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Decadal resurvey of long-term lobster experimental sites to inform *Centrostephanus* control

Final contracted report for the Abalone Industry Reinvestment Fund (AIRF Project
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Funded by the Abalone Industry Re-investment Fund (AIRF), this report details the 2020 resurvey of long-term lobster experimental sites to inform *Centrostephanus* control (AIRF project 2019/08). The long-term sites were established in 2008 via the Fisheries Research and Development Corporation project no. 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' (Johnson et al. 2013).

The following staff/ students at the Institute for Marine & Antarctic Studies contributed to the AIRF resurvey of experimental sites in 2020: Scott Ling, John Keane, Paul Armstrong, Stuart Isles, German Soler, Lachie Tainsh, David Faloon, Aiden Dudgeon, Jennie Smith, Masayuki Tatsumi.

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HIGHLIGHTS

1. Lobster populations can be rebuilt on extensive *Centrostephanus* barrens providing lobster fishing is relaxed, however rebuilt lobster populations on extensive barrens (following complete closure to lobster fishing) did not control urchin populations within 12-yrs to the point where kelp could recover (previous modelling indicates >50-yrs for any control by lobsters on extensive barrens).
2. Lobster populations can be rebuilt within kelp beds containing incipient barrens providing lobster fishing is relaxed, and following complete closure to lobster fishing, naturally high abundances of large lobsters can decrease urchin abundance and mitigate barrens expansion.
3. To minimize the risk of barrens formation, the rebuilding of large-sized and abundant lobster populations within largely intact kelp beds should be prioritised.
4. Alternative management interventions are required to rehabilitate extensive barrens in the near-term.

NON-TECHNICAL SUMMARY

Aims: We conducted two simultaneous long-term (12-year) experiments to assess the effectiveness of rebuilding large predatory lobster populations (≥ 140 mm carapace length) to:

- 1) Recover kelp beds on extensive *Centrostephanus* barrens.
- 2) Prevent barrens formation in largely intact kelp beds with incipient *Centrostephanus* barrens.

Approach: Rebuilding of lobster populations occurred within designated research areas closed to lobster fishing, i.e. lobster-rebuilding 'impact' sites, encompassing (1) extensive barrens (Elephant Rock research area, Figure 1a,b), and (2) kelp beds with incipient barrens (North Bay research area, Figure 1a,c). Lobster-rebuilding 'impact' sites were closed to lobster fishing for 12-years following an initial accelerated rebuilding via translocation of $\sim 1,000$ large lobsters to each research area during the first year of closure to lobster fishing, representing the extreme case of possible lobster management options. For the extensive and incipient barrens experiments, monitoring of lobster, sea urchin and abalone populations, as well as barrens coverage, was performed 'Before' and 'After' lobster rebuilding for the 'Impact' and adjacent 'Control' sites open to fishing. An initial experimental set-up and intensive monitoring period of 3.5 years (from 2008 to 2011, i.e., FRDC Project #2007/045) indicated a rapid and encouraging decline in sea urchins inside at least one of the research areas (Johnson et al. 2013). This prompted continuation of the fisheries research areas for purposes of confirming early trends and to enable the effect of rebuilding lobster populations on urchin population dynamics to be established over a more ecologically meaningful timescale. Subsequently, given the ongoing nature of the fisheries research areas, an additional survey of the 'impact' and 'control' sites was achieved in 2014 and recently in 2020 (this project, funded by AIRF), enabling a 12-year assessment of the effectiveness of lobster rebuilding as a strategy for controlling *Centrostephanus*.

Results: We show that lobster population rebuilding, via closure of reefs to fishing, was achievable on both extensive and incipient urchin barrens reef. Notably, large resident lobsters (≥ 140 mm carapace length) rapidly rebuilt such that after 3.5 years they were more numerous within closed areas than the $\sim 1,000$ large lobsters initially translocated to accelerate rebuilding. Relative to control sites, the lobster-rebuilding increased urchin predation potential within the research areas, yet after 12 years, no effect of the lobster-rebuilding was detected on extensive barrens. In contrast, lobster-rebuilding within largely intact kelp beds with incipient barrens had a significant effect in reducing *Centrostephanus* abundance and cover of incipient barrens relative to control sites. For the incipient barrens experiment, the native sea urchin *Heliocidaris erythrogramma* was also significantly reduced by the lobster-rebuilding relative to control populations. Further demonstrating that lobster-rebuilding can mitigate barrens-formation, the number of incipient barrens in the lobster-rebuilding research area was largely stable through time, while the abundance of barrens approximately doubled at the control sites over 12-years. The size of individually monitored incipient barrens patches also more than doubled, on average, whereas incipient barrens within the research area remained stable.

