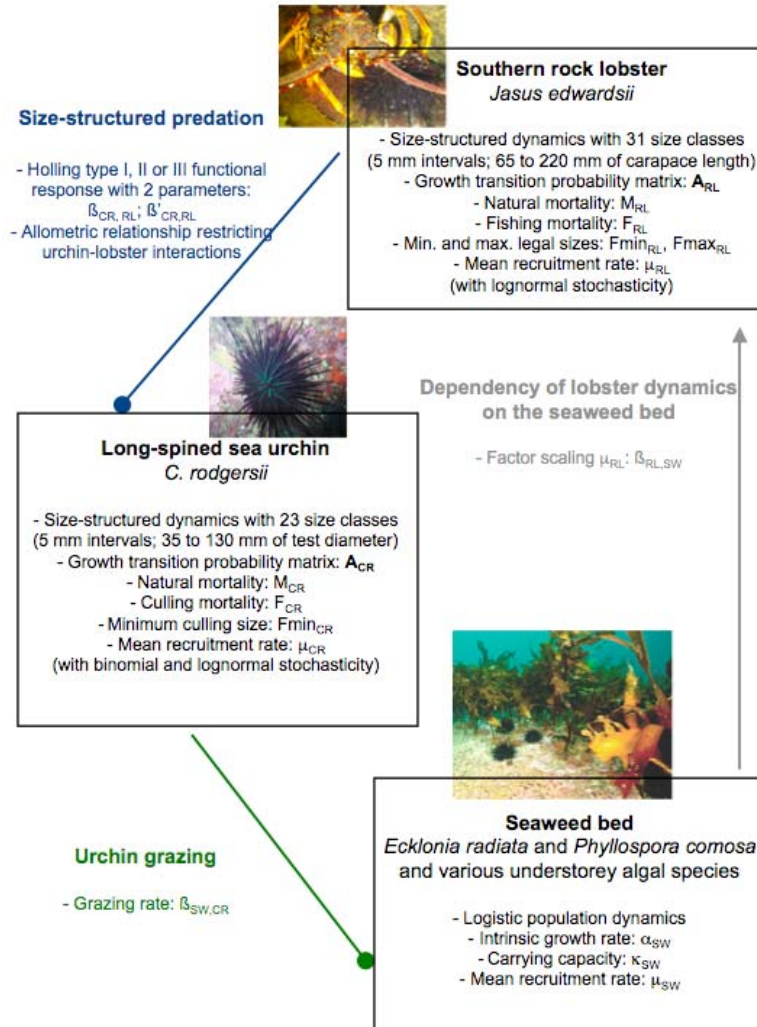
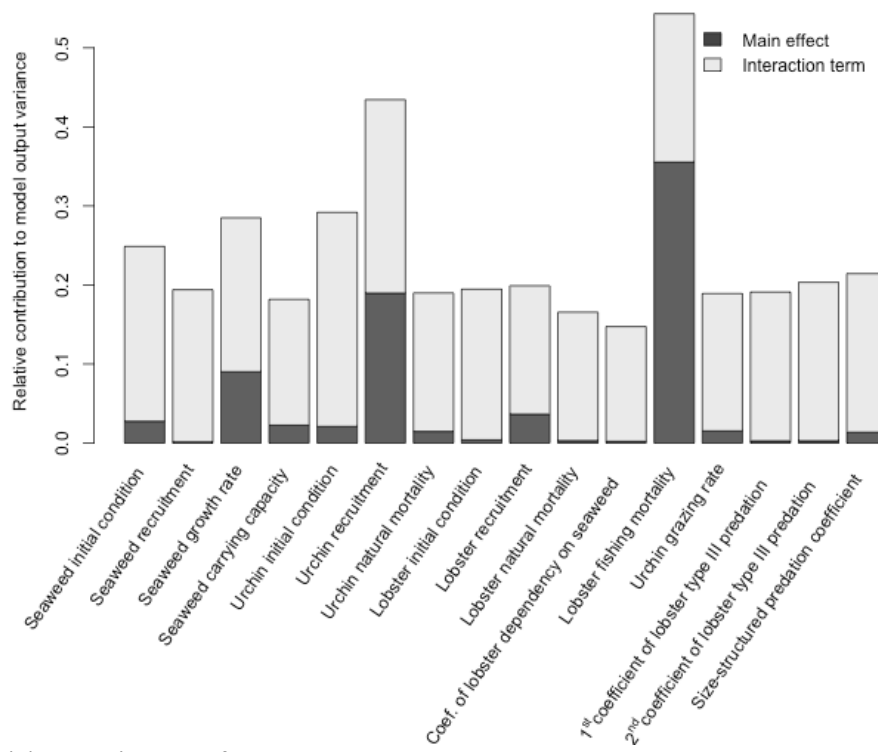
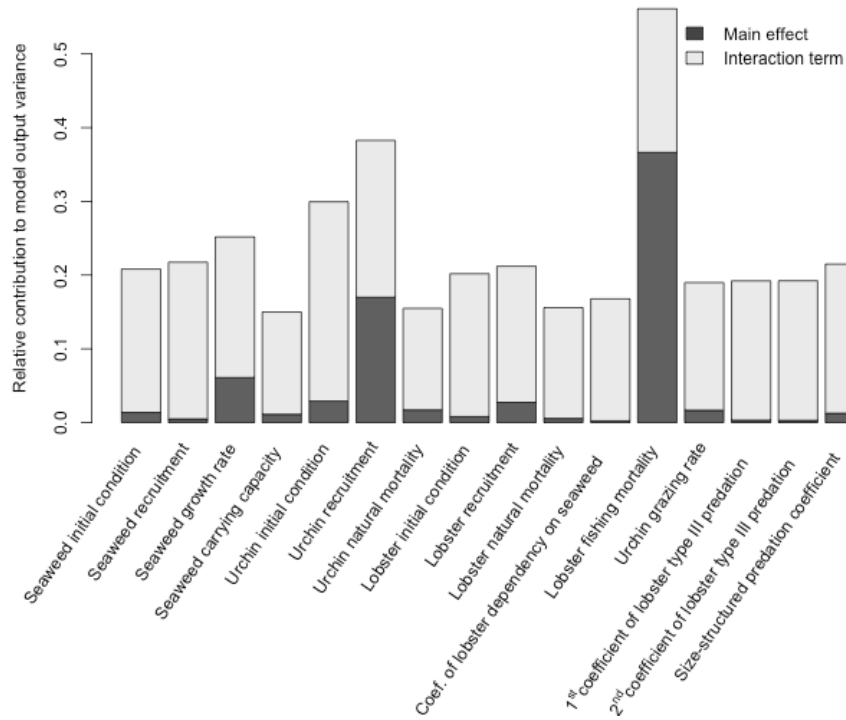


Figure A8.1. Conceptual diagram of TRITON, a model of local community dynamics on rocky reefs in eastern Tasmania. The boxes represent the three functional groups or species explicitly interacting in TRITON, namely southern rock lobster, long-spined sea urchin and the seaweed assemblage. Each box lists all the parameters defining the dynamics of each group. Interactions between the three groups are represented as arrows, where a full circle at the end of lines indicates a negative effect to the adjacent group while an actual arrow head points to a group positively affected in this interaction. Photography credits: Scott D. Ling.

(a) Holling's Type I functional response



(b) Holling's Type II functional response



(c) Holling's Type III functional response

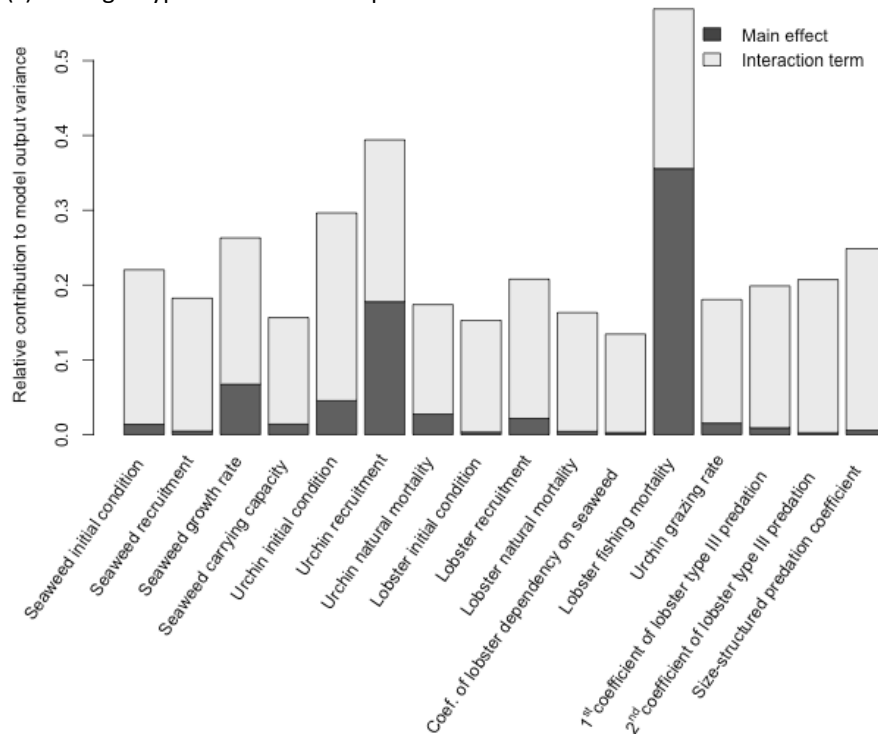


Figure A8.2. Extended FAST indices quantifying the contribution of input parameter values to model output variance, using the first principal component from the PCA (accounting for 73% of the total variance) on mean-centred normalised biomass density outputs, under alternative formulations of the functional response of lobster predation on sea urchin, assuming either Holling Type I (a), II (b) or III (c) relationships. Figure 3 provides a graphical summary of final model state across the three model groups.

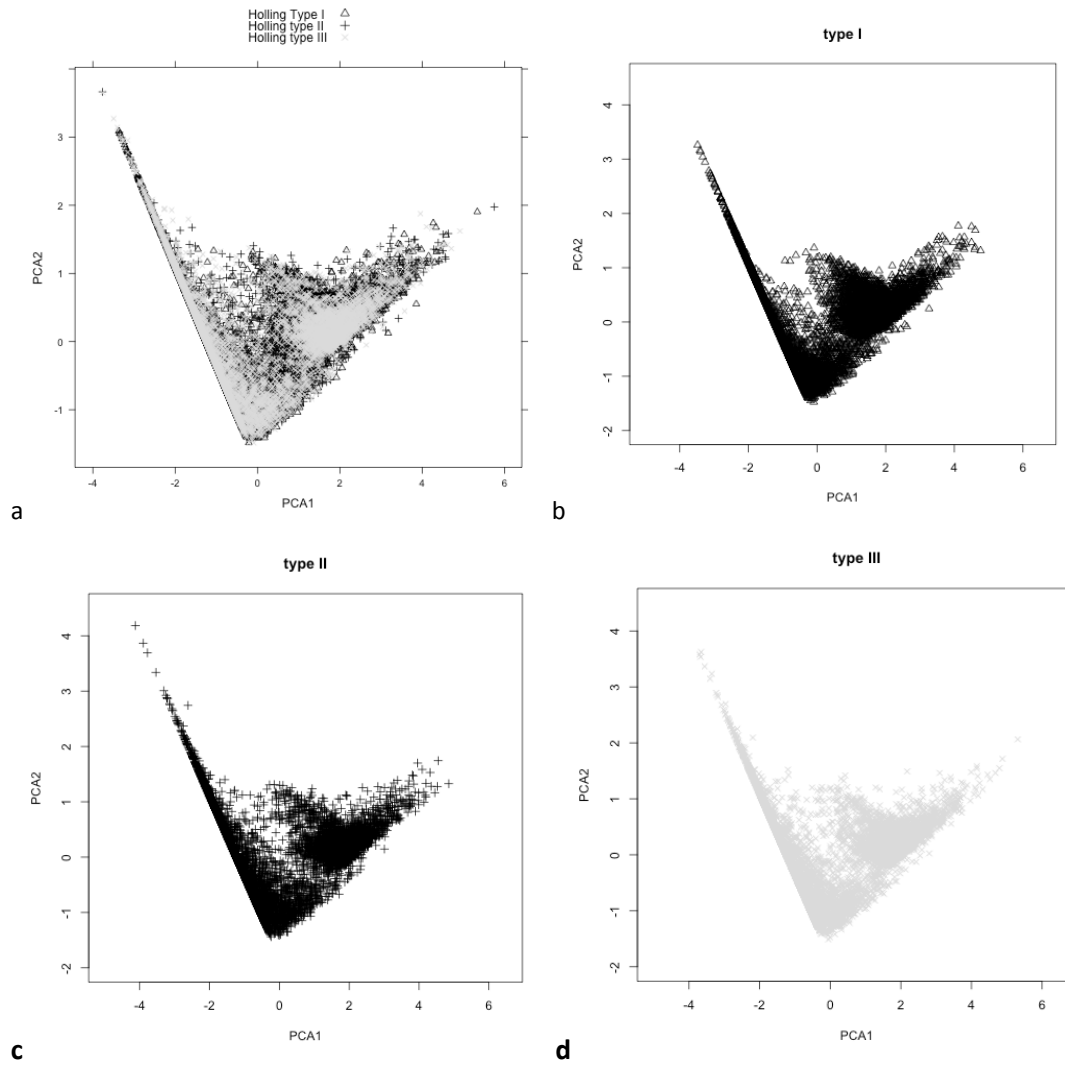
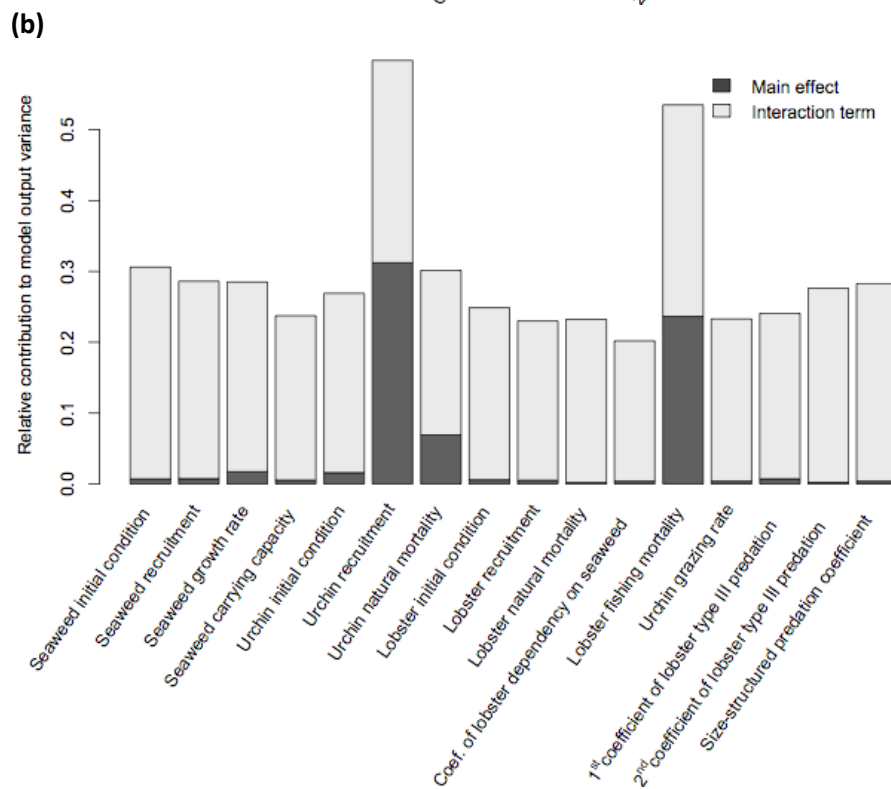
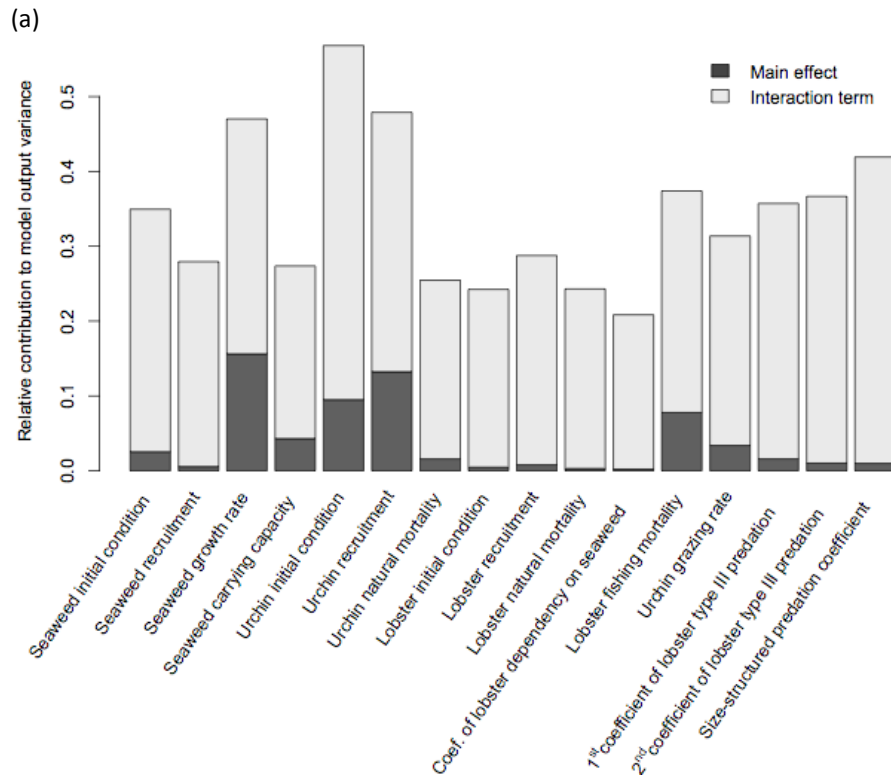


Figure A8.3. Effect of different formulation of lobster predation rate on the scores of simulation outcomes on the first two axes of the PCA, which capture 87.4% of the total variance. Scores are plotted for all functional responses (a) then respectively for Holling Type I (b), II (c) and III (d) functional responses.