Results show that lobster-rebuilding will be more effective in preventing overgrazing in the first instance compared to attempts to recover kelp beds once extensive urchin barrens have formed. We observed low lobster CPUE at the control sites open to fishing showing that east coast lobster stock rebuilding is not evenly distributed across the wider coast. Local areas sampled here were accessible for fishing and remain depleted, particularly for large predatory-capable lobsters, despite seven years of stock rebuilding along the wider east coast. Proactive management for local-scale resilience of kelp beds against overgrazing, by rebuilding natural size and abundance of predatory lobsters, will be far more effective than reactive attempts to restore natural predators once collapse to extensive barren grounds has occurred. For managing extensive barrens, rebuilding natural predators will be ineffective for restoring kelp beds in the near-term noting that previous modelling indicated >50 -yrs may be required for predatory lobsters to reduce urchins to the point of kelp recovery on extensive barrens (Johnson et al 2013).

Key findings: In summary, this long-term research demonstrates that “*An ounce of prevention is worth a ton of cure*” when it comes to controlling destructive overgrazing by *Centrostephanus*. That is, the longer time series obtained through this latest survey extends and consolidates the trends detected in previous research (Johnson et al. 2013). Confirming early-signals from the initial research, the rebuilding of lobsters as a control strategy for sea urchins must prioritise the rebuilding of lobster populations (e.g., aided by lobster translocations) at sites with largely intact kelp beds, which show early-signs of barrens formation, before it is too late. The results thus reconfirm the ecological role of rock lobsters as a preventative means of controlling urchin populations and the value of the overall rebuilding strategy implemented in 2013. To recover kelp beds on extensive barrens, much larger and costly management interventions will be required to ‘re-set’ productive kelp beds (e.g., urchin harvesting, culling and/ or quickliming). Providing kelp beds can be ultimately restored on extensive barrens, management of restored areas must explicitly focus on maximizing natural predators to ensure resilient and sustainable kelp bed ecosystems are maintained into the future.

BACKGROUND

Need: In response to a rapidly warming coastal ocean environment, the habitat-modifying sea urchin *Centrostephanus rodgersii* (Diadematidae) has extended its range south to eastern Tasmania where it is causing widespread destructive grazing of productive kelp beds and causing phase-shift to extensive sea urchin barrens habitat (Ling 2008, Ling et al. 2009, 2015). Since first detection at St. Helens in 1978, the population of *Centrostephanus* in eastern Tasmania reached an estimated 20 million individuals by 2017 (Ling & Keane 2018). Critically, when the abundance of *Centrostephanus* builds to more than ~2 individuals per square metre, productive kelp beds are collapsed to extensive urchin barren grounds (Ling et al. 2015). Representing an alternative stable state of collapsed kelp beds, the impoverished barren grounds persist as urchins avoid eating themselves out of house and home by switching diet to feed on encrusting/ filamentous/ microscopic algae (Ling & Johnson 2009). Based on current trajectories of unmitigated population growth and barrens expansion (from 3% to 15% cover in 15 years), *Centrostephanus* threatens to form barrens across ~50% of nearshore reefs in eastern Tasmania by as soon as ~2030 (Ling & Keane 2018). Collapse of kelp beds at this scale, would further reduce productivity of lucrative Tasmanian abalone and lobster fisheries, plus continue wholesale collapse of biodiversity associated with kelp beds.

Globally, there is a wealth of evidence that initiation of sea urchin barrens is triggered by the removal of urchin 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). In Tasmania, large southern rock lobsters (≥ 140 mm CL) are the chief predator of *Centrostephanus* (Ling et al. 2009a; Ling & Johnson 2012). Lobsters of this large predatory-capable size are abundant inside long-term marine protected areas but occur in extremely low abundance across much of eastern Tasmania where shallow reefs (<30m depth) are intensively fished by commercial and recreational sectors (Ling et al. 2009a; Ling & Johnson 2012). The capacity to rebuild lobster populations on reefs impacted by urchin grazing, and critically the potential for lobster-rebuilding as a natural control of *Centrostephanus*, is needed to support the 'East Coast Rock Lobster Rebuilding Strategy' which, as part of its explicit benefits, focusses on rebuilding the number of predatory lobsters towards increasing natural mortality of urchins.

Objectives

The "Decadal re-survey of long-term lobster experimental sites to inform *Centrostephanus* control" project, made possible by AIRF funding, enabled an important opportunity to examine long-term (12-year) lobster-rebuilding trends on extensive barrens and within kelp beds containing incipient barrens; and to critically examine the longer-term effectiveness of rebuilding predatory lobsters as a means of controlling urchin abundance to recover extensive barrens and/ or prevent barrens formation. Achieving this, the current report provides an assessment of the status and population trend of *Centrostephanus* and its grazing impact on eastern Tasmanian reefs from 2008 to 2020 at lobster-rebuilding 'Impact' (Elephant Rock and North Bay research areas) and adjacent 'Control' sites (open to lobster fishing) to test the effectiveness of rebuilding large predatory lobster populations to: 1) Recover kelp beds on extensive barrens; and 2) Prevent barrens formation in intact kelp beds with incipient barrens. The assessment involved surveying the rebuilding of lobster populations in the research area 'impact' sites and resultant ecological changes in abundance of urchins (*Centrostephanus* and the native *Heliocidaris erythrogramma*), blacklip abalone (*Haliotis rubra*), and flow-on changes in barrens coverage relative to adjacent 'control' sites.

METHODS

Effectiveness of lobster-rebuilding

Rebuilding of lobster populations occurred within designated research areas, i.e. lobster-rebuilding ‘Impact’ sites, encompassing (1) extensive *Centrostephanus* barrens (Elephant Rock, Figure 1a,b), and (2) kelp beds with incipient *Centrostephanus* barrens (North Bay, Figure 1a,c). The lobster-rebuilding research areas, i.e., impact sites, were closed to lobster fishing for a total of 12-years following an initial accelerated rebuild via translocation of ~1,000 large lobsters (≥ 140 mm carapace length) to each research area during the first year of closure. For each of the ‘Extensive Barrens’ and ‘Incipient Barrens’ experiments, two adjacent ‘fished’ control sites were selected based on similar depth, wave exposure, reef substratum type and the presence of extensive or incipient barrens for the respective experiments (Fig. 1a). The control sites for the extensive barrens lobster-rebuilding ‘impact’ at Elephant Rock were St Helens Island and Sloop Rock, while controls for the incipient barrens lobster-rebuilding ‘impact’ at North Bay were Cape Paul Lamanon and Fortescue Bay (Table 1, Figure 1).

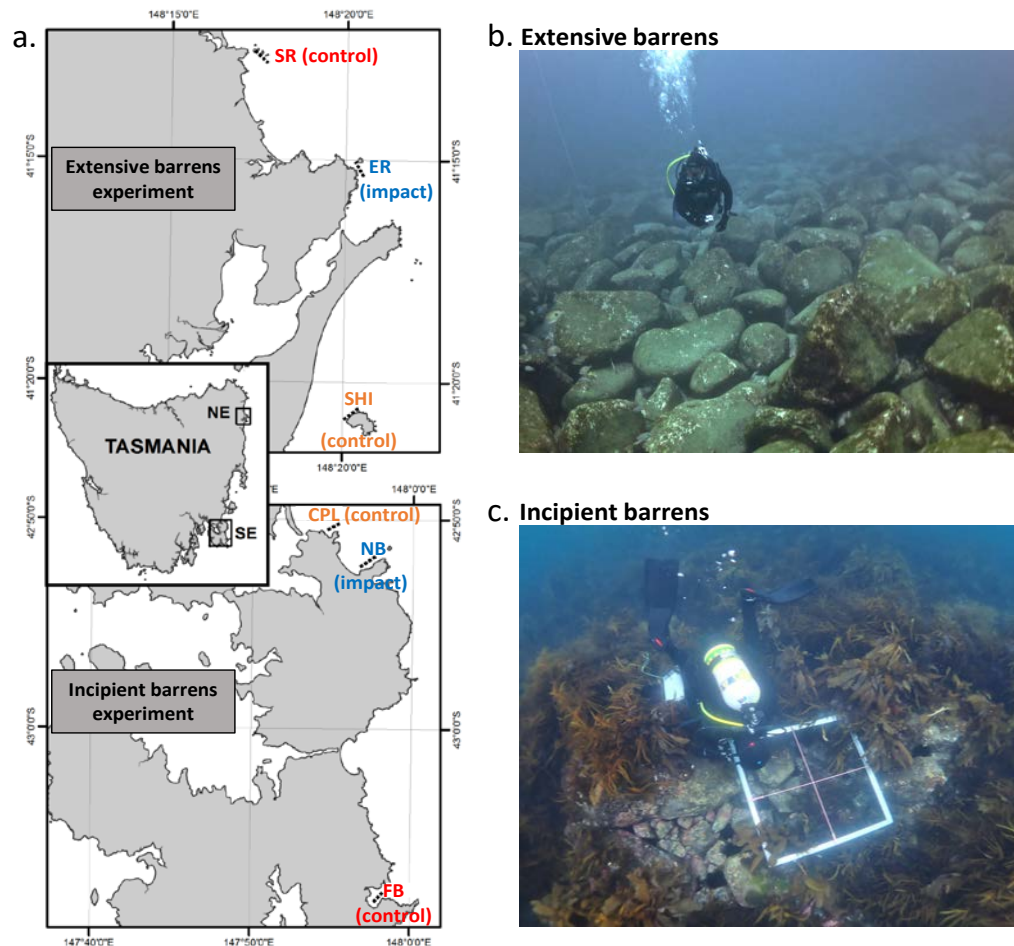


Figure 1. (a.) Map showing lobster-rebuilding ‘impact’ and adjacent ‘control’ sites (open to fishing) for examining the effectiveness of lobster-rebuilding on rehabilitating extensive barrens, i.e., the ‘Extensive Barrens Experiment’ (north east Tasmania), and the effectiveness of lobster-rebuilding on mitigating barrens-formation, i.e., the ‘Incipient Barrens Experiment’ (south east Tasmania). The impact sites at Elephant Rock (ER) and North Bay (NB) were closed to fishing in April 2008 and April 2009 respectively, while respective control sites of Sloop Rock (SR), St. Helens Island (SHI), Cape Paul Lamanon (CPL) and Fortescue Bay (FB) remained open to fishing throughout the study. Reefs where the research was undertaken are indicated by heavy dotted lines.