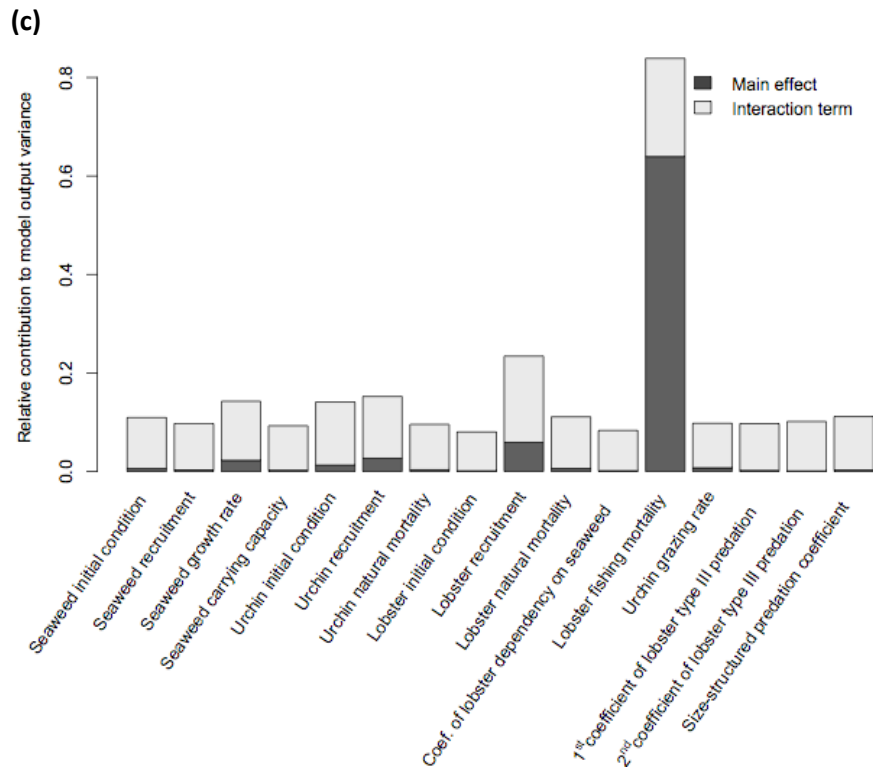
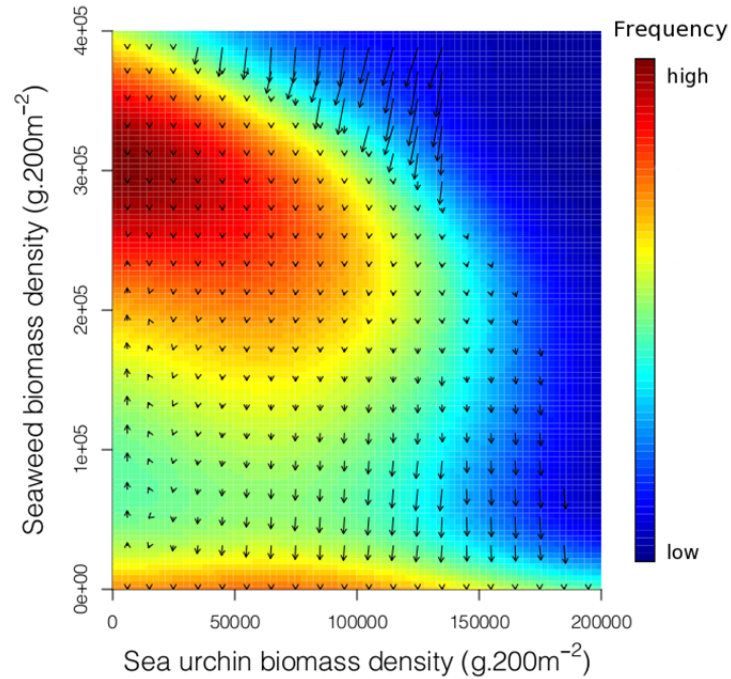


Figure A8.4. Sensitivity analysis based on extended FAST indices quantifying the contribution of all model input parameter values to model output variance. Final biomass densities of (a) seaweeds, (b) sea urchins and (c) rock lobster at the end of 50-year simulations with unconstrained initial conditions are used as model outputs.

(a)



(b)

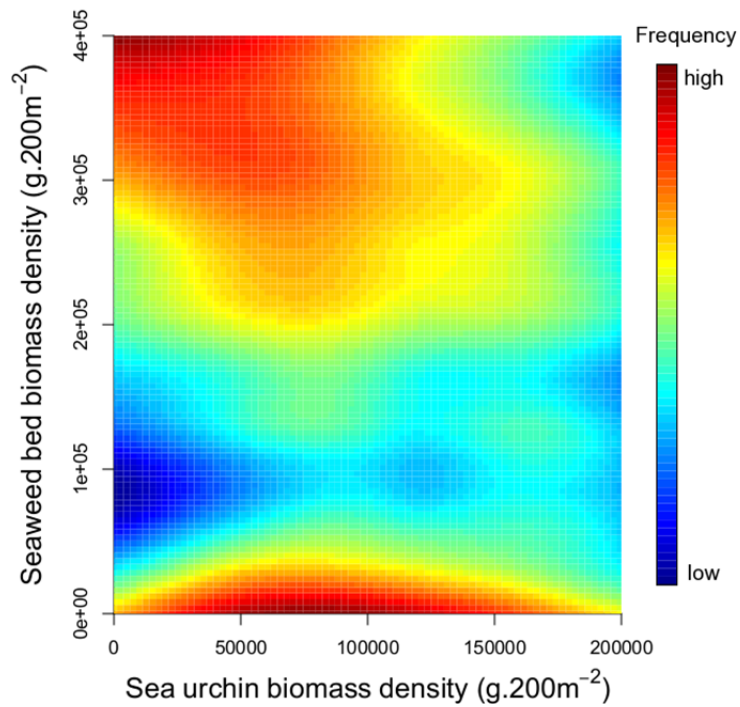


Figure A8.5. Frequency (logarithmic scale) of community states as a function of sea urchin versus seaweed bed biomass densities from (a) the 8000 Monte-Carlo simulations with TRITON and from (b) large-scale surveys on the east coast of Tasmania (Johnson et al., 2005; Johnson et al., 2011; this study). Arrows in (a) represent the mean simulation trajectory in terms of fortnightly change in sea urchin and seaweed bed biomass densities.

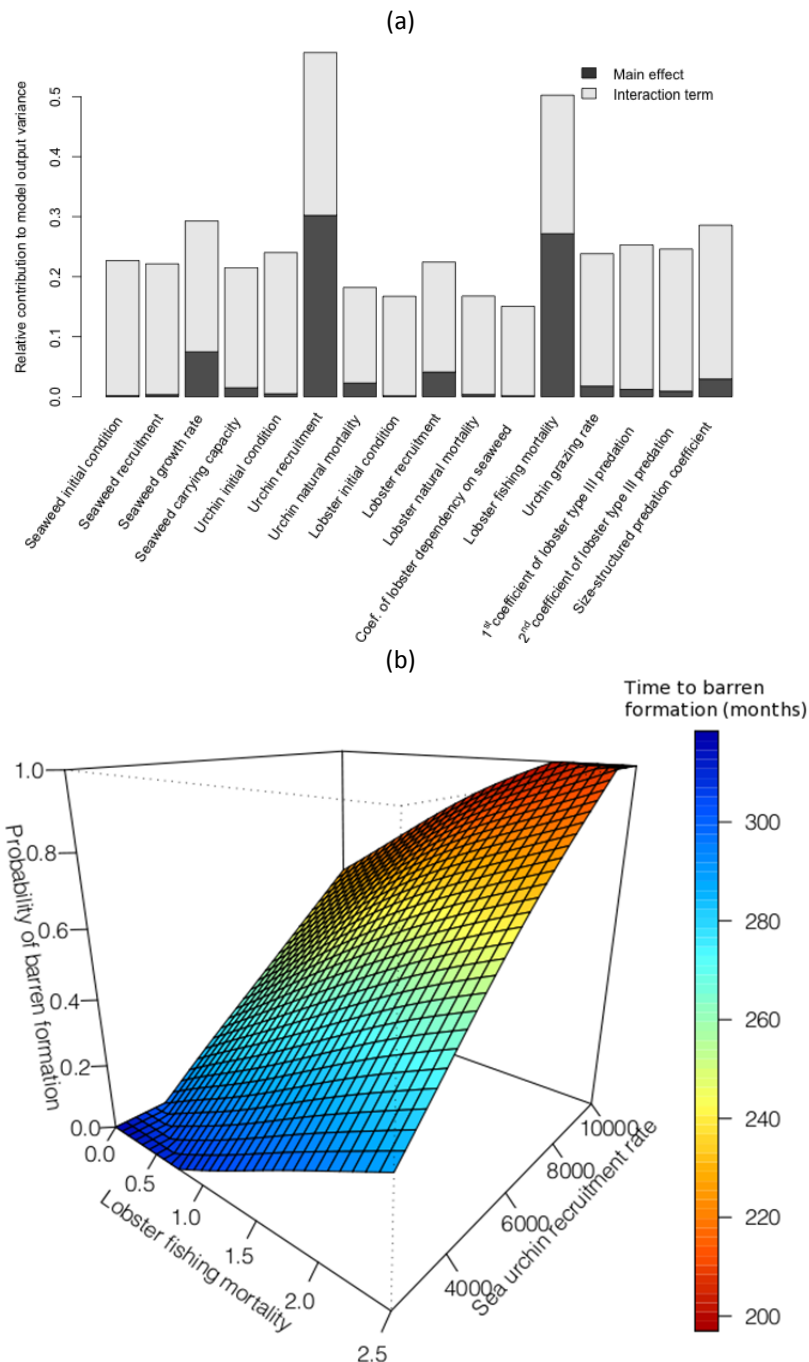


Figure A8.6. Sensitivity of the ‘forward’ shift (from high seaweed biomass to sea urchin barrens habitat) to model input parameters (i.e. this analysis was restricted to those simulations in which the ‘forward’ shift occurred). Initial conditions correspond to the seaweed bed state with seaweed cover at >50%, low initial sea urchin density (< 40000 g. 200 m⁻²) and random rock lobster biomass density. (a) Extended FAST indices quantifying the contribution of input parameters to model output variance in overall community structure (described as the first PC from the PCA on mean-centred normalised biomass density outputs of all groups) for 50-year simulations. (b) 3D plot representing both the probability of (z axis) and the time for (colour scaling) barrens establishment (in months) as a function of the two parameters most influential in affecting the likelihood of the transition to barrens, viz. sea urchin recruitment rate (in g. 200 m⁻². year⁻¹) and lobster fishing mortality (in year⁻¹).

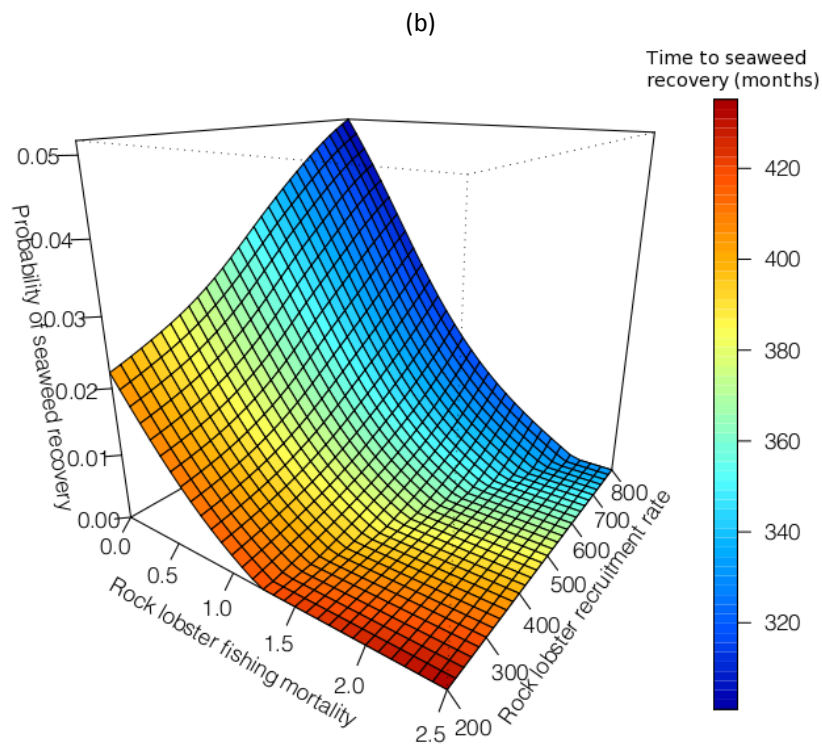
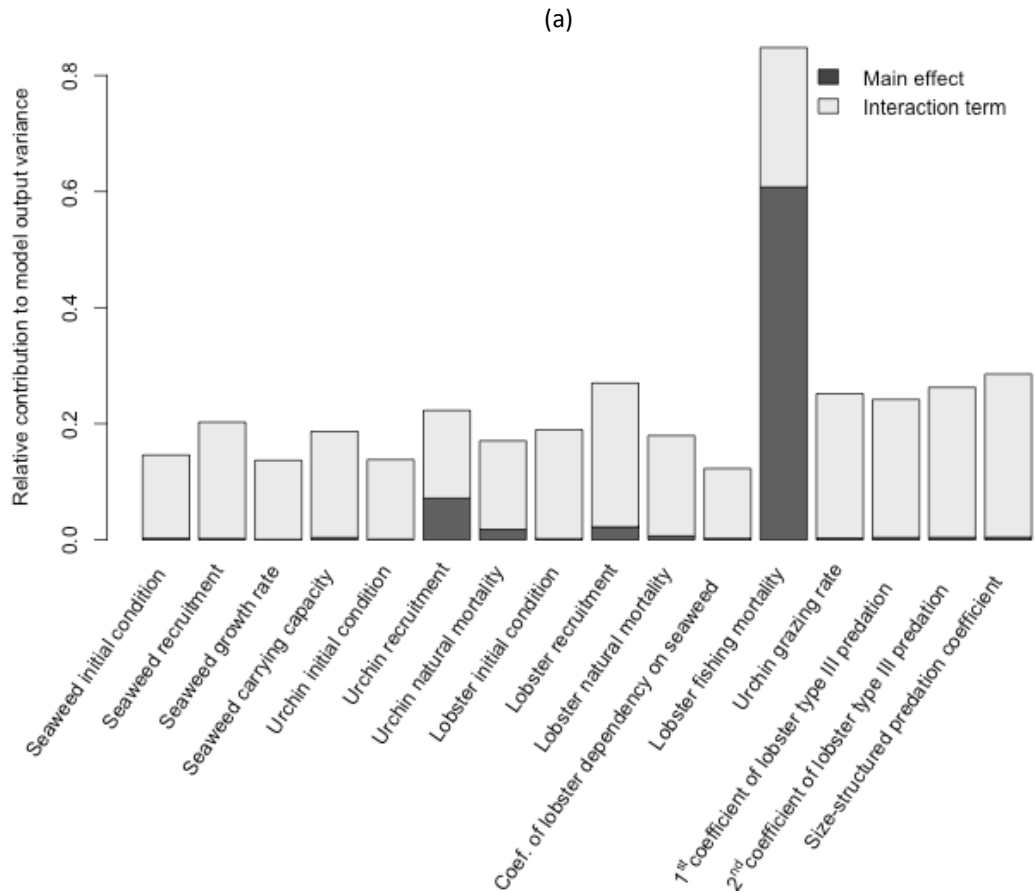


Figure A8.7. Sensitivity of the 'backward' shift (from sea urchin barrens to recovery of dense seaweeds) to model input parameters (i.e. this analysis was restricted to those simulations in which the 'backward' shift occurred). Initial conditions correspond to sea urchin barrens habitat, with seaweed cover <10% of carrying capacity, initial urchin density > 70000 g. 200 m⁻² and random rock lobster biomass density. (a) Extended FAST indices quantifying the contribution of input parameters to model output variance in overall community structure (described as the first PC from the PCA on mean-centred normalised biomass density outputs of all groups) for 50-year simulations. (b) 3D plot representing both the probability of (z axis) and the time to (colour scaling) seaweed bed recovery from sea urchin barrens (in months) as a function of the two parameters most influential in affecting the likelihood of the transition from established barrens back to dense seaweed cover, viz. lobster recruitment rate (in g. 200 m⁻². year⁻¹) and lobster fishing mortality (in year⁻¹).