Impact of lobster-rebuilding on urchins, barrens and abalone

For impact and control sites in both extensive and incipient barrens experiments, monitoring of lobster, sea urchin, and abalone populations, plus barrens coverage was performed once 'Before' (early-2008) and on six occasions 'After' (mid-2008, 2009, 2010, 2011, 2014, and 2020) the lobster-rebuilding 'Impact' was brought into effect (i.e., translocation of large lobsters and concomitant closure of the research areas, see Table 1). Fixed belt transects (50m length), which were repeatedly placed at the same start and end GPS positions in each sampling period, were used to record size-graded counts of rock lobsters (*Jasus edwardsii*), sea urchins (*Centrostephanus* and *Heliocidaris erythrogramma*), abalone (*Haliotis rubra*), and planar percentage cover of barrens habitat. Counts and percentage cover was recorded by divers in 5 m long × 1m wide blocks along each side of the transects (covering 100 m² per transect), except for 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). Percentage cover of barrens was recorded to the nearest 5% within each 5 m by 1 m block, with cover <5% recorded as present.

In the final sampling year of 2020, lobster populations within impact and control sites were also assessed by calculating the average size-graded catch rate per baited trap-lift (i.e., CPUE of 'craypot' lifts), based on 40 'fishery-independent' research trap-lifts per site using 1 cousta head (*Thysites atun*) and 1 jack mackerel (*Trachurus declivis*) as bait in each trap. Note that potential declines in lobsters and abalone at control sites were not independent of fishing mortality since control sites were open to commercial and recreational harvest over the duration of the study, while both lobster-rebuilding 'impact' sites in northeast and southeast Tasmania respectively were, in addition to being no-take for lobsters, also closed to abalone fishing. Notably, while variable harvesting of *Centrostephanus* has occurred in Tasmania since 2009, this harvest has focused on the take of urchins from within kelp beds and at the shallow interface between barrens/ kelp beds in approx. 10-12m depth. The extensive barrens surveyed as part of this study occurred at a mean depth ≥18m, which remains largely unharvested and harvesting was not apparent within this depth range at the extensive barren sites. Originally shallow kelp beds were surveyed as part of the experiment in the north east (Johnson et al. 2013); however, extensive harvesting was apparent on shallow reef (8-12m depth), and these areas were therefore excluded from experimental surveys since 2014. Harvesting of sea urchins did not occur at the incipient barrens sites in southeast Tasmania which ranged between 6 and 18 m depth.

Geo-referenced surveys of incipient barrens patch size and abundance

For the incipient barrens experiment, the density and size of incipient *Centrostephanus* barrens patches were surveyed 'Before' and on 6 occasions 'After' establishment of the lobster-rebuilding 'impact' site at North Bay and at adjacent control sites using two independent and non-overlapping replicate 45-minute geo-referenced swims on SCUBA. Divers, towing a float with GPS (logging the dive track), recorded the time a barrens patch was encountered enabling the density of incipient barrens to be standardized per 100m distance swum by the diver. The geo-referenced swims were conducted parallel to the coast within a depth range of ~4-10m and the approximate position of each replicate swim were maintained across sampling periods.

Marked incipient barren patches

For the incipient barrens experiment, the dynamics of individually marked incipient barrens patches (using star-pickets & GPS) at impact and control sites were monitored in each survey period. A 1 by 1m quadrat frame, sub-divided into four 0.25m² sub-quadrats, was placed over the central peg for calibration and the area (planar dimension) of the barrens patch estimated by a diver hovering squarely above the

quadrat. At lobster-rebuilding impact site (North Bay) 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 by the end of the experiment due to overgrowth by kelp. At each control site, 10 patches were initially marked with all patches located again by final sampling in 2020.

Size-structure of Centrostephanus at experimental sites in 2020

To assess evidence for potential predator-driven change to size structure of *Centrostephanus*, in the final year of sampling the size-distribution of ~300 individual *Centrostephanus* was measured *in situ* at the impact and control sites by using digital underwater calipers to measure urchin test-diameters (shell width). Due to a lack of 'Before' estimates of size-structure of *Centrostephanus* at all experimental sites, a 'Before' vs 'After' comparison of urchin sizes at impact and control sites was not possible. Size-distributions were compared across impact and control sites for each of the extensive barrens and incipient barrens experiments in 2020 using Kolmogorov-Smirnoff tests on pre-planned comparisons between impact and control populations. Notably, the most vulnerable urchin size class to lobster predation is the newly emergent 'medium' size-class, i.e., 70-90mm test diameter (Ling et al. 2009; Ling & Johnson 2012), and therefore relative abundances of this vulnerable size-class were also explicitly compared between impact and control populations.

Table 1. Survey design for monitoring changes in sea urchin abundances and barrens cover in response to rebuilding large lobster populations on (a.) extensive barrens in north-east Tasmania; and (b.) incipient barrens in south-east Tasmania. Note that accelerated rebuilding of large lobsters was performed at each impact site during the first year of the study in 2008, i.e., 933 and 732 large lobsters were translocated to the lobster-rebuilding impact sites defined by the Elephant Rock and North Bay research areas, respectively. All sites were surveyed 'Before' (early-2008) and 'After' (mid-2008, 2009, 2010, 2011, 2014 and 2020) establishment / translocation of large lobsters at impact sites.

Reef habitat	Location	Site name	Lobster-rebuilding treatment	Closed to fishing/ large lobster translocation
a. Extensive barrens	North-east	Elephant Rock	Impact	Apr 2008
		St. Helens Island	Control 1	-
		Sloop Rock	Control 2	-
b. Incipient barrens	South-east	North Bay	Impact	Apr 2009
		Cape Paul Lamanon	Control 1	-
		Fortescue Bay	Control 2	-

Statistical analyses

Change in benthic invertebrates and barrens cover

For both extensive barrens and incipient barrens experiments, data were analyzed by examining change 'Before' (2008) vs 'After' (2020) for 'Impact' vs 'Control' sites. That is, change in *Centrostephanus* abundance, barrens cover, *H. erythrogramma* and *H. rubra* abundances for the 'After' (2020) minus 'Before' (2008) sampling periods were compare between 'Impact' and 'Control' sites using pre-planned 1-

way ANOVA contrasts (Impact vs Control 1, Impact vs Control 2, and Impact vs Controls pooled where change at controls were not significantly different from each other). Data from belt transects were aggregated at the transect level (i.e., densities of urchins and abalone, and cover, were averaged across the twenty contiguous 5 m × 1 m blocks per transect). For the incipient barrens experiment, change of incipient *Centrostephanus* barren abundance and patch-size, and change in size of individually marked incipient barrens patches, were analysed 'Before' (2008) vs 'After' (2020) for 'Impact' vs 'Control' sites. That is, change in barrens size and abundances per replicate timed-swims, or change in marked barrens sizes for the 'After' (2020) minus 'Before' (2008) sampling periods were compare between 'Impact' and 'Control' sites using pre-planned 1-way ANOVA contrasts as above. Size-distributions of *Centrostephanus*, as measured in 2020 only, were compared between impact and control sites using pre-planned Kolmogorov-Smirnoff tests; and the proportion of vulnerable emergent 'medium-sized' urchins was compared by pooling the proportions of this size-class across impact and control sites to achieve replication (n=2 for impact, and n=4 for control sites across extensive and incipient barrens experiments).

RESULTS

Effectiveness of lobster-rebuilding

Designated closure of research areas to fishing, in combination with lobster translocation, enabled rapid and ongoing population rebuilding of large lobsters on reef containing extensive barrens (Fig. 2a) and incipient barrens (Fig. 2b). The density of all sizes of lobster also increased within the research areas (Fig. 2c,d). Trap-sampling in 2020 also demonstrated effectiveness of lobster population rebuilding for extensive and incipient barrens experiments for large (Fig. 2e,f) and all lobster size-classes (Fig. 2g,h).