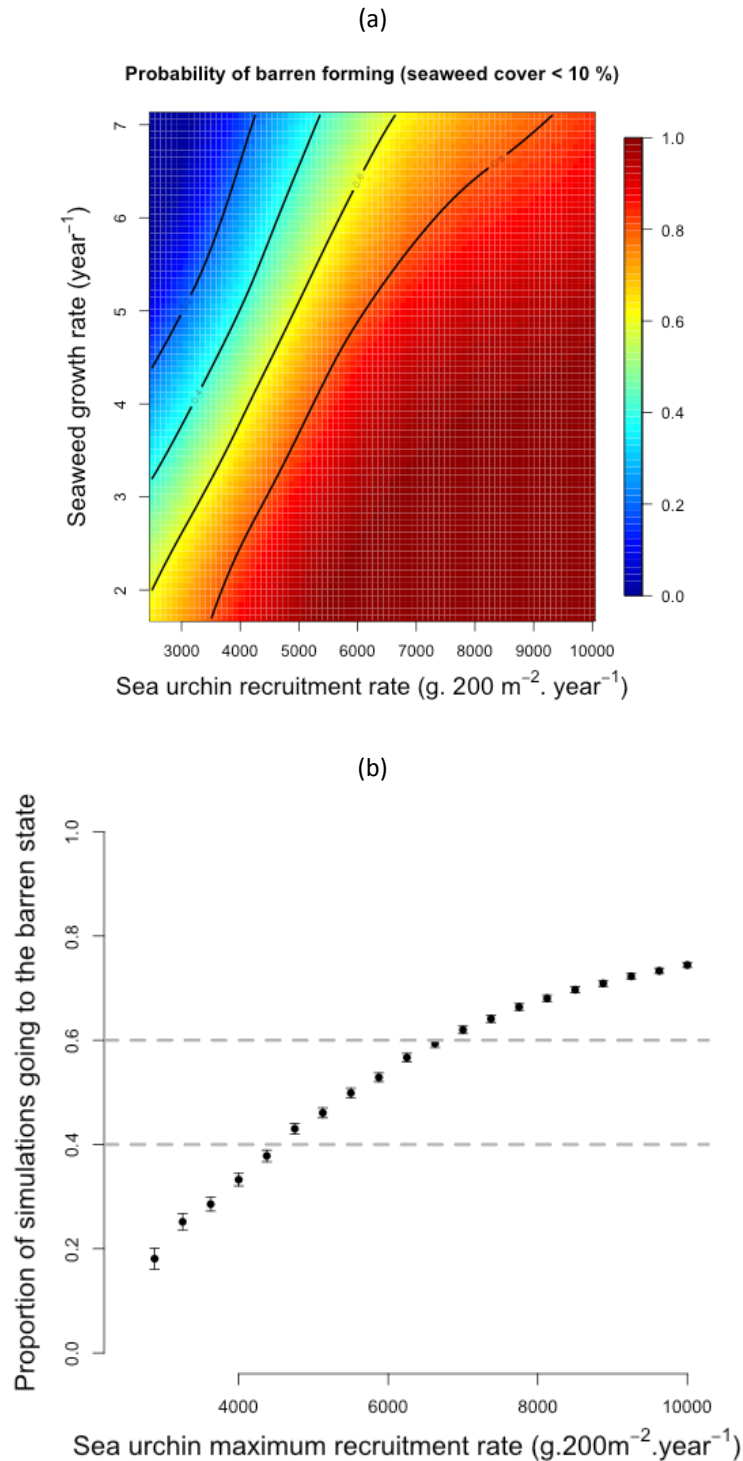


Figure A88. Results from 50-year-long Monte-Carlo simulations used to calibrate ranges in sea urchin recruitment from the model's propensity to shift to sea urchin barrens under historical rock lobster fishing conditions. (a) Probability of barren formation as a function of the two most influential input parameters, sea urchin recruitment rate and seaweed growth rate; (b) Probability of the shift from seaweed bed to sea urchin barren as a function of sea urchin maximum recruitment rate with fixed coefficient for size-structured allometric relationship. The dashed horizontal lines mark the observed range of sea urchin barren cover across rocky reefs in New South Wales (Andrew and O'Neill, 2000) and Tasmania (Johnson et al., 2005, 2011, this study) where *C. rodgersii* is long established and where populations of reef predators have been depleted by fishing.

TECHNICAL APPENDIX AT8: Derivation of parameter estimates for the TRITON (Temperate Rocky reef communities In Tasmania with lobsters and urchins) model of the local dynamics of Tasmanian rocky reefs.

Introduction

Context of the model: units, temporal and spatial scales, programming languages

The variables in this local model of Temperate Rocky reef communities In Tasmania with lobsters and urchins (TRITON) are expressed in biomass density ($\text{g} \cdot 200 \text{ m}^{-2}$). 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).

Model time is discrete because it is more computationally efficient than using continuous time, and also more flexible to implement using the object-oriented Python programming language (Python Software Foundation, 2008). The extended FAST method was implemented using the sensitivity package of the R software for statistical computing (R Development Core Team, 2010). Using Rpy2, a high-level interface between R and Python (Python Software Foundation, 2008), we automated all sensitivity analyses between R and the TRITON simulation model. A two-week time-step was adopted as a compromise between computational efficiency and adequate convergence between discrete- and continuous-time dynamics (Deng et al., 2008). All figures were produced in R (R Development Core Team, 2010).

Functional groups

The number of groups and/or species in the model is kept to a minimum (seaweed assemblage, sea urchin, rock lobster) 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). 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.

Appendix structure

This additional technical appendix (to Appendix 8) details the parameterisation of all the processes explicitly modelled in TRITON and is organised in four main sections: population dynamics of each of the three groups; trophic interactions; model closure and factors implicitly accounted for in TRITON; and limitations and guidance for future research.

Population dynamics

Logistic population dynamics

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

$$\frac{dB}{dt} = \alpha B \times \frac{(K-B)}{K} \quad \dots \text{(Equ. A1)}$$

with B, biomass density (g. 200 m⁻²); K, carrying capacity (g. 200 m⁻²); α , intrinsic growth rate (year⁻¹); t, time (in years).

Defining logistic population dynamics

The following equation defines an analytical solution to $\frac{dB}{dt} = \alpha B \times \frac{(K-B)}{K}$

Equ. A1 (Kot, 2001):

$$B(t) = \frac{K}{1 + \beta \exp(-\alpha t)} \quad \dots \text{(Equ. A2)}$$

with $\beta = (K - B_0)/B_0$, where B_0 is the initial biomass density at time $t=0$.

Using observations of population biomass density through time (e.g. Fig. AT8.2 for the seaweed bed) standardised to a 200 m² area, the intrinsic growth rate α , the carrying capacity K and the constant β from Equ. A2 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. AT8.1).

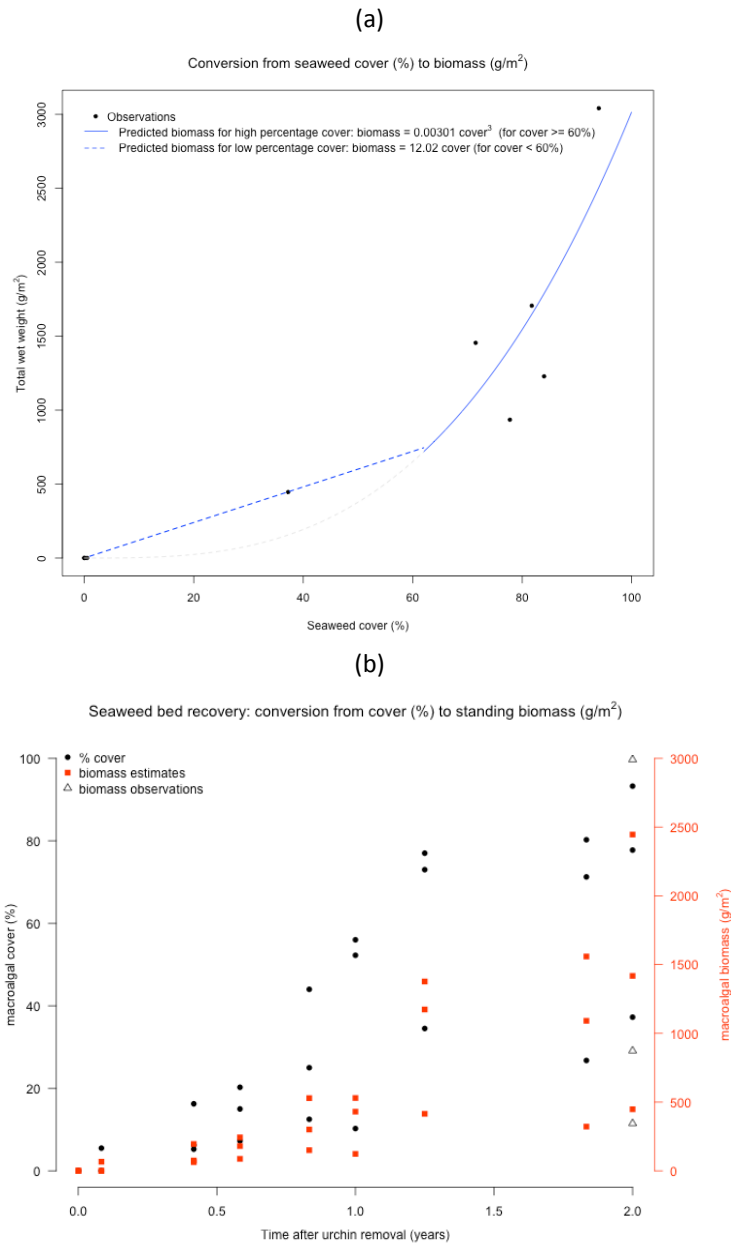


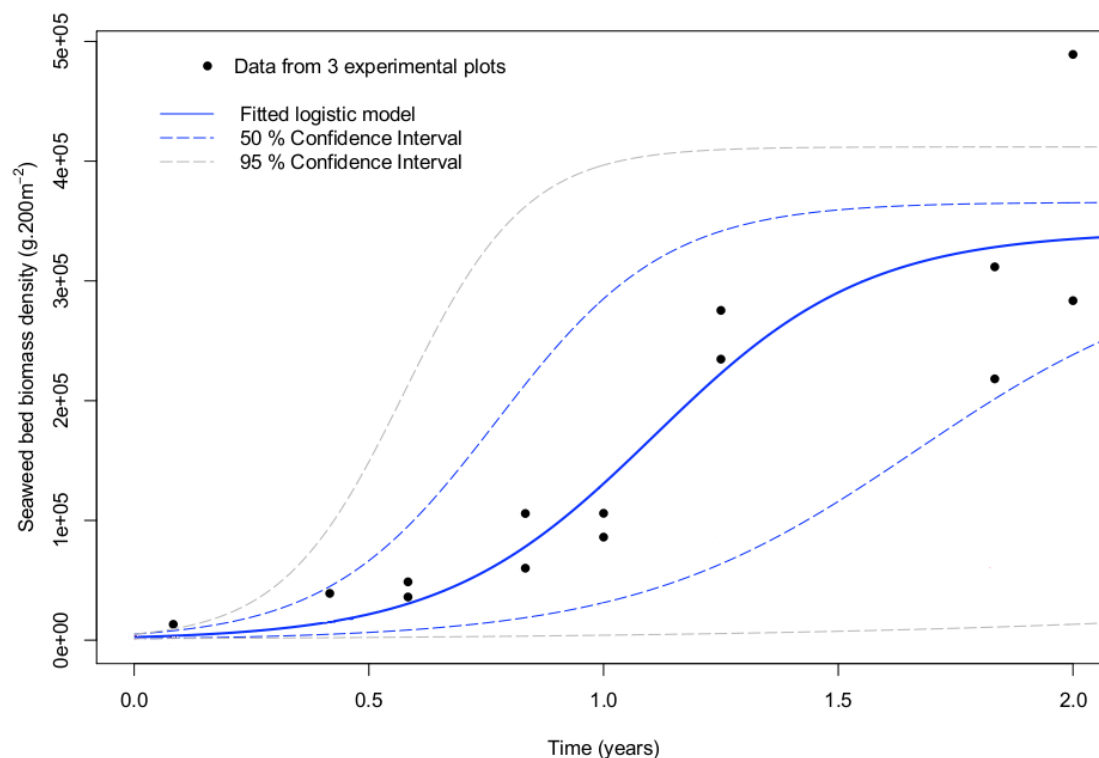
Figure AT8.1. a) Conversion from percentage cover (%) to biomass density ($\text{g} \cdot \text{m}^{-2}$) for Tasmanian seaweed beds (*Ecklonia radiata*, *Phyllospora comosa*, etc.; Ling, unpublished data). b) Seaweed bed recovery data from Ling et al. (2008), aggregated across quadrats for 3 experimental sites. The data originally in percentage cover (in %; black dots) were converted to biomass density (in $\text{g} \cdot \text{m}^{-2}$; red squares).

- 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. AT8.2). Parameter estimates for seaweed bed logistic dynamics (Equ. A2) are given in Table AT8.1

Table AT8.1. Parameter estimates for the seaweed bed logistic growth function (Equ. A2).

	Estimate	Std. 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 AT8.2.** 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 distal tip of the blade where it erodes (Sanderson, 1990). Both tissue production and erosion can be measured for *E. radiata* seaweed beds (Kirkman, 1984; 1989). However, the effects of urchin grazing on individual macroalgae are poorly known. Thus, TRITON only represents the mean dynamics of *E. radiata* beds without explicitly capturing individual plant growth. 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, 2011; Ling et al., 2009b), information about sea urchin population age and biomass density could be derived at different sample sites to describe population growth (Fig. AT8.3). 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.

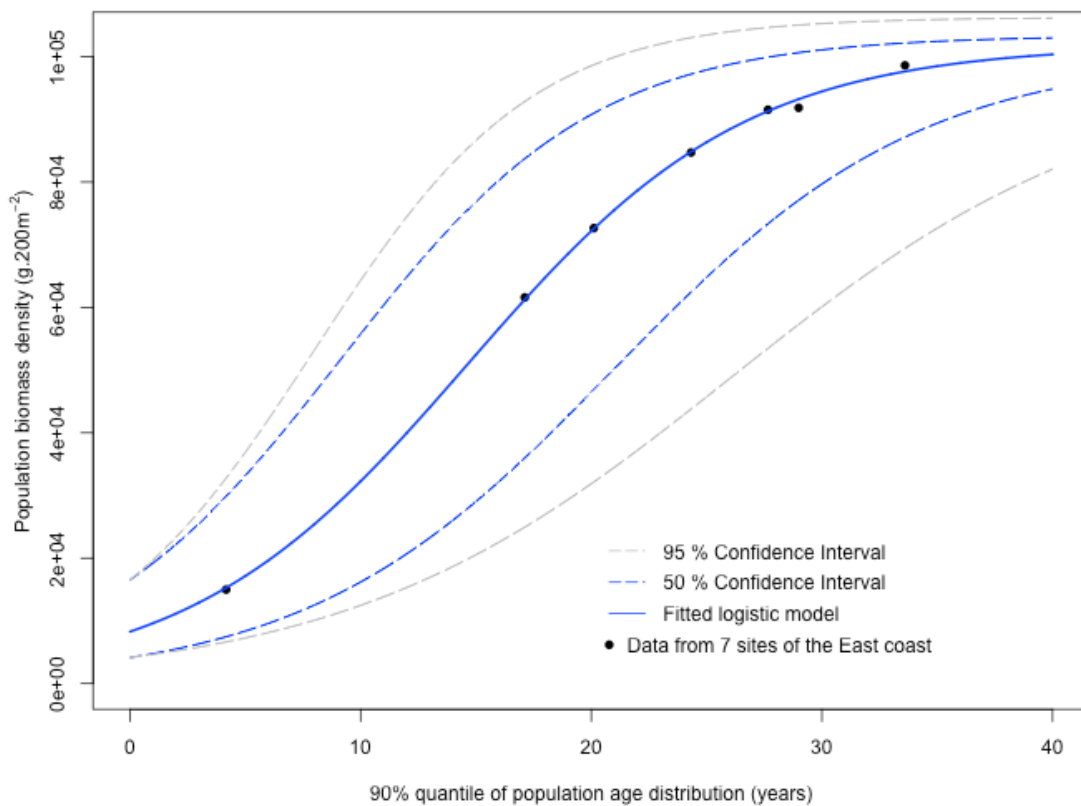


Figure AT8.3. Logistic growth model (with 50% and 95% confidence intervals) fitted to data from large-scale survey of *C. rodgersii* population on the east coast of Tasmania (Johnson et al., 2005; Ling et al., 2009b). The 90% quantile of population age distribution is used as a proxy for the time elapsed 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. AT8.4) is derived from size-structured survey of invertebrate abundance using the length-weight relationship for southern rock lobster (*Jasus edwardsii*) given as $B = 0.000271 L^{3.135}$ (Punt et al., 1997) relating individual lobster biomass (B) in grams to carapace length (L) in mm.

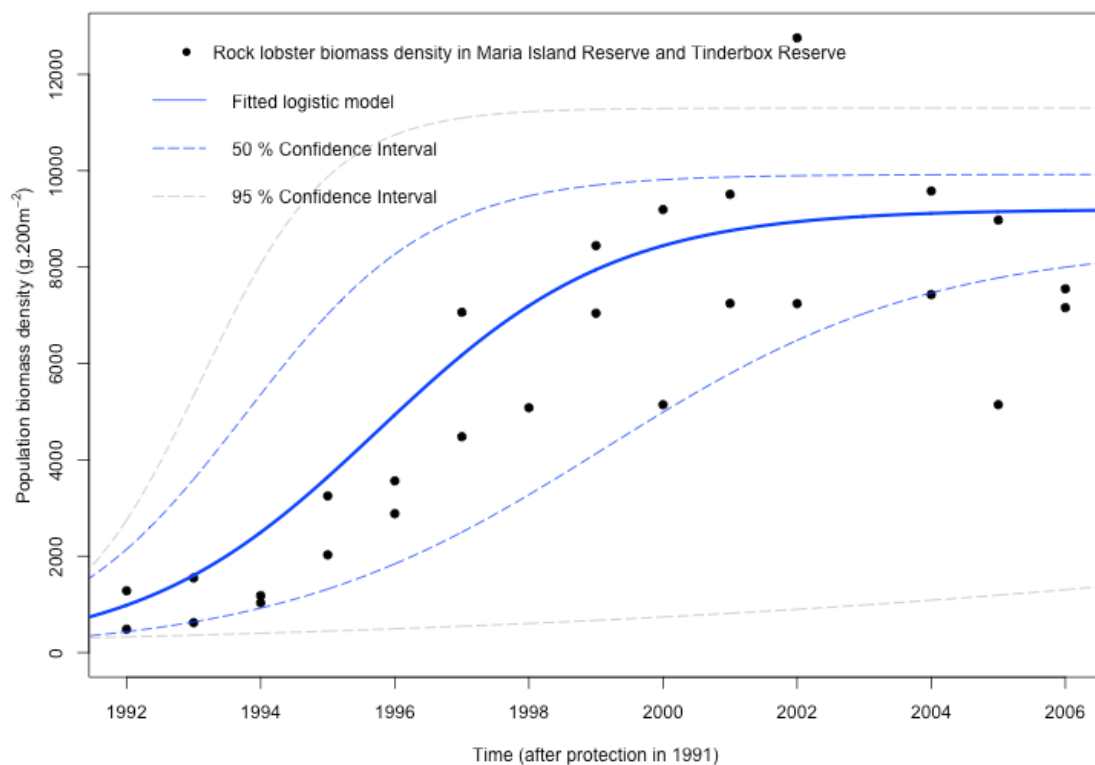


Figure AT8.4. Logistic growth model (with 95% confidence intervals) fitted to data from surveys of rock lobster mean biomass density in Maria Island and Tinderbox marine reserves following protection in 1991 (Barrett et al., 2007; Edgar et al., 2009).

Both sea urchin and rock lobster dynamics are size-structured in TRITON. Thus, while Figs. AT8.3 and AT8.4 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 accommodate 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:

$$B_{s,t+1} = r_t + B_{s,t} \times \exp(-\beta) + \sum_{j=1}^{j < s} (\delta'_{s,j} \times B_{j,t}) - \left(\sum_{i > s}^N \delta_{i,s} \right) \times B_{s,t} \quad \dots \text{(Equ. A3)}$$

with $B_{s,t}$, biomass density of size class s at time t ($\text{g} \cdot 200 \text{ m}^{-2}$); $\delta'_{i,j}$, biomass-based growth transition probability from size class j to i (year^{-1}); $\delta_{i,j}$, abundance-based growth transition probability from size class j to i (year^{-1}); β , natural mortality (year^{-1}); r_t , recruitment rate to the first size class (only if $s=1$) at time t ($\text{g} \cdot \text{year}^{-1} \cdot 200 \text{ m}^{-2}$).

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 Equ. A4). Lognormal stochastic recruitment rate at time t can be written as:

$$r_t = \mu \exp(\gamma + \sigma \cdot \varepsilon) \quad \dots \text{(Equ. A4)}$$

with μ , mean recruitment rate ($\text{g} \cdot \text{year}^{-1} \cdot 200 \text{ m}^{-2}$); γ and σ , mean and standard deviation of the lognormal stochastic function defining the magnitude of interannual recruitment variability; and ε , a random term following a normal distribution of mean 0 and standard deviation of 1. The parameters γ and σ can be derived from the mean m and the variance v of the observed lognormally-distributed variable as:

$$\gamma = \log(m^2) / \sqrt{v + m^2} \text{ and } \dots$$

$$\sigma = \sqrt{\log(v/(m^2 + 1))}.$$

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 (Figs. AT8.3, AT8.4).

- Growth transition probability matrix

Transition probability matrices are derived from individual growth functions describing size-specific growth increments (Punt et al., 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 (Equ. A3) are defined as:

$$\delta_{i,j} = \begin{cases} 0, & \text{if } i < j, \\ \Pr\left(L_j + \Delta_j \in \left[L_i - \frac{c}{2}; L_i + \frac{c}{2}\right]\right), & \text{if } i \geq j. \end{cases} \quad \dots \text{ (Equ. A5)}$$

with $\delta_{i,j}$, abundance-based transition probability from size class j to i (year^{-1}); L_i , mean individual length in size class i (mm); Δ_i , annual growth increment in size class i follows a normal distribution with mean and standard deviation derived from the individual growth function ($\text{mm}\cdot\text{year}^{-1}$); and 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 $\delta'_{i,j} = \delta_{i,j} \times B_i / B_j$ with $\delta'_{i,j}$, biomass-based transition probability from size class j to i (year^{-1}); $\delta_{i,j}$, 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 (Equ. A3) is fitted to time series of species biomass density in order to estimate the most likely set of recruitment and natural mortality rates. We assessed model fit under different combinations of these two parameters, the ranges of which were defined from published studies (for the natural mortality) and from the logistic population dynamics models fitted previously (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. AT8.5). A binomial function brings stochasticity to sea urchin annual recruitment with a 0.4 probability of successful recruitment in any given year (proportion of winters with sea surface temperature above 12°C; see Fig AT8.5).

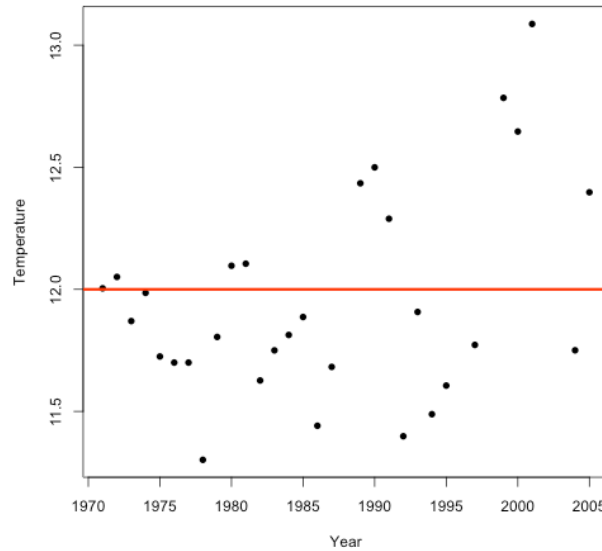


Figure AT8.5. Time line of mean sea surface temperature at Maria Island during winter months (August-September, i.e. time of spawning for *C. rodgersii*). The red line represents the 12°C threshold for urchin larvae to develop.

A lognormal stochastic function ($\nu_{CR} = -0.15$; $\sigma_{CR} = 0.5$) is applied to scale the magnitude of annual recruitment rate in successful years. It captures the remaining inter-annual 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. observations) 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 length ΔL as a function of jaw length L_t at time t , as follows:

$$\Delta L_t = \frac{\Delta L_{max} \Delta t}{1 + \exp \left[\log(19) \frac{L_t^m - L_{50}^m}{L_{95}^m - L_{50}^m} \right]} + \varepsilon_{L_t}$$

with $\Delta L_{max} = 2.599$, maximum annual growth increment; 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; and ε_{L_t} , additive and normal error term of mean 0 and standard deviation σ_{L_t} defined as:

$$\sigma_{L_t} = \frac{\sigma_{max} \Delta t}{1 + \exp \left[\log(19) \frac{L_t^m - L_{50}^m}{L_{95}^m - L_{50}^m} \right]} \text{ with } \sigma_{max} = 0.244.$$

- 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 $0.05-0.22 \text{ year}^{-1}$, after Lauzon-Guay et al. (2009); mean recruitment rate μ_{CR} in $1000-20000 \text{ g.200 m}^{-2} \cdot \text{year}^{-1}$). 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. AT8.3; data from Ling et al. (2009b)). Table AT8.3 provides the 10% most likely sets of mean recruitment and natural mortality parameters for the sea urchin size-structured dynamics model. Figure A14 compares the distribution of sea urchin biomass density across all size classes obtained from simulations with observations in northeastern Tasmania on long-established barrens grounds (Ling et al., 2009b). Table A3 gives the mean estimates of natural mortality and recruitment rates on which the simulated distribution is based.

Table AT8.3. Parameter estimates for sea urchin (*C. rodgersii*) size-structured population dynamics model (cf. Equ.A3 and Equ. A4).

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

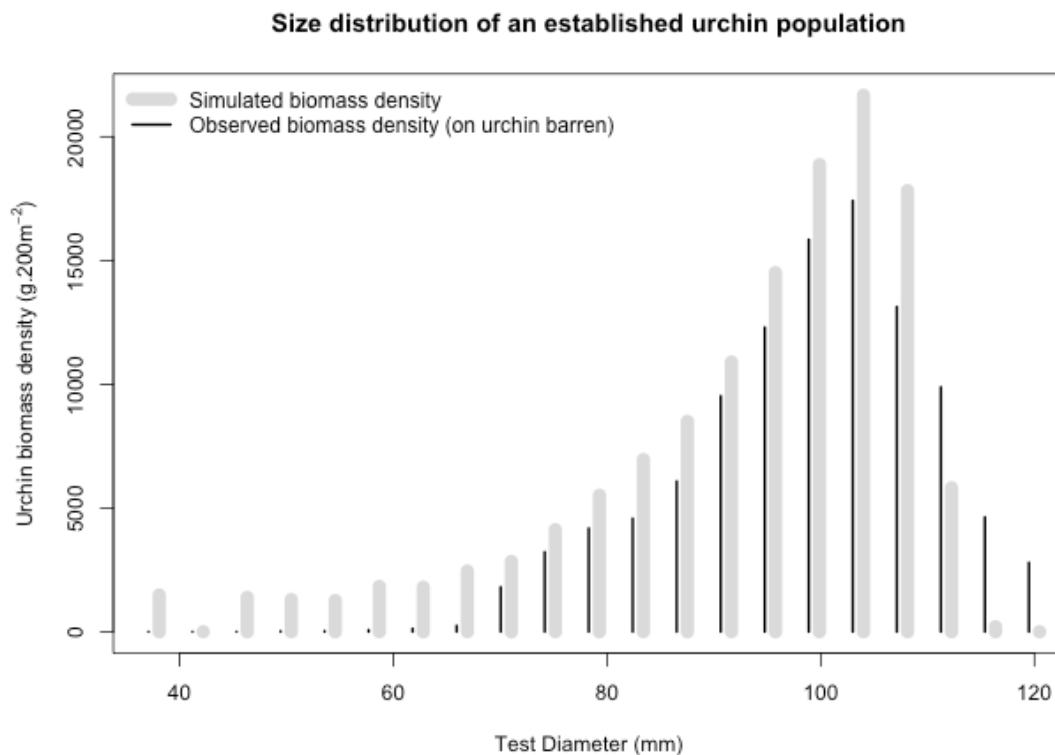


Figure AT8.6. Distribution of sea urchin biomass density across all modelled size classes for a fully-established urchin population (barrens state). Biomass densities (in g.200 m^{-2}) are from simulations using mean parameter estimates from Table A3 (in grey), and from surveys at St Helens, northeastern Tasmania (in black; after Ling et al., 2009b).

- Length-weight and allometric relationships

Jaw length (JL in mm) can be converted to test diameter (TD in mm) as follows: $TD = 4.12 JL$ (Ling et al., 2009b).

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

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 Equ. 4). Estimates of lobster recruitment are available from puerulus collectors on the east and southeast coast of Tasmania (Fig. AT8.7 a, b) and from the southern rock lobster stock assessment model for the central east coast of Tasmania (Fig. AT8.7c). A lognormal stochastic function with standard deviation σ_{RL} of 0.6 (mean of the different estimates from Table A4) defines inter-annual variability in lobster recruitment.

Table AT8.4. 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 $\sigma_{RL} = 0.55$ Equ. A4).

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

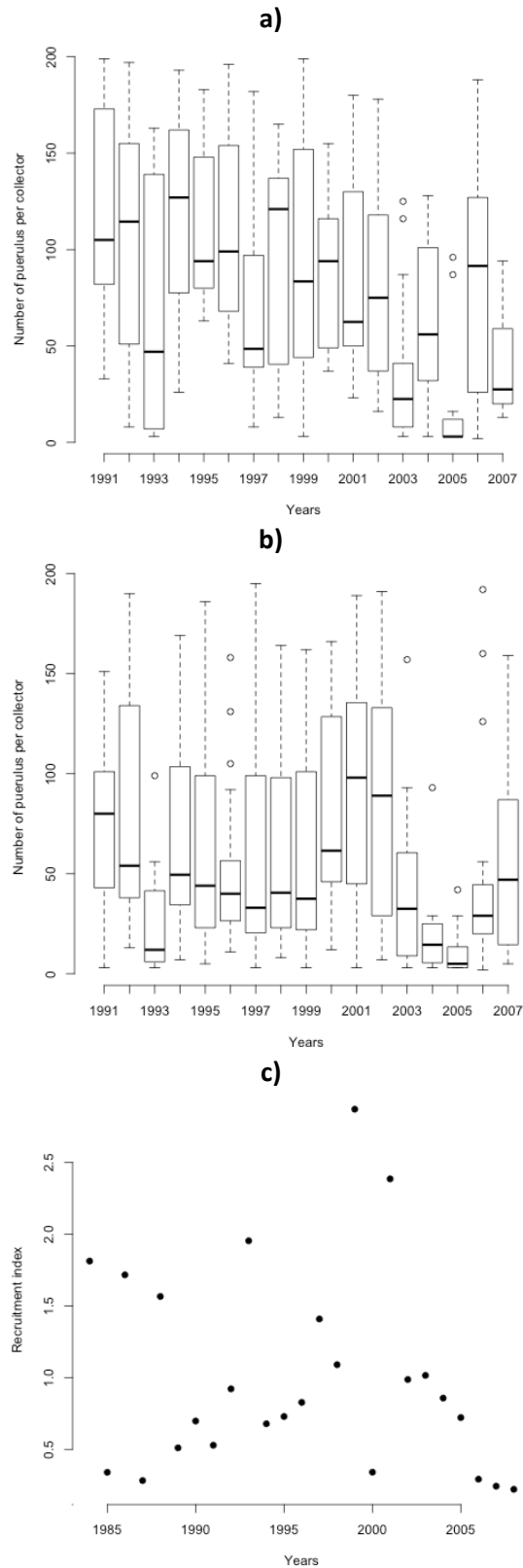


Figure AT8.7. Estimates of mean annual lobster recruitment on the east coast of Tasmania from puerulus collectors (Frusher, unpublished data) in a) Bicheno and b) in southeastern Tasmania from 1991 to 2007 and c) from the lobster stock assessment for management block 2, central east coast of Tasmania (Gardner, unpublished data).