Resurvey of long-term experimental sites to inform sea urchin control

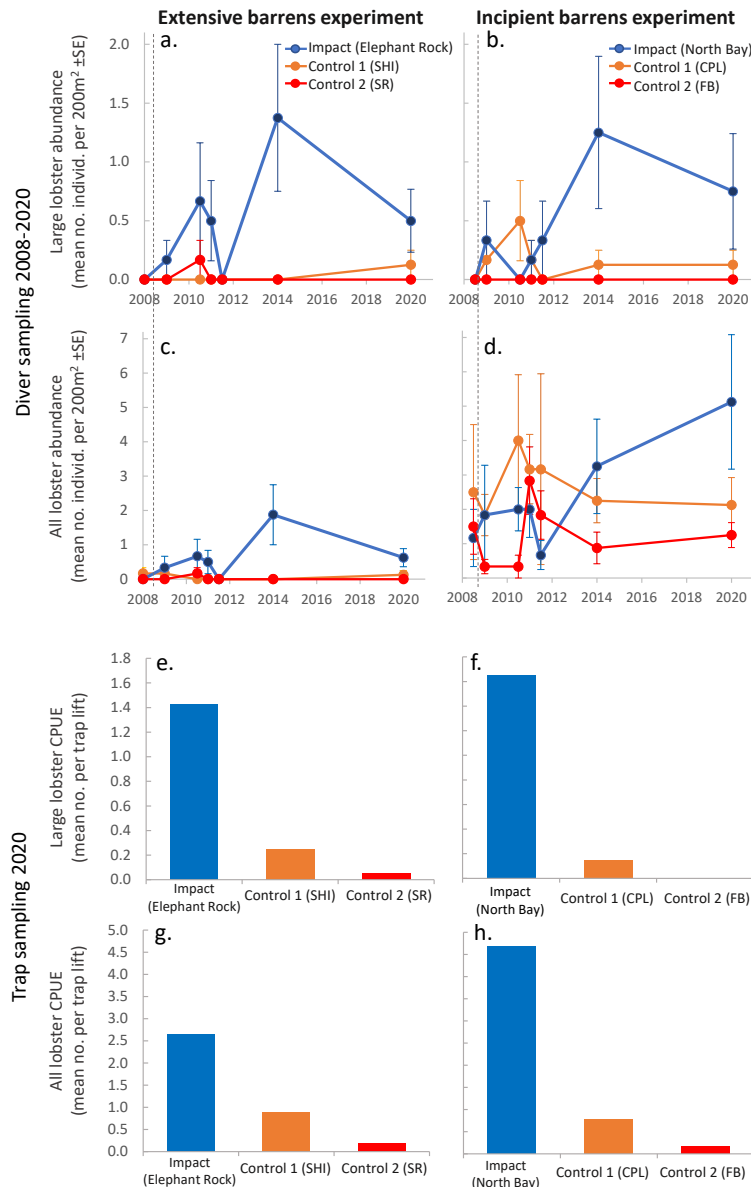


Figure 2. Rebuilding of lobster populations within research areas (i.e., impact sites) relative to control sites open to fishing for extensive barrens (left-hand column, a, c, e, g) and incipient barrens (right-hand column, b, d, f, h)) experiments from 2008 to 2020. Diver transect assessment of large lobster abundance (a,b) and all lobster size-classes (c,d) show clear population rebuilding of lobsters relative to controls, diver sampling data points represent means of six replicate transects \pm SE. Trap sampling in 2020 also showed clear evidence of large-lobster rebuilding (e,f) and of all lobster size-classes (g,h). For (a-d), dashed vertical lines indicate timing of research area closure defining the lobster-rebuilding impact sites, with data to left of this line representing the ‘Before’ period in 2008, while data to the right represent successive ‘After’ periods up until 2020. Codes for control sites are: SHI= St. Helens Island, SR=Sloop Rock; and CPL=Cape Paul Lamanon, FB=Fortescue Bay.

Impact of lobster-rebuilding on urchins, barrens and abalone

Response of *Centrostephanus* populations

For the extensive barrens experiment, *Centrostephanus* populations showed non-significant decline at the lobster-rebuilding ‘Impact’ site (i.e., Elephant Rock Research Area) relative to the control sites (Fig. 3a; for ANOVA summary see Appendix 1a). In contrast, for the incipient barrens experiment, densities of *Centrostephanus* within the lobster-rebuilding ‘Impact’ site (i.e., North Bay Research Area) showed

decline, which was significantly different to control populations of *Centrostephanus* that steadily increased from 2008 to 2020 (Fig. 3b; Appendix IIa).

Response of barrens coverage

On extensive barrens, there was no effect of lobster-rebuilding on barrens cover through time where barrens remained stable at >90% cover at 'Impact' and 'Control' sites from 2008 to 2020 (Fig. 3c; for ANOVA summary see Appendix Ib). For the incipient barrens experiment, the cover of barrens declined at the 'Impact' site from 2008 to 2020, which contrasted significantly with the control sites, where large increases in barrens cover were observed (Fig. 3d; Appendix IIb).

Response of native urchins and abalone populations

Heliocidaris erythrogramma generally occurs at low densities on extensive *Centrostephanus* barrens and there were no detectable differences in changes between the impact and control sites (Fig. 3e; for ANOVA summary see Appendix Ic). In contrast, for the incipient barrens experiment, *H. erythrogramma* were abundant in the 'Before' (2008) period but declined dramatically within the lobster-rebuilding 'Impact' site at North Bay, which was significantly different to control populations that remained stable through time (Fig. 3f; Appendix IIc). Abalone were extremely rare on extensive barrens, and there were no significant differences between change in abalone density between 'Before' and 'After' periods for 'Impact' and 'Control' sites (Fig. 3h; Appendix Id). For the incipient barrens experiment, abalone were highly variable and there were no statistical differences in change of abalone between the lobster-rebuilding impact and fished control sites through time (Fig. 3i; Appendix IId).

Dynamics of incipient patch barrens

Changes in the mean size of incipient *Centrostephanus* barrens patches, as assessed 'Before' (2008) vs 'After' (2020) were not different between impact and control sites (Fig. 4a; for ANOVA summary see Appendix IIIa). However, while the average abundance of incipient barrens patches remained stable at the impact site, this contrasted significantly with increases in abundance of incipient barrens at the control sites (Fig. 4b; Appendix IIIb). Similarly, while there was stability in the mean size of individually marked incipient barrens at the impact site, this contrasted significantly with the control sites where barrens patches on average approximately quadrupled in size from 2008 to 2020 (Fig. 4d; Appendix IIIc).