- 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 $M_{s,z,t}$ can thus be computed for each sex s , zone z and period t of the year following Equ. A5. 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 detail was unnecessary in our ecological model of Tasmanian reef dynamics) as follows:

$$M_z = \frac{1}{2} \sum_{s=1}^2 \left[\prod_{t=4}^1 M_{s,z,t} \right] \quad \dots \text{ (Equ. A6)}$$

For all simulation results presented in this paper, 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.200 m⁻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. AT8.3; data from Barrett et al., 2009; Edgar et al., 2009). Table AT8.5 provides statistics of the 10% most likely sets of mean recruitment and natural mortality parameters for the lobster size-structured dynamics model. Fig. AT8.10 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., 2007). Note that due to the low sample sizes 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. AT8.10). 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 AT8.5. Parameter estimates for southern rock lobster size-structured population dynamics model (*cf.* Equ. A3 and Equ. A4).

	Unit	Mean	Range
Natural mortality β_{RL}	year ⁻¹	0.23	0.2-0.26
Mean recruitment rate μ_{RL}	g.200 m ⁻² . year ⁻¹	350	200-800

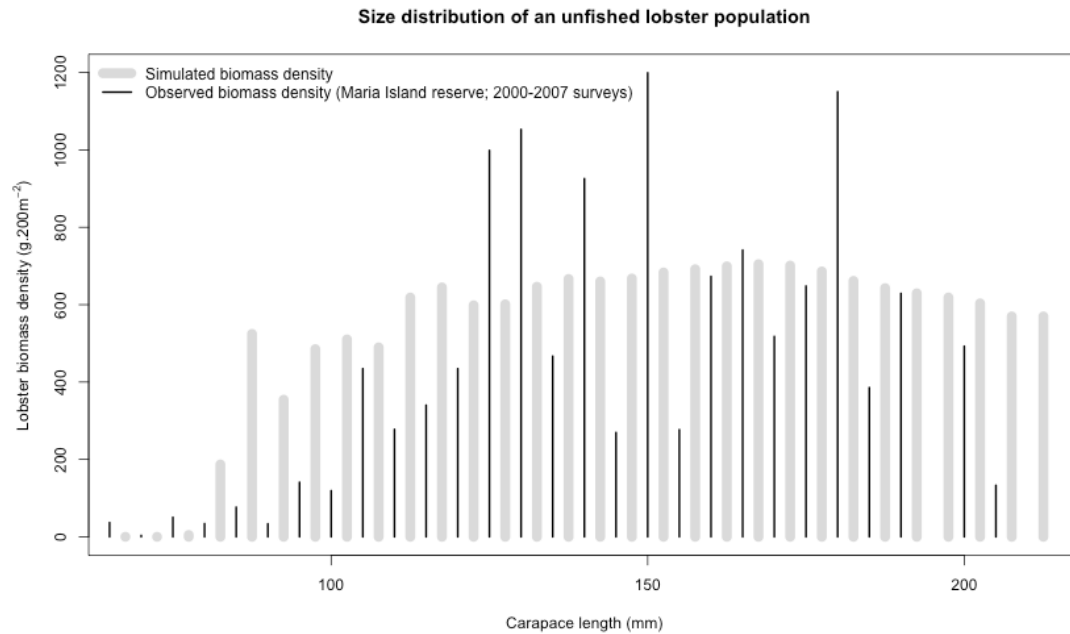


Figure AT8.8. Distribution of rock lobster biomass density across all modelled size classes. Biomass density (in g.200 m⁻²) is from simulation based on mean parameter estimates from Table A (in grey), and from *in situ* visual surveys in Maria Island in 2000-2007 (in black; after Barrett et al. (2009)).

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 populations (Johnson et al., 2005; Ling, 2008).

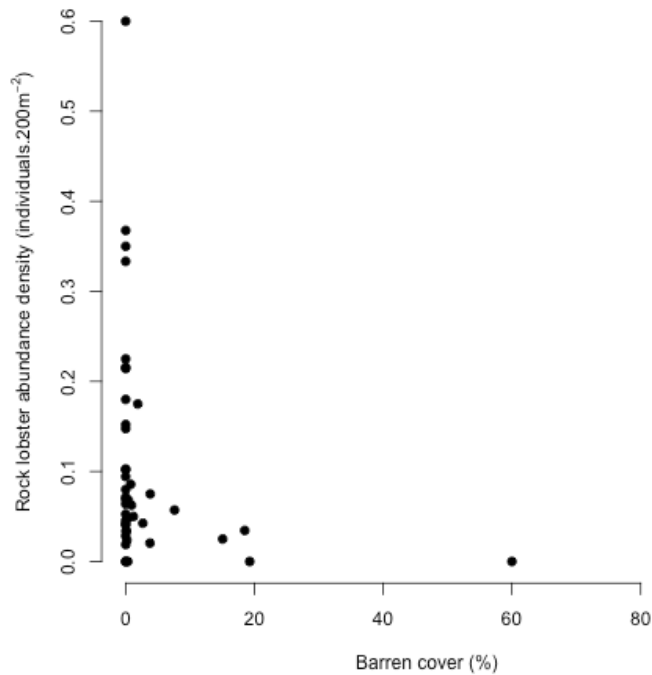


Figure AT8.9. Sea urchin barrens percentage cover against rock lobster density. These data from large-scale surveys of *C. rogersii* barrens on the east coast of Tasmania are aggregated by subsite (Johnson et al., 2005, 2011).

- 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, 2011). Sampling was hierarchically structured with 16 primary sites (13 on Tasmanian mainland; 3 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. AT8.9.

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. AT8.1. Size was not reported for lobster individuals, so we assumed a linear relationship between abundance and biomass density. 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 (Koenker and Park, 1996; Thomson et al., 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 (α , β , γ) of a n^{th} power function defined as: $B_{\text{RL}} = \alpha + \beta B_{\text{SW}}^{\gamma}$ with B_{RL} rock lobster relative density and 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 three years to gauge the efficiency of translocating deep-sea lobsters (carapace length (CL) >140 mm) as a management option to restore seaweed habitat from fully-established urchin barrens. 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 along its shallow edge (<12 m depth), 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 lobsters being more catchable on barrens grounds where they are more mobile and possibly forage more actively. Capture-mark-recapture modelling of tagged animals in the Elephant Rock experimental site provides habitat-specific estimates of catchability coefficients (as a percentage of the population sampled through potting) across all size classes of lobster. The estimated percentage of the population sampled by pot fishing varies between 4.40 (+/- SE=0.17) % in the kelp bed or 4.90 (+/- SE=0.17) % on barrens habitat (this study), which gives a mean catchability ratio between the two habitats (kelp bed *versus* barrens ground) of 0.898. Similar work on habitat-specific (barrens *versus* kelp bed) catchability for American rock lobster in Nova Scotia suggests a ratio of 0.766 of catchability in kelp beds relative to barrens habitat (Miller, 1989).

Fig. AT8.10 shows the size-structured distribution of catch per unit 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 pot lift). Additionally, only the abundance of smaller size classes of lobster (carapace length <140mm) is lower on barrens ground than in adjacent kelp beds (see Fig AT8.10). 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 A5) 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.

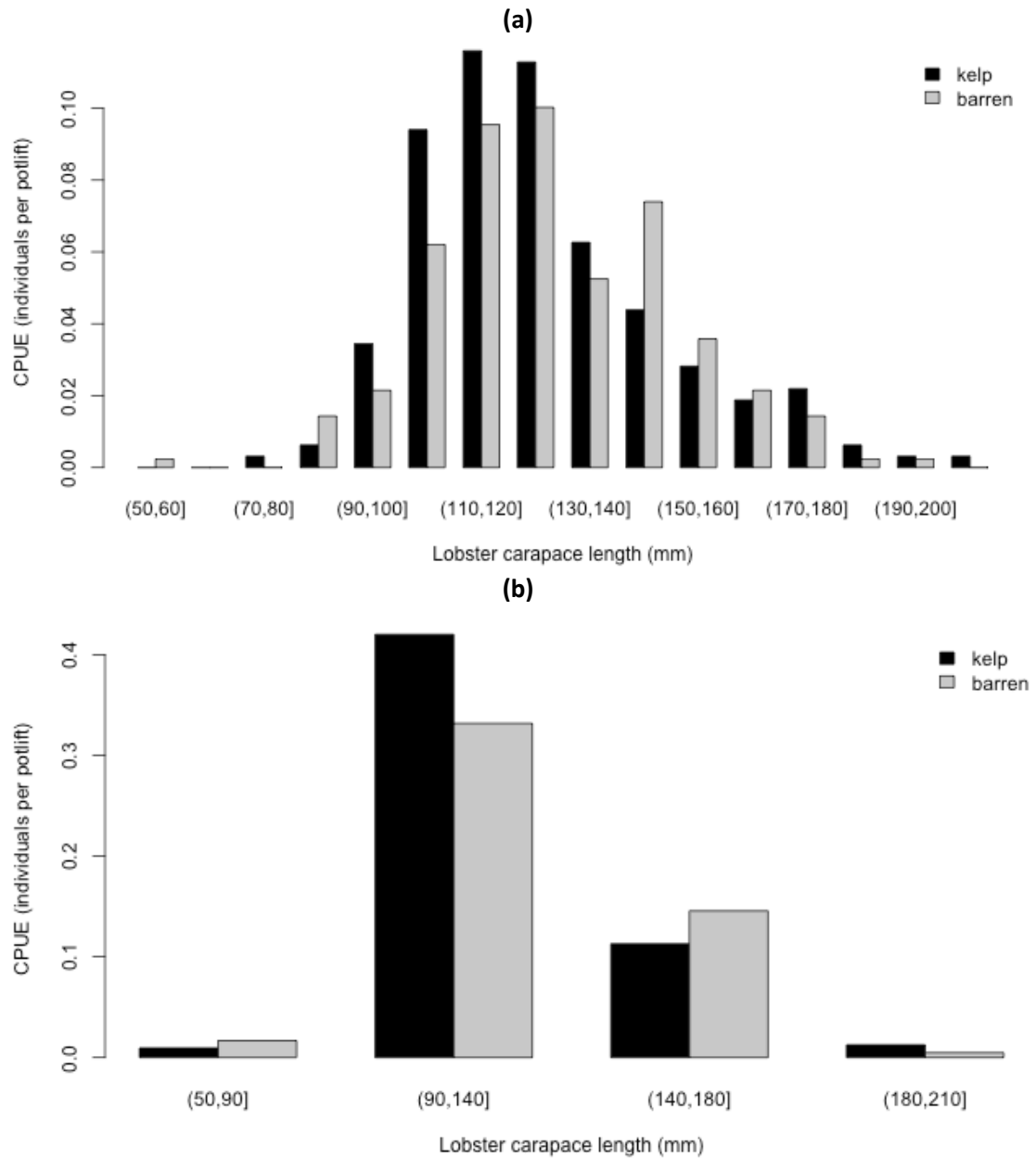


Figure AT8.10. Size-structured catch per unit of effort (individuals per pot lift) in the Elephant Rock experimental area following protection from fishing in both seaweed (black) and barrens (grey) habitats.

Table AT8.6. Size-structured catch per unit effort (CPUE; the unit is individuals per pot lift) at the St Helens experimental site following protection from fishing for resident lobsters only (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 corrected CPUE account for differences in catchability in the two habitats; indeed, catchability estimates from Elephant Rock suggest that 4.40 % of the resident population was sampled through potting in the kelp bed against 4.90 % on barrens ground.

	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}	1.52	0.67	1.100	0.32

Lobster CL	Width of size classes	CPUE _{barren} / CPUE _{kelp} (+/- Std. deviation)
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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)
140-180 mm	10 mm	1.01 (+/- 0.36)

Trophic interactions

Sea urchin grazing on seaweed

- Data

The estimate of *C. 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 fresh weight (Hill et al., 2003). Using the length weight relationship for *C. rodgersii* in Tasmania ($B = 0.00267 TD^{2.53}$ 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 (+/-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 activity 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 about 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). 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. In TRITON, grazing of macroalgae is simply assumed to be linearly proportional to sea urchin biomass density. This assumption of constant per capita grazing rate is supported by empirical observations of 'barrens' formation in eastern Tasmania (Flukes et al., 2012). The use of this simple representation of urchin grazing on seaweed is also 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 (Johnson et al. 2005; 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, in calm weather *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 through transport. 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.

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., 2009a). 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 urchins can be derived from this data (Table AT8.7) but it is essential to keep in mind that the density of urchin was very low in this experiment.

- Data from two experimental sites where large rock lobster individuals were translocated onto sea urchin barrens

Large predatory rock lobsters (CL > 140mm) were translocated onto two experimental sites (Redd, unpublished data) at Elephant Rock near St Helens and North Bay on the Forestier Peninsula, where extensive and incipient sea urchin barrens occur respectively (this study). Both sea urchin and rock lobster population densities were monitored over the three years of these experiments (this study), and estimates of predation rate were derived from the observed decline in sea urchin density (this study), which we attributed to the large predation-capable lobsters (CL > 140mm). Note that density of *C. rodgersii* at the translocation sites with elevated densities of large lobsters declined significantly over the study period while there was no consistent trend in urchin densities, and changes were not significant, at the control sites without added lobsters. Across the two experimental sites, the mean biomass-based estimate of lobster predation rate on *C. rodgersii* is 7.5 (+/- 2.6; standard deviation) year⁻¹ (i.e. g of urchin/ g of lobster/ year). Site-specific estimates of predation from these translocation experiments are given in Table AT8.7.

- Estimates of predation rates

Overall, the different estimates of lobster predation from predation experiments 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 AT8.7).

Table AT8.7. 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 ≥ 140 mm.

Data source	Mean	Std. Dev.
	Tagging experiment	
All lobster	0.29	0.14
Large lobsters	0.64	0.3
	Translocation of large predatory lobsters on sea urchin barrens	
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 AT8.8). 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 AT8.8).

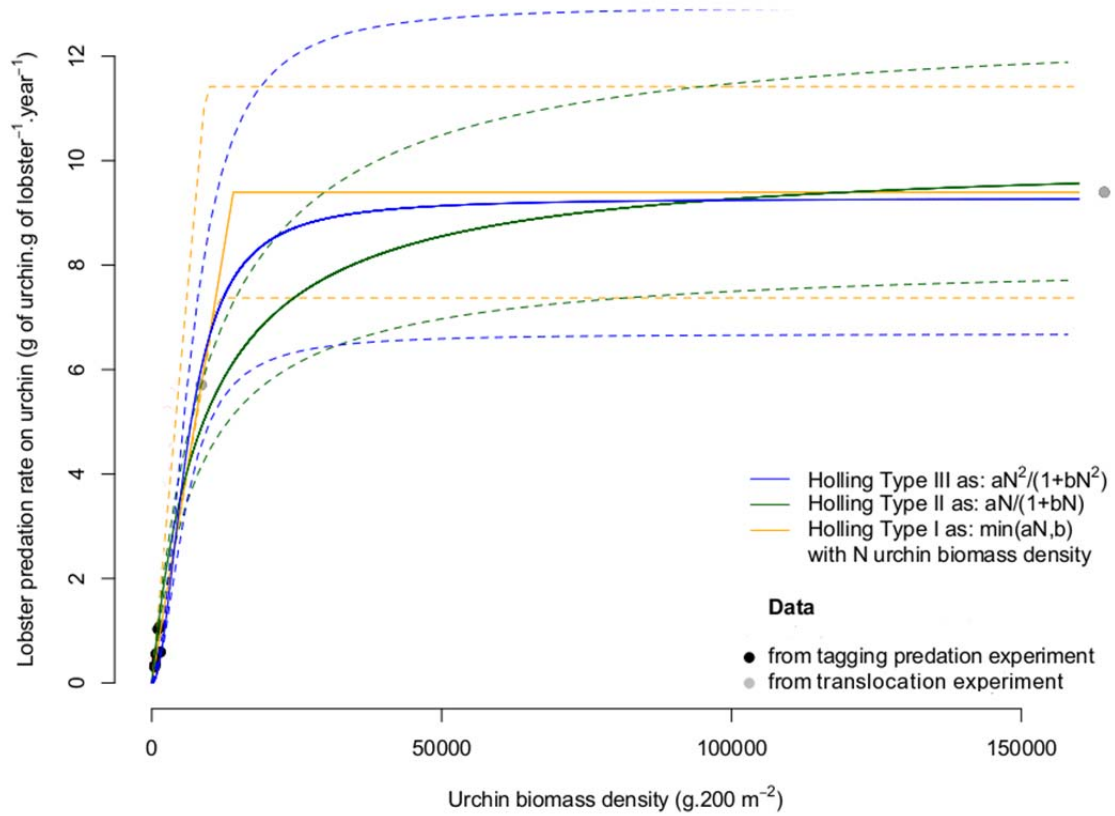


Figure AT8.11. Estimates of lobster predation rate on *C. rodgersii* and fitted Holling Type I (orange curve), II (green curve) and III (blue curve) functional responses to urchin density. Data from predation experiments (Ling et al., 2009a) in marine reserves are shown in black and data from translocation of large predatory lobsters onto sea urchin barrens (this study) in grey. The dotted lines represent the 50% confidence interval of the fitted functional responses.

Table AT8.8. 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 <i>H. americanus</i>	Green sea urchin <i>S. droebachiensis</i>	Type III	All size	(Breen, 1974; Evans and Mann, 1977) (Hagen and Mann, 1992)
American lobster <i>H. americanus</i>	Green sea urchin <i>S. droebachiensis</i>	Type II	Large prey only	(Breen, 1974; Evans and Mann, 1977) (Hagen and Mann, 1992)
Shore crabs <i>C. maenas</i>	Mussel <i>M. edulis</i>	Beddington-DeAngelis (predator density-dependence)		(van der Meer and Smallegange, 2009) (Smallegange and van der Meer, 2010)
Shore crabs <i>C. maenas</i>	Mussel <i>M. edulis</i>	Type III		(Griffen and Delaney, 2007)
Blue crab <i>C. sapidus</i>	Clams <i>M. arenaria, M. balthica</i>	Type III (field)		(Seitz et al., 2001)
Crab <i>C. irroratus</i>	Scallop <i>P. magellanicus</i>	Type II (lab.) Type III (field)	Evidence of size-structured interactions	(Barbeau et al., 1998) (Wong et al., 2010) (Wong and Barbeau, 2006)
Crabs <i>C. sapidus</i>	Clams <i>M. arenaria, M. balthica</i>	Type III (lab.) Type II (field)		(Eggleston et al., 1992) (Iribarne et al., 1995)
Crab <i>C. sapidus</i>	Oysters <i>C. virginica</i>	Type III		(Eggleston, 1990)

- Parameter estimates

Table AT8.9 presents parameter estimates for the Holling Type I, II and III functional responses of lobster predation on urchin.

Table AT8.9. 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.200 m⁻²) and where β and β' are scalars defining the shape of the functional response. Data from *in situ* predation experiments (Ling et al., 2009a; Ling and Johnson, 2012) and translocation of large predatory lobsters onto sea urchin barrens (this study).

	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 $\beta_{CR,RL} = \beta N / (1 + \beta' N)$				
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 II as $\beta_{CR,RL} = \beta N^2 / (1 + \beta' N^2)$				
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., 2009a). 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., 2009a) as $CL_{min} = \alpha \log(TD) - \beta$ with $\alpha = 43.48$ and β in [48.91;71.01] (mean of 59.96; standard deviation of 15.63).

Table AT8.10. Parameter estimates and confidence intervals used in Monte-Carlo simulations with TRITON. Data sources used to define (a) seaweed bed logistic growth, (b) sea urchin size-structure dynamics, (c) rock lobster size-structured dynamics, (d) lobster dependency on the seaweed bed, (e) urchin grazing rate, (f) rock lobster predation and (g) allometric relationships are also specified.

a) Seaweed bed logistic growth with α , intrinsic growth rate; K, carrying capacity; μ , mean annual recruitment rate.

(Fitted against observations of seaweed bed recovery following the removal of grazers; Ling, 2008)

Parameter	Units	Estimate	Std. error	Conf. interval
α_{SW}	year ⁻¹	4.43	1.65	1.72-7.14
K_{SW}	g SW.200 m ⁻²	3.4e+05	3.6e+04	2.8e+05-4e+05
μ_{SW}	g SW.200 m ⁻² year ⁻¹	5000		2500 - 10000

b) Sea urchin size-structured population growth with a growth transition matrix derived from an inverse logistic growth function (Ling et al., 2009b); β_{CR} , annual natural mortality; μ_{CR} , mean annual recruitment rate. The annual stochastic recruitment function follows a binomial with a 0.4 probability of success, which is combined with a lognormal of mean $\gamma_{RL} = -0.15$ and standard deviation σ_{CR} of 0.5.

(Fitted against large-scale population surveys; Johnson et al., 2005; Ling et al., 2009b)

Parameter	Units	Estimate	Conf. interval
β_{CR}	year ⁻¹	0.11	0.1-0.15
μ_{CR}	g CR.200 m ⁻² . year ⁻¹	4100	2500-10000

c) Lobster size-structured population growth with a growth transition matrix derived from polynomial growth functions (McGarvey and Feenstra, 2001); β_{RL} , annual natural mortality; μ_{RL} , mean annual recruitment rate. The annual stochastic recruitment function follows a lognormal of mean $\gamma_{RL} = -0.15$ and standard deviation σ_{RL} of 0.6.

(Fitted against observation of population recovery following protection from fishing; Barrett et al., 2009)

Parameter	Units	Estimate	Conf. interval
β_{RL}	year ⁻¹	0.23	0.20-0.26
μ_{CR}	g CR.200 m ⁻² . year ⁻¹	350	200-80

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

(Johnson and Ling, unpublished data)

Parameter	Units	Estimate	Std. error	Conf. interval
$\beta_{SW,RL}$	constant	0.64	0.11	0.46 - 0.83

e) Urchin grazing rate

(After in situ experiments by Hill et al., 2003)

Parameter	Units	Estimate	Std. error	Conf. interval
$\beta_{SW,CR}$	g SW.g CR ⁻¹ . year ⁻¹	5.94	1.10	4.13-7.75

f) Functional responses of lobster predation on urchin with B_{CR} , urchin biomass density ($g \cdot 200 m^{-2}$)

(Fitted against predation estimates from Ling et al., 2009a and K. Redd, unpublished data)

- Holling Type I as $\beta_{CR,RL} = \min(\beta N, \beta')$

Parameter	Units	Estimate	Std. error	Conf. interval
β	$g RL^{-1} \cdot year^{-1}$	6.68e-04	2.27e-05	6.31e-04 - 7.05e-04
β'	$g CR \cdot g RL^{-1} \cdot year^{-1}$	9.40	3.00	4.46 - 14.33

- Holling Type II as $\beta_{CR,RL} = \beta N / (1 + \beta' N)$

Parameter	Units	Estimate	Std. error	Conf. interval
β	$g RL^{-1} \cdot year^{-1}$	11.09e-04	1.68e-04	8.34e-04 - 13.85e-04
β'	$g CR^{-1}$	1.10e-04	0.20e-04	7.76e-05 - 14.19e-05

- Holling Type III as $\beta_{CR,RL} = \beta N^2 / (1 + \beta' N^2)$

Parameter	Units	Estimate	Std. error	Conf. interval
β	$g CR^{-1} \cdot g RL^{-1} \cdot year^{-1}$	2.35e-07	0.55e-07	1.46e-07 - 3.25e-07
β'	$g CR^{-1} \cdot g CR^{-1}$	2.50e-08	0.60e-08	1.47e-08 - 3.60e-08

g) Allometric and other size-based relationships

Length-weight relationship for the long-spined sea urchin (Ling, unpublished data)

 $B = 0.00267 \times TD^{2.534}$ with B, urchin individual weight (g); TD, urchin test diameter (mm).

Length-weight relationship for the southern rock lobster (Punt and Kennedy, 1997)

 $B = 0.000271 \times CL^{3.135}$ with B, lobster individual weight (g); CL, lobster carapace length (mm).

Size-structured predation of lobster on urchin (after Ling et al., 2009a)

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

Implicitly accounting for other factors in the model

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 lobsters) or intraspecific competition.

Abiotic factors: temperature, seasonality, habitat and depth

Seasonality and temporal variability

Several model parameters are likely to change seasonally, *viz.* growth, recruitment (following spawning, development and settlement of pelagic larvae) and trophic interactions (catchability of southern rock lobster varies throughout the year and relates directly to lobster foraging activity). However, the current version of the model does not incorporate seasonality because implementing seasonal processes (e.g. autoregressive stochastic functions; Annan, 2001) considerably increases model complexity in terms of parameterisation, and specific information about the seasonality of the different model processes is lacking. Moreover, the temporal scale of the issues addressed by the model is of the order of several years to several decades, so that seasonal fluctuations are largely irrelevant and using annual averages is a valid approximation.

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. AT8.5; Ling et al., 2008).

- Discrepancies in lobster growth

Lobster growth rates increase 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 et al., 1997). For simplicity, the observed growth rate on 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 and presumably sea urchin and lobster behaviour; ii) habitat structure, which can significantly influence sea urchin survival (Ling and Johnson, 2012). 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.

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. It also illuminates lack of information about ecosystem processes which helps 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.

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 these estimates. Additionally, it may be useful to represent different guilds of seaweeds (e.g. turfing species, other understorey species, canopy species) 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

Some 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.

Dependency of lobster dynamics on 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.

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 quantitative data are currently available to quantify density dependence of the grazing rate on either the seaweed bed cover or sea urchin density.

Predation rate

Further field experiments across a wider range of sea urchin densities could help refine our current estimate of rock lobster predation on 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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APPENDIX 9: Application of the TRITON ecosystem model – Identifying thresholds in community dynamics and assessing management intervention to limit destructive grazing of sea urchins

This component of the project has been developed for submission to *Ecology Letters*. The title and authorship is:

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

Authors: Martin P. Marzloff, Craig R. Johnson, L. Rich Little

Presented here are the elements of this paper necessary to provide the broad academic context of the work, and a technical outline of the methodology to augment and complement the more general outline given in the main body of the report.

Abstract

Like many shallow temperate marine systems worldwide, Tasmanian inshore rocky reefs can occur in alternative persistent community states. The shift from dense productive seaweed beds to sea urchin 'barrens' habitat significantly affects ecosystem structure and functioning. Along with dramatic loss of habitat and species diversity, the establishment of extensive barrens habitat constitutes an immediate threat to the productivity of Tasmanian fisheries. Effective management requires estimates of key thresholds in community dynamics and assessment of the effectiveness of alternative management scenarios. However the transition to barrens habitat can be swift and extremely difficult to study empirically.

Through Monte-Carlo simulations with a model that realistically captures rocky reef community dynamics in eastern Tasmania and the potential for both 'forward' shifts from dense seaweed beds to sea urchin barrens and 'backward' shifts from barrens habitat to seaweed recovery, we identify thresholds in community dynamics, reference points for management and assess the effects of alternative management interventions on community state and fishery productivity. The different tipping points for forward and backward shifts reflect a hysteresis in dynamics, i.e. once sea urchin barrens form extensively, restoration of dense seaweed beds becomes much more difficult to achieve than prevention of their formation in the first place. The risk of barrens formation increases significantly with fishing mortality on predatory lobster. Direct culling of sea urchin populations combined with reduced lobster fishing pressure is likely to be more effective in terms of both ecological outcomes and improved fishery performance than intervention aimed only at rebuilding populations of predatory lobsters to control the urchins. The model highlights the risk of Tasmanian rock lobster fishery management relying solely on a single-species orientation focussing on maximum sustainable yield or maximum economic yield, and the need to accommodate a more conservative ecologically sustainable yield that accounts for the ecosystem services delivered by rock lobsters to reef communities.

Context

Variability is a key characteristic of ecological dynamics (Doak *et al.* 2008). In some ecological systems, in addition to relatively short-term space-time variability in dynamics (e.g. seasonal, 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 & Carpenter 2003; Carpenter *et al.* 2011). These abrupt changes in community dynamics can dramatically alter ecosystem functioning and have disastrous consequences for the human activities that rely on them. These phase shifts are challenging to anticipate and their consequences difficult to predict (Doak *et al.* 2008; Fung *et al.* submitted manuscript), so that systems with the potential for these shifts represent particular challenges for ecologists and managers alike (Sutherland *et al.* 2009).

Phase shifts are often swift and are usually observed *a posteriori*, i.e. after the community has shifted to the alternative state. Hence, thresholds in the dynamics of marine ecosystems with alternative persistent states are notoriously difficult to identify empirically (de Young *et al.* 2008; Doak *et al.* 2008; Hastings & Wysham 2010). Additionally, experimental assessment of the effects of alternative management scenarios on community state is hardly ever achievable in marine ecosystems at an appropriate scale. For these reasons, and because the triggers and behaviours of phase shifts are unique to each ecosystem, tailored case-specific simulation models represent a valuable tool to explore ecological dynamics with alternative community states, test the effects of management scenarios and inform decision making for particular circumstances (Scheffer & Carpenter 2003; de Young *et al.* 2008). Several ecological models developed to capture the essential dynamics of marine ecosystems with alternative community states have been developed over the last decade, and include some designed explicitly for application in management support (see Mumby *et al.* 2007; Melbourne-Thomas *et al.* 2010; Fung *et al.* 2011 for some coral reef examples).

We developed the TRITON model (for **T**emperate **R**eefs **I**n **T**asmania with **L**obsters and **u**rchi**N**s) of the dynamics of seaweed-based reef communities in eastern Tasmania (see Appendix 8). In this region, shallow (< 40 m depth) exposed rocky reef communities essentially occur in one of two alternative persistent states: (1) as a dense cover of macroalgae; or (2) as sea urchin 'barrens' habitat characterised by a poorly productive and largely bare rock habitat following destructive grazing of the seaweeds and sessile benthic invertebrates by the long-spined sea urchin (*Centrostephanus rodgersii*). The establishment of these widespread sea urchin barrens results from the combined effects of climate-driven range extension of the sea urchin from Australia's mainland to Tasmania via strengthening eddy activity of the warm East Australian Current (Johnson *et al.* 2005; Ling *et al.* 2009b; Johnson *et al.* 2011) and depletion of biomass of large southern rock lobster (*Jasus edwardsii*) as the only effective predator of the long-spined sea urchin in Tasmania (Ling *et al.* 2009a). 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 (Johnson *et al.* 2005, 2011; Ling 2008). Thus, the spread of sea urchin barrens in eastern Tasmania has been identified as a major threat to the sustainability of the important lobster fishing industry (Johnson *et al.* 2005, 2011; Pecl *et al.* 2009).

Here we address a range of important questions for the management of Tasmanian reef communities using Monte-Carlo simulations with the TRITON model:

Having developed, calibrated and validated the TRITON ecosystem model, here we apply the model using Monte-Carlo simulations to address several important questions focused on management of Tasmanian reef communities:

1. What are the characteristic thresholds in community dynamics? Identifying the tipping points is critical for sound management, but they cannot easily be observed empirically. The simulation-based estimates of these thresholds from TRITON are intended to help define essential reference points for the Tasmanian rock lobster fishery so as to minimise the risk of barren formation or

facilitate the recovery of seaweed beds from a state of extensive barrens.

2. What are the merits and overall effectiveness of alternative management scenarios to either prevent the establishment of sea urchin barrens habitat, or restore dense seaweed beds from sea urchin barrens? Here we test, both independently and in combination, the effectiveness of available management levers: reducing lobster fishing, implementing a maximum legal size to protect large lobsters as key predators of the sea urchins, and culling of sea urchin populations and translocating large lobsters from deep reefs to shallow reefs that are exposed to sea urchin destructive grazing.

3. How do the different management scenarios affect the performance of the rock lobster fishery in eastern Tasmania, estimated from simulated catches with TRITON and overlain with a version of the current Tasmanian rock lobster stock assessment model? Over the last two decades, fisheries scientists have increasingly emphasised the need to account for the ecosystem effects of fishing, and to shift management practises away from a traditional single species focus towards an ecosystem-based approach (Smith *et al.* 2007; Smith *et al.* 2011). It is in this context that this question is addressed. With this simple example in which lobsters play an important ecological role as predators of sea urchins, we illustrate some of the misleading assumptions of a single-species focus when 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 ecological services delivered by commercial species, and suggest that these targets may need to be revised to maintain ecosystem functioning. This will be particularly important for ecological systems in which the dynamics are characterised by alternative community states with hysteresis, i.e. where phase shifts are particularly difficult to reverse.

Methods

The TRITON model

A detailed account of the development of the TRITON model is presented earlier in the report, and a technical outline is given in Appendix AT8. There are two additional elements to introduce here.