Resurvey of long-term experimental sites to inform sea urchin control

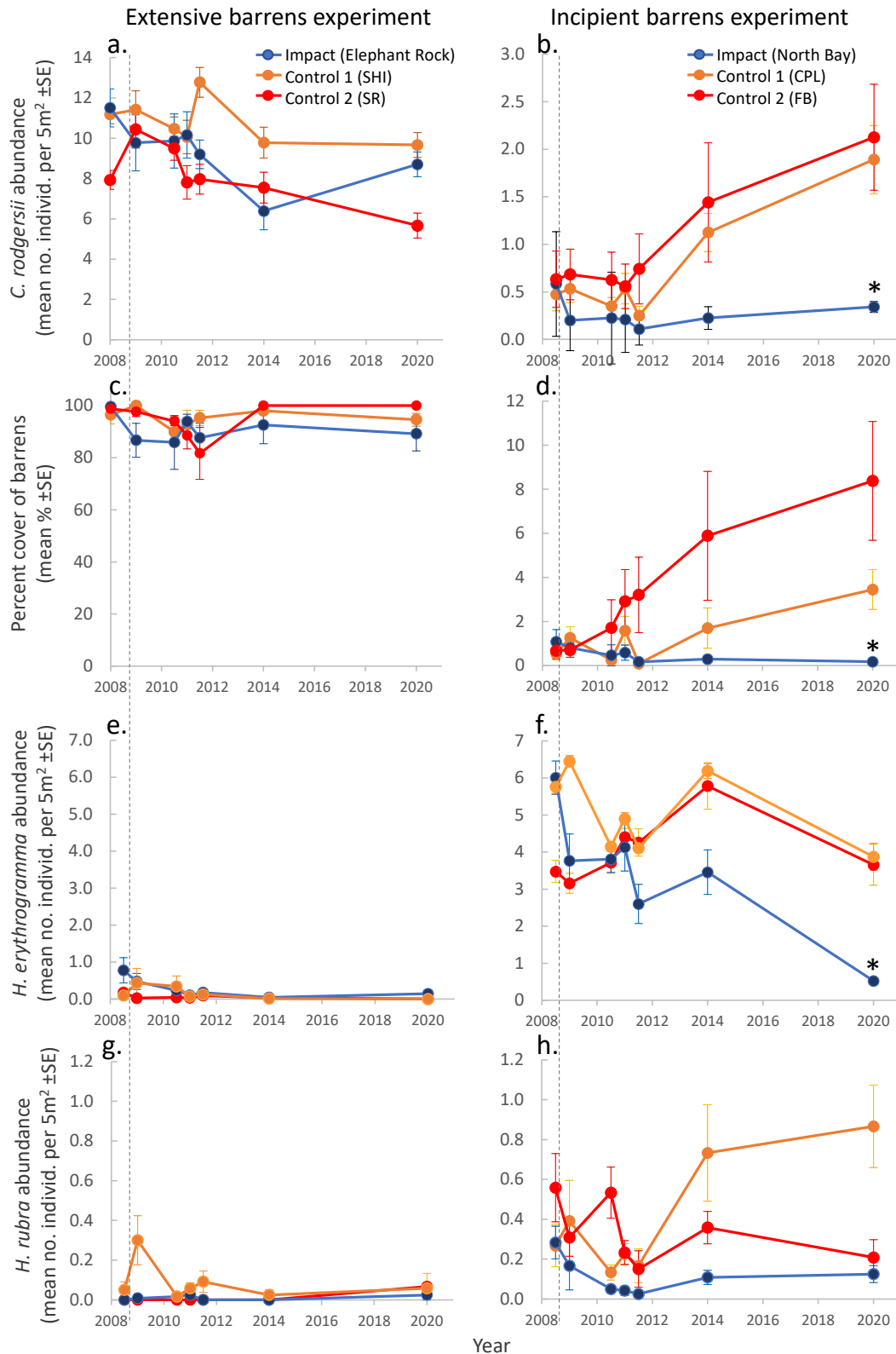


Figure 3. Trends in *Centrostephanus rodgersii* (a,b), urchin barrens (c,d), *Heliocidaris erythrogramma* (e,f) and *Haliotis rubra* (g,h) abundance at lobster-rebuilding impact and control sites for the extensive barrens experiment (left-hand column, a,c,e,g) and the incipient barrens experiment (right-hand column, b, d, f, h). Dashed vertical lines indicate declaration of research area closure, with data to left of this line representing the ‘Before’ period in 2008, while data to the right represent successive ‘After’ periods up until 2020. Data points represent means of six replicate transects ± SE. Asterisks indicates significant differences “Before” vs “After” between impact and control sites at alpha < 0.05.