First, in comparing predicted future catches in the rock lobster fishery on the east coast as estimated by TRITON with predicted catches based on a single-species approach, we used a slightly simplified version of the current rock lobster stock assessment model used in the Tasmanian rock lobster fishery (Punt & Kennedy 1997; Hartmann *et al.* 2012) as the ‘single species’ model. In this, lobster population dynamics follows Equation A9.1’ (below), which is similar to TRITON’s equation defining rock lobster dynamics (see Appendix 8) except that stochastic recruitment to the first size class is assumed to be lognormal and independent of both the local biomass density of lobster (i.e. we assume large-scale regional supply of larvae) and local extent of sea urchin barrens habitat.

$$\begin{aligned}
 RL_{s,t+1} = \max & \left\{ 0, \underbrace{\left\langle \text{If } s = 1: r_{RL} \right\rangle}_{\text{Recruitment to the first size class gets reduced as barren habitat expands.}} + \underbrace{RL_{s,t} \times \exp(-\beta_{RL})}_{\text{Natural mortality}} \right. \\
 & \left. + \underbrace{\left(\sum_{j=1}^{j < s} (\delta_{s,j}^{\sigma} \times RL_{s,t}) - \left(\sum_{i>s}^{N_{RL}} \delta_{i,s} \right) \times RL_{s,t} \right)}_{\text{Growth between different size classes accounts for individual weight gain}} - \underbrace{\left(1 - \exp(-F_{RL_s}) \right) \times RL_{s,t}}_{\text{Fishing mortality}} \right\} \quad \dots \text{ (Equ. A9.1')}
 \end{aligned}$$

where $RL_{s,t}$ denotes biomass of rock lobster in size class s at time t ($g \cdot 200 m^{-2}$); r_{RL} , lobster recruitment rate ($g \cdot year^{-1} \cdot 200 m^{-2}$), with mean recruitment rate μ_{RL} varying stochastically following a lognormal stochastic function of mean 0 and standard deviation ϵ_{RL} ; $\delta'_{s,j}$, biomass-based transition probability from size class j to s , or element of the s^{th} row, j^{th} column of the transition probability matrix ($year^{-1}$ or $g \cdot g^{-1} \cdot year^{-1}$); $\delta_{i,s}$, abundance-based transition probability from size class s to i ($year^{-1}$ or $individual \cdot individual^{-1} \cdot year^{-1}$); SW , seaweed biomass ($g \cdot 200 m^{-2}$); F_{RLs} , fishing mortality for lobster of class s ($year^{-1}$).

The second element to outline concerns the logistic binomial models we fitted to relate seaweed cover or the probability of community shift (i.e. extensive barren formation or restoration of the seaweed bed) to the standing biomass density of different model groups. The binomial GLM routine estimates the coefficients α and β in: $\log\left(\frac{p}{1-p}\right) = \alpha + \beta \cdot x$ where p is the predicted variable (probability of community shift, or seaweed relative cover expressed as the ratio of seaweed standing biomass density on seaweed carrying capacity) and x is the explanatory variable (standing biomass density of large lobsters [carapace length ≥ 140 mm] or sea urchins). We use α and β to characterise thresholds and reference points as $x = \frac{\log\left(\frac{p}{1-p}\right) - \alpha}{\beta}$.

Characteristics of the different sets of Monte-Carlo simulations

Tables A9.1 and A9.2, respectively, describe the characteristics of the Monte-Carlo simulations used to assess the effects of alternative management interventions (e.g. sea urchin culling, maximum legal size for rock lobster) (Table A9.1); and the initial conditions for simulations focusing either on the ‘forward’ shift from dense seaweed bed to extensive sea urchin barrens, or the ‘backward’ shift of seaweed bed regrowth on extensive sea urchin barrens (Table A9.2).

Table A9.1. Characteristics of the different sets of Monte-Carlo simulations considering sea urchin culling or harvesting, establishment of a maximum legal size for lobsters, for a particular mean lobster recruitment rate. Lobster fishing mortality F_{RL} is varied between 0 and 2.5 $year^{-1}$ in all the scenarios.

	Sea urchin cull rate F_{CR} ($year^{-1}$)	Maximum legal size F_{maxRL} (mm)	Lobster recruitment rate μ_{RL} ($g \cdot 200 m^{-2} \cdot year^{-1}$)
Range	0 – 2.5	135 – 165	200 – 800
Low	0 – 0.5	135 – 145	200 – 400
Moderate	0.5 – 1.5	145 – 155	400 – 600
High	1.5 – 2.5	155 – 165	600 – 800

Table A9.2. Initial conditions for simulations focusing on the ‘forward’ or the ‘backward’ shift, where the initial community state corresponds either to the seaweed bed, or to sea urchin barrens habitat, respectively. Biomass densities are given in $g \cdot 200 m^{-2}$.

	Dense seaweed cover	Sea urchin barrens
Seaweed assemblage	$2 \times 10^5 - 4 \times 10^5$ (i.e. more than 50% cover)*	$0 - 4 \times 10^4$ (i.e. less than 10% cover)*

Sea urchins	0 – 4 × 10 ³ (i.e. marginal population biomass density)	7– 1.4 × 10 ⁵ (i.e. more than 50% of mean biomass density observed on extensive barrens)
Rock lobsters	0 - 1.2 × 10 ⁴	0 - 1.2 × 10 ⁴

* The same values are used to define presence (1) or absence (0) of a shift to the alternative state at the end of a simulation: a persistent shift to sea urchin barrens is assumed if the seaweed bed drops below 10% cover, while recovery of seaweeds corresponds to the seaweed bed re-growing above a 50% of cover. These values of seaweed proportional cover, which determine the presence or not of a shift to the alternative state, were defined based on the examination of TRITON's mean behaviour across Monte-Carlo simulations (See Fig. 39, main body of report).

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APPENDIX 10: Modelling *Centrostephanus rodgersii* and rock lobster population dynamics and 'barrens' habitat in eastern Tasmania

Here is presented a more technically detailed and complete version of the methods used to develop and apply the projection matrix model of *Centrostephanus rodgersii* dynamics, and the projections predicting the distributions of urchin densities and cover of barrens habitat for particular densities and predicted temporal trajectories of abundances of large (>140 mm CL) lobsters.

We adopt two broad (and complementary) approaches, based on the population dynamics of *Centrostephanus rodgersii* and rock lobsters, to address the feasibility of managing the rock lobster fishery to affect the abundance of large predatory-capable lobsters to control *C. rodgersii* in eastern Tasmania. In the first, we model long term dynamics to identify the level of mortality from predation by large lobsters that is necessary to achieve particular target densities of urchins associated with different levels of risk of formation of extensive *C. rodgersii* barrens. This work is focused on intact seaweed beds and incipient urchin barrens, and preventing their transition to extensive barrens.

In the second approach we reverse the question and estimate the level of urchin barrens we can expect in eastern Tasmania for a given density of large predatory capable lobsters. In addressing this question, we first consider the general case and predict expected barrens cover in the long term for a given density of predation capable lobsters, and then address the outcome of specific rock lobster management scenarios over short (10 years) and medium (21 years) terms. Given the strong hysteresis in dynamics, outcomes of specific management scenarios are considered separately for intact seaweed beds or incipient urchin barrens, and for extensive barrens. For the case of incipient barrens we estimate the expected distribution of barrens cover in 2021 (10 year prediction) and 2032 (21 year prediction) for each management scenario. In addressing extensive barrens, for each management scenario we estimate the probability density profile across a range of *C. rodgersii* densities and compare this with the target density of urchins necessary to realize regrowth of seaweeds.

While analysis of the consequences of specific short- and medium-term approaches to managing the rock lobster industry are of most immediate interest, the general case provides a context for interpretation of specific scenarios, and the combined approach provides a comprehensive assessment of the likely short and long term state of shallow reefs in eastern Tasmania given an 'acceptable' level of risk of barrens formation. All approaches rely on the same underlying model of *C. rodgersii* population dynamics, which is developed based on both our long term observations in eastern Tasmania as well as data obtained from the present study.

A model of population dynamics of *C. rodgersii* on the east coast of Tasmania

Given the nature of data available for *C. rodgersii* populations in eastern Tasmania, for which there is robust information on densities and age and size structure, a simple and appropriate model is based on a stochastic projection matrix. The stability obtained from the ergodic behaviour of this kind of model allows greater insight to be obtained in our application, and suggests the approach as 'fit for purpose'. In this approach age-specific survivorship and recruitment are parameters of critical importance.

Key elements of population dynamics are survivorship and recruitment, estimates of which are outlined below prior to introducing the model *per se*.

Annual survivorship and mortality of C. rodgersii

Survivorship is expressed as age-specific survival (transition) probabilities. We estimated the proportion of each age class surviving to the next year from the age-frequency pattern for eastern Tasmania obtained from pooling population age-structure data from all sites for which these data are available (See Ling et al. 2009b; Johnson et al. 2011). These data show an exponential decay over age classes 8-50 years (Fig. A10.1) which, scaling from an initial emergent population of 1000 urchins at 8 years old, is given as $y = 2404.9 * \exp(-0.1169 * x)$ (adjusted $R^2 = 0.925$, SE of exponent = ± 0.005).

This indicates a remarkably constant decay rate of 0.1103 y^{-1} , or annual survival rate of 0.8897, irrespective of age class. We assume that this describes the background mortality rate in fished areas outside of reserves that, given their scarcity on shallow reefs (<25-30 m depth) in eastern Tasmania, is largely independent of predation by large lobsters (>140 mm CL). This estimate is identical to the estimate of overall annual *C. rodgersii* mortality (of 0.11 y^{-1}) that we derived in developing the TRITON model, based on fitting a logistic growth model to the relationship between sea urchin population biomass density and the 90th quantile of the population age distribution (used as a proxy for the time elapsed since settlement of the urchins) as observed for populations in eastern Tasmania. That these two quite different approaches based on two different data types yield the same result gives us confidence in the estimate.

Note however that while available data provides the estimate of annual mortality, the model is implemented in daily time steps (see below). Thus in the model daily mortality was scaled to yield the estimated annual mortality rate.

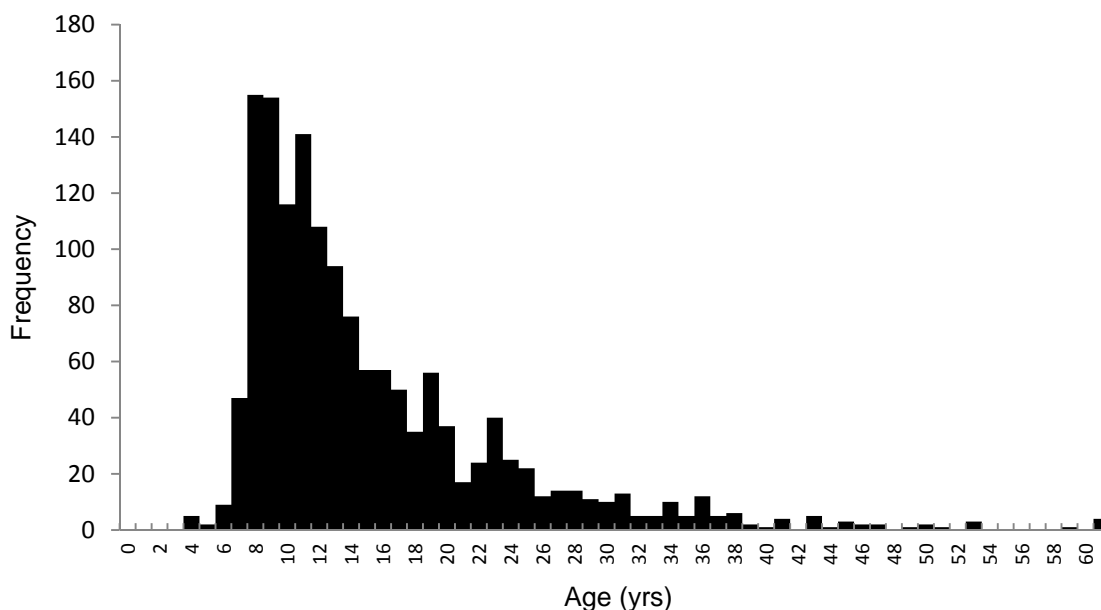


Figure A10.1. Age –frequency of *C. rodgersii* in eastern Tasmania determined from data pooled across several sites ($N = 1706$; after Ling et al. 2009b; see also Johnson et al. 2011). Annual mortality rates from an age of 8 years are constant at 0.1103 y^{-1} (determined from fitting exponential decay; scaled to an initial population of 1000, population size is given as $2404.9 * \exp(-0.1169 * \text{time})$, adjusted $R^2 = 0.925$).

Recruitment

Recruitment in the model is defined as recruitment to the emergent size class. While occasionally small individuals (e.g. 40 mm TD) are found emergent on reefs, and 50 mm TD animals can be observed in non-cryptic habitat at night, size-frequency distributions of emergent animals from the Kent Group (Johnson unpublished data, $N=298$ animals), and east coast of Tasmania (Ling et al. 2009b) are consistent in showing the smallest emergent sizes as predominantly 75 mm and 70 mm TD respectively. Given the large spatial extent over which these data were obtained (i.e. several 100 km of coastline), this result is unlikely to

represent development of a single cohort. Assuming emergence at 70 mm TD, this equates to an expected modal age of emergence of 7 years (Johnson et al. 2005, 2011; Ling and Johnson 2009; Ling et al. 2009b).

Recruitment rates of *C. rodgersii* to any size or age class have not been monitored directly, so it is necessary to estimate this critical population parameter. We follow the procedure followed for the TRITON model in determining recruitment as the combination of a binomial and lognormal distribution. Annual recruitment r to the 7+ age class is given as:

$$r = [0,1] * \mu * \exp(\gamma + \sigma * N(0,1)) \quad \text{equation (A10.1)}$$

where:

[0,1] defines a binary outcome from the binomial distribution (see below);

μ is an absolute recruitment population size chosen randomly from a uniform distribution ranging between minimum and maximum values and which is unchanged for any given single modeled population trajectory, i.e. variability in μ reflects variability between reefs, based on observations that some reefs (e.g. on headlands) are likely to receive on average more recruits than others (e.g. those in bays; see Ling et al. 2009b);

γ is a lognormal scaling quantity that introduces additional inter-annual stochastic variation into the recruitment signal where γ and σ are the mean and standard deviation respectively of the lognormal distribution; and

$N(0,1)$ is a random term following a normal distribution with mean = 0 and standard deviation = 1.

The binomial term determines whether a recruitment event will occur *at all* in any given year, and is based on $Prob = 0.4$ as the probability that a recruitment event can occur in any one year. This acknowledges that from 1970-2007 only ~4 in 10 years achieved water temperatures sufficiently warm to support larval development (Ling et al. 2008), although we acknowledge that this frequency is likely to increase into the future (Johnson et al. 2011).

In defining the range of absolute recruitment (μ in equation A10.1), we adopted the estimates used in parameterising recruitment in the TRITON model, but required to transform them from total biomass density recruiting to the 3+ year class to density of individuals recruiting to the 7+ year class (Table A10.1). For the TRITON model we estimated minimum and maximum recruitment rates from the lower and upper 95% confidence interval of a logistic growth model fitted to the relationship between sea urchin population biomass density and the 90th quantile of the population age distribution (used as a proxy for the time elapsed since settlement of the urchins), as observed in eastern Tasmania. In this way we estimated the range in recruitment rates to the 40 mm size class (equivalent to 3.46 years old, which we conservatively assume as the 3+ age class; after Ling et al. 2009b) as 2,500-10,000 g.200 m⁻². For the projection model we converted biomass density of the 3+ age class to density of individuals in the 7+ age class (the modal age class at emergence from the reef matrix). Biomass (B) conversion is described by the power function $B = a * TD^b$ where $a = 0.00267$ ($\pm SD = 0.00042$) and $b = 2.534$ ($\pm SD = 0.00042$) (after Ling & Johnson 2009), i.e. the mean fresh weight of individuals at 40 mm TD is 30.63 grams. To transcribe from recruitment into the 3+ age class to recruitment into the 7+ age class, mortality of 0.1103 y^{-1} (see above) was applied (Table A10.1).

Table A10.1. Conversion of recruitment parameters as biomass density of animals 40 mm TD (used in parameterising the TRITON model) to density of individuals per hectare in the 7+ year class. In the model we rounded minimum and maximum values to 2,500 and 10,000 ha⁻¹ respectively. '#' refers to numbers of individuals; * indicates assumption of annual mortality = 0.1103 y⁻¹ (see above).

Biomass (g.200 m ⁻²) (parameters for TRITON model)	Conversion to #.200 m ⁻² at 40 mm TD	*Recruitment to 7+ year class (#.ha ⁻¹)
2,500 (lower)	81.62	2556
4,100 (mean)	133.86	4192
10,000 (upper)	326.49	10224

The final parameters to estimate in describing recruitment are for the lognormal distribution which adds stochastic annual variability. Despite that recruitment of *C. rodgersii* has not been monitored directly in Tasmania, we have observed two significant recruitment events over the period 1998-2011. Significant recruitment events once or twice a decade is consistent with a planktotrophic life history in which larvae are advected in the plankton for ~3 months and, in line with other echinoids, where there is a finite and relatively narrow competency period (Huggett et al. 2005). For the parameters of the lognormal, we used the estimate of $\gamma = -0.15$ and $\sigma = 0.5$ as in TRITON, and checked that (1) this provides a significant recruitment event approximately 'once or twice in a decade', (2) and yields a long term stable density of urchins similar to that observed in eastern Tasmania on developed *C. rodgersii* barrens (see below). We can define that a significant recruitment event requires the lognormal scaling quantity

$$\exp(\gamma + \sigma * N(0,1)) > 1.0.$$

Simulation (10,000 random draws from $N(0,1)$) indicates that for $\gamma = -0.15$ this condition is satisfied with $Prob = 0.378$ (the distribution of the scaling quantity is given in Fig. A10.2). By this definition, the overall probability of a significant recruitment event is $0.4 * 0.378 = 0.151$ or, on average, 1.5 times per decade. Alternatively, it is also defensible to define a significant recruitment as an elevated recruitment signal 'boosted' >100%, e.g. 120% (i.e. the lognormal scaling factor >1.2). The probability of a significant recruitment event by this definition is $0.4 * 0.243 = 0.097$, or on average, $0.97 \approx 1$ time per decade. Despite obvious subjectivity in defining what constitutes a 'significant' recruitment event, the key point is that the selected values of γ and σ for the stochastic lognormal component of the recruitment function produce a frequency of events that is ecologically sensible. Furthermore, the predicted asymptotic density of sea urchins under a *status quo* scenario (i.e. negligible urchin mortality due to predation by large lobsters) of 1.9 m⁻² is in line with mean densities observed on extensive *C. rodgersii* barrens in NE Tasmania (see below; Fig. 5 in main body of report).

The projection model of C. rodgersii population dynamics

The model simulates population dynamics on a hectare of reef, reflecting an appropriate spatial scale for the ecological and management questions to which the model is applied.

The projection commences from an initial population of *C. rodgersii*, which may contain zero individuals. Initial populations that are non-zero are structured to the age distribution given in Fig. A10.1. There are 45 age classes representing ages 7-50 years, while the oldest age class represents individuals 51+ and older. Choice of the oldest age class to model is to some extent arbitrary, however the model is not sensitive to a sensible range in this choice. Note also that given the ergodic nature of this kind of model, the model converges to the asymptotic density irrespective of the initial population density.

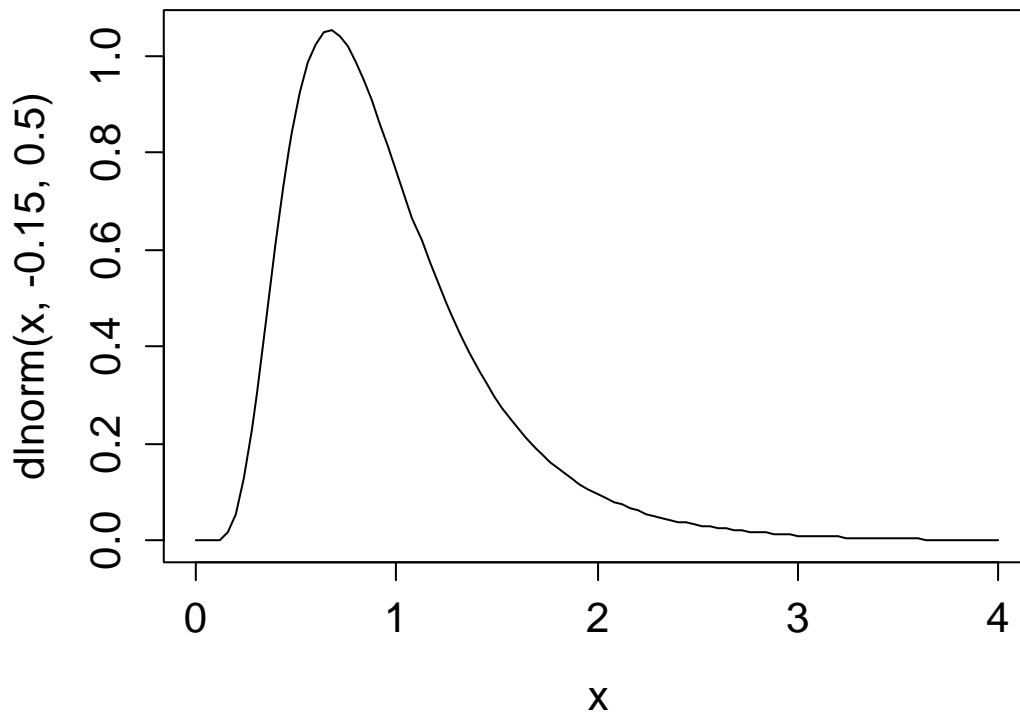


Figure A10.2. Distribution of the lognormal scaling coefficient that introduces stochastic variation in the year-to-year recruitment signal on a given reef, based on parameters λ (mean) = -0.15 and σ (standard deviation) = 0.5.

Variability in population size is driven largely by recruitment, which is annual. Accordingly, population dynamics from run to run can vary significantly depending on recruitment. We emphasise again that in simulating recruitment, each run accounts for (1) variability in the large scale oceanographic environment (in some years winter temperatures are too cold for larval development), (2) spatial variation from reef-to-reef (some reefs have consistently better recruitment than others), and (3) stochastic annual variability. Note that while it is straightforward to also introduce stochastic variation into the background mortality term, since the standard error of this estimate is so small, it makes little difference to model behaviour and for simplicity background mortality is treated as a constant.

Projection matrix models, by definition, use a finite time step. To avoid bias leading to inflated urchin numbers, particularly as mortality due to lobster predation increases, it is necessary to use a daily time step. Thus, mortality takes place with a daily time step such that estimated total annual mortality rates (determined as the sum of 'background mortality' m_b and mortality due to predation by large lobsters m_l) are preserved. Scaling annual mortality to a daily rate is achieved by considering the equation for exponential decay:

$$N_t = N_0 * e^{-\lambda t} \text{ and, by rearranging, } N_t/N_0 = e^{-\lambda t}$$

N_t/N_0 is the annual survival rate S (where $S = 1 - m_A$, and where m_A is annual mortality rate); for a daily time step, t is on average is 365.25; and λ is the daily mortality rate to be estimated. Rearranging further, λ is given as:

$$e^{-\lambda t} = S$$

$$\therefore -\lambda * t = \ln(S)$$

$$\therefore \lambda = -((\ln(1-m_A))/t).$$

Each year there is opportunity of recruitment to the emergent 7+ age class (as described above), and mortality is applied daily to each age class. Annual background mortality m_B is constant at 0.1103 y^{-1} (as described above) and is assumed not to include significant mortality due to predation by large lobsters. Annual mortality due to predation by large lobsters is a separate term (m_L) such that $m_A = m_B + m_L$. For scenarios focused on extensive urchin barrens, predation rates are scaled linearly to that observed within the Elephant Rock Research Reserve which, over the entire study period, averaged 18.55 large (>140 mm CL) lobsters ha^{-1} , resulting in a mean instantaneous annual mortality rate on the *C. rodgersii* population of 0.0394. For scenarios focused on incipient barrens or fully intact kelp beds, predation rates are scaled linearly to that observed within the North Bay Research Reserve which, over the period of the study, averaged 37.66 large (>140 mm CL) lobsters ha^{-1} imposing a mean instantaneous annual mortality rate on the *C. rodgersii* population of 0.4919. The linear scaling assumes that, at the densities of urchins and lobsters encountered in Nature, lobsters do not interfere with each other in foraging. (At this point we remind that constant mortality rates will result in exponential decline in the prey population).

Predation mortality is applied equally across all age classes, i.e. it assumes that large lobsters in the system are large enough to tackle any urchin they encounter, that emergent urchins are distributed randomly at the scale of a lobster's home range, and that lobsters do not select urchins on the basis of their age. A constant *rate* of mortality is consistent with observations from *in situ* experiments showing exponential decline of tagged urchins subject to lobster predation (after Ling et al. 2009a; Ling & Johnson 2012). These data indicate that the time taken by a lobster to encounter a sea urchin, and the absolute number of urchins consumed by a fixed population of lobsters in a year, depends on the density of sea urchins, which is ecologically sensible.

Given the underlying management imperative, what is required from a particular parameterization of the model is the overall likely 'steady state' population size and density (i.e. the mean asymptotic population) or the urchins, which is given as the mean of a Monte Carlo simulation of 1,000 runs ($\pm 95\%$ confidence interval) (results of a typical run are presented in Fig. 6 of the main report). Since the asymptotic mean density is invariably reached within 30 years irrespective of the starting density of *C. rodgersii*, each run simulates 100 years of population development, and the asymptotic density is calculated as the mean of the last 70 years of the averages of the Monte Carlo. Given variability in recruitment, in the context of risk of widespread barrens development and management considerations, the mean asymptotic density defined by the upper 95% confidence interval is also calculated as an important quantity worthy to consider.

Estimating predation rates of lobsters on *Centrostephanus rodgersii* and target densities of predation-capable lobsters

Given target densities of urchins necessary to realize low risk of extensive barrens formation or to rehabilitate extensive barrens (see above), and knowledge of predicted (asymptotic) densities of urchins for a given mortality rate, annual mortality rates from lobster predation necessary to achieve particular target densities of urchins can be ascertained (see above). By scaling this with known predation rates of large lobsters on urchins it is possible to estimate the target density of large (>140 mm CL) lobsters necessary to, on average, achieve particular long term urchin target densities. In other words, by defining urchin target densities from which necessary levels of lobster predation can be inferred, it is possible to identify target densities of lobsters necessary to maintain *C. rodgersii* populations in healthy seaweed beds at sufficiently low densities to provide low risk of incipient barrens developing into extensive tracts of barrens habitat, and to rehabilitate extensive *C. rodgersii* barrens. It remains only to estimate absolute rates of predation of large lobsters on *C. rodgersii*.

There are three ways to estimate absolute predation rates of large lobsters on urchins based on observations at the two experimental reserves: (1) from fitted models of change in urchin abundance related to lobster abundance at the experimental reserve sites, taking into account all data from all surveys of urchin abundance during the study, (2) from the change in urchin abundance related to lobster abundance but based only on the initial and final estimates, and (3) based on results of screening lobster faecal pellets for evidence of *C. rodgersii* DNA. The first two approaches are justified on the basis that the observed changes showed a statistically significant decline in *C. rodgersii* densities at the North Bay Research Reserve, a notable decline in urchin density at the Elephant Rock Research Reserve⁴, while at control sites there was no consistent trend either up or down in urchin numbers and changes in density were not statistically significant.

For the first two approaches we assume exponential decline in urchin numbers based on observations at the experimental sites and our earlier work with predation on a population of tagged urchins. Ling et al. (2009) and Ling & Johnson (2012) showed that a population of tagged *C. rodgersii* subject to predation within a marine reserve (at Maria Island) containing relatively high densities of large lobsters declined exponentially, i.e. that the mortality rate was remarkably constant ($R^2 = 0.97$) over the ~180 days of the experiment. For the North Bay Research Reserve where lobster predation had most impact (present study), fitting an exponential decay model to changes in urchin numbers based on all observations gives a slightly better fit (adjusted $R^2 = 0.81$) than a linear model (adjusted $R^2 = 0.78$), but moreover is a significant improvement over the linear model in describing the trend in urchin density (ANOVA, $F_{1,3} = 18.00$, $P=0.024$). At the experimental site at Elephant Rock (present study), the decline in urchin numbers over the study period is described equally well by a linear or exponential decline (adjusted $R^2 = 0.51$ in both cases), and the exponential model does not offer a significant improvement over the linear one (ANOVA, $F_{1,3} = 5.17$, $P=0.108$). On this basis, in calculating annual mortality rates, we assume changes in urchin numbers are exponential. Thus, within habitat types, it follows that a given lobster density will exert a constant annual mortality rate on *C. rodgersii* across the range of urchin densities likely to be encountered on the east coast of Tasmania and that the absolute encounter rate of lobsters with urchins depends on urchin density, i.e. a fixed density of lobsters will consume greater numbers of urchins as urchin densities increase. Similarly, we assume that lobster predation scales linearly with lobster density over the range of densities likely to be realized on the east coast of Tasmania (i.e. that twice as many lobsters in a given location will consume on average twice as many urchins at a given density at an instant in time). Effectively, this assumes that lobsters do not interfere with each other in prey capture and feeding over the densities encountered on east coast Tasmania.

Of the three approaches, the first is most robust in utilizing all available data – thus providing the greatest precision of the trend – to describe changes in *C. rodgersii* density at the two experimental sites. However, for completeness, and because the modelling approaches also require assumptions, we present results based on all three. For the model based estimates, there is risk of underestimating predation rates because in the absence of site-specific data it is necessary to assume zero recruitment of urchins to the emergent population over the study period, and in the other direction there is risk of overestimating predation rates because we assume sources of mortality other than from lobster predation are negligible (on the basis of no trends or significant changes in urchin density at the control sites). As discussed earlier in the report, the DNA based estimates are most problematic given the likelihood of inflated positive assays as a result of lobsters ingesting urchin DNA from scavenging or from ingesting urchin faecal pellets in the sediments. Detection rates of urchin DNA in faeces of lobsters from North Bay indicates ingestion other than through direct predation since the *C. rodgersii* population at that site could not sustain the predation rate indicated from the DNA-based approach. Lobster target densities for extensive barrens and incipient barrens are developed separately since it cannot be assumed that the same dynamics apply to both habitats.

⁴ Paired t-tests showed the decline in *C. rodgersii* at ERRR between the initial and final samplings, but not the corresponding changes at control sites, as statistically significant (after controlling level to maintain an overall Type I error rate = 0.05), while ANCOVA across all sampling dates indicates the change at ERRR was not significant although this approach has low power given 5 sampling occasions. See earlier section on estimating predation rates.

The inverse problem – estimating urchin density and extent of barrens cover for given lobster density

Assuming that lobster predation rates observed at the North Bay and Elephant Rock Research Reserves (in incipient barrens and extensive barrens respectively) scale linearly over the range of densities of lobsters and urchins likely to occur in eastern Tasmania, then the projection model can be run to estimate asymptotic urchin densities (and the 95% CI) for a given lobster density. Using this approach we first examined the general case of long term dynamics (based on asymptotic behaviour), in which long term mean urchin density, and the upper 95%CI of the mean, is predicted dependent on lobster density. By considering the observed relationship between urchin density and the extent of urchin barrens (See Fig. 5, main report), this is readily converted to an estimate of barrens cover. Using this approach, four different relationships describing the expected cover of urchin barrens dependent on lobster density are derived, representing all combinations of using the asymptotic mean or upper 95% confidence interval of urchin density dependent on lobster density, with both the median and upper 95% prediction interval describing the relationship between urchin density and barrens cover. Management might be guided by any of these four relationships depending on the level of risk of barrens cover deemed acceptable.

While predicted long term dynamics can provide guidance to, and an overall context for, management, key decisions are more usefully informed by reference to specific scenarios. In consultation with managers and industry, several potential scenarios for management of the rock lobster fishery were considered. For each scenario the trajectories of rock lobster biomass on the east coast of Tasmania (in areas 1-3 combined; see Fig. 7, main body of report) over two decades (to 2032) was predicted using the Tasmanian rock lobster stock assessment model (Hartmann et al. 2012). Scenarios included the extreme cases of the status quo and closing the fishery entirely, and a variety of scenarios between these extremes allowing total catch across both the commercial and recreational sectors combined from areas 1-3 to range from 160-240 t pa. In each scenario the mean biomass density of 140+ mm CL lobsters is predicted to increase until 2032, but the increase occurs at different rates (Fig. 8, main body of report). For the simulations, biomass density was converted to density in terms of numbers of large (140 = mm CL) predatory capable lobsters per hectare of reef.

The projection model was modified to include an annual change in mortality from rock lobster predation as the density of 140 + mm CL animals changed over the simulation period 2012-2032. The change in density of large lobsters is described as annual increments, consistent with a circumscribed period for the annual moult. For scenarios with incipient barrens, lobster densities are converted to an annual predation mortality rate on the urchins based on the observed impact of large lobsters on *C. rodgersii* at North Bay (from the present project) and assuming linear scaling, i.e. that lobsters do not interfere with each other's feeding over the range of lobster densities considered. As previously, in all these simulations we use an annual mortality rate of urchins at the North Bay site of 0.4919 (see Tables 25, 26 in main body of report), and an initial *C. rodgersii* density of 0.1 m^{-2} , similar to that observed at North Bay at the commencement of the study. Similarly, for scenarios with extensive barrens, lobster densities are converted to an annual predation mortality rate on the urchins based on the observed impact of large lobsters on *C. rodgersii* at the Elephant Rock Research Reserve, and the initial density of urchins in all cases was as observed on the extensive barrens at Elephant Rock at the beginning of the project in 2008 (2.3 m^{-2}). All scenarios are explored through Monte Carlo simulation ($n = 5000$ runs).

For each scenario, simulations for incipient barrens (and intact seaweed beds) predict changes in urchin density over the simulation period, and the probability density of urchin barrens in 2021 and 2032. These distributions are most appropriately interpreted as the likely distribution of extent of barrens at local scales (10^2 - 10^4 m^2) across the east coast. In the case of extensive barrens, the predicted probability distribution of urchin density in 2021 and 2032 was related to the maximum target density of *C. rodgersii* ($= 0.25 \text{ m}^{-2}$) at which recovery of seaweed cover is expected to commence.

All modelling and analysis, excepting the rock lobster assessment model, was undertaken using the *R* package, version 2.14.1.