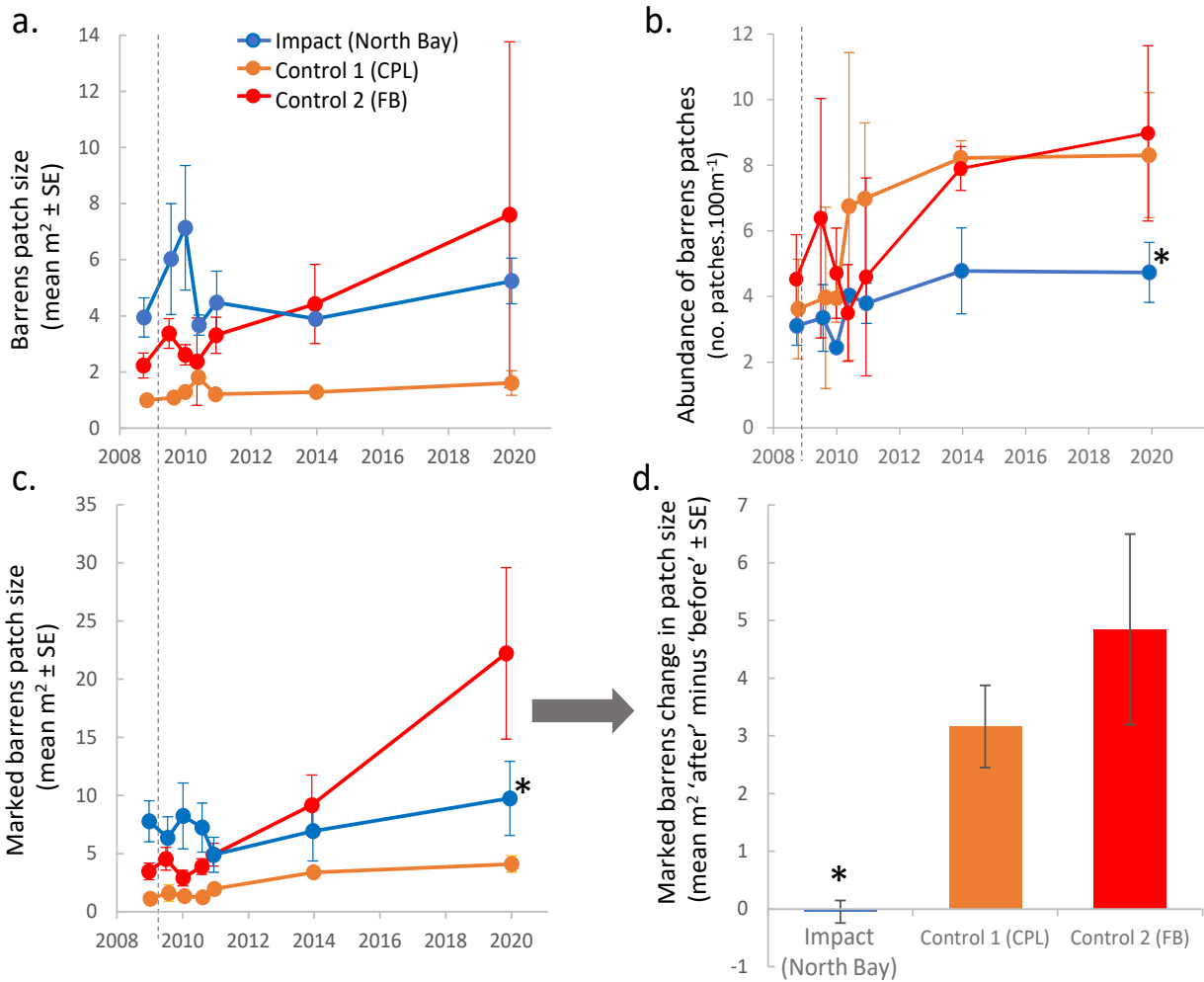


Figure 4. Dynamics of incipient *Centrostephanus rodgersii* barrens in south east Tasmania at lobster-rebuilding impact and control sites. (a) mean size of barrens patches observed during geo-referenced timed-swims, (b) abundance of barrens patches observed during geo-referenced timed-swims, (c) mean size of individually marked incipient barrens patches through time, (d) change in marked incipient barrens patches from before lobster-rebuilding (2008) to final sampling (2020) at impact and control sites. For (a & b), data points are means of two replicate geo-referenced 45-minute timed swims. For (c & d), data are means of n=10 marked patches for each control site and n=18 for the impact site. Asterisks indicates significant differences “Before” vs “After” between impact and control sites at alpha <0.05.

Size-structure of Centrostephanus at experimental sites in 2020

While analysis of change in size-distributions for impact and control sites was not possible as sizes were not measured in the before period (making it impossible to discern local effects on size-structure from lobster-rebuilding impacts), examination of *Centrostephanus* sizes at impact and control sites in 2020 revealed similar overall size distributions between impact and control sites for extensive barrens (Fig. 5a-c) and incipient barrens experiments (Fig. 5d-f; for Kolmogorov-Smirnoff test summary see Appendix IVa). Nevertheless, consistent with high vulnerability of emergent 'medium-sized' *Centrostephanus* to predation, the medium size-class was observed to be reduced at the lobster-rebuilding impact sites relative to control sites (a mean of 19% vs 34% across all impact and control populations respectively), however this difference was non-significant (Fig. 5; for ANOVA summary see Appendix IVb).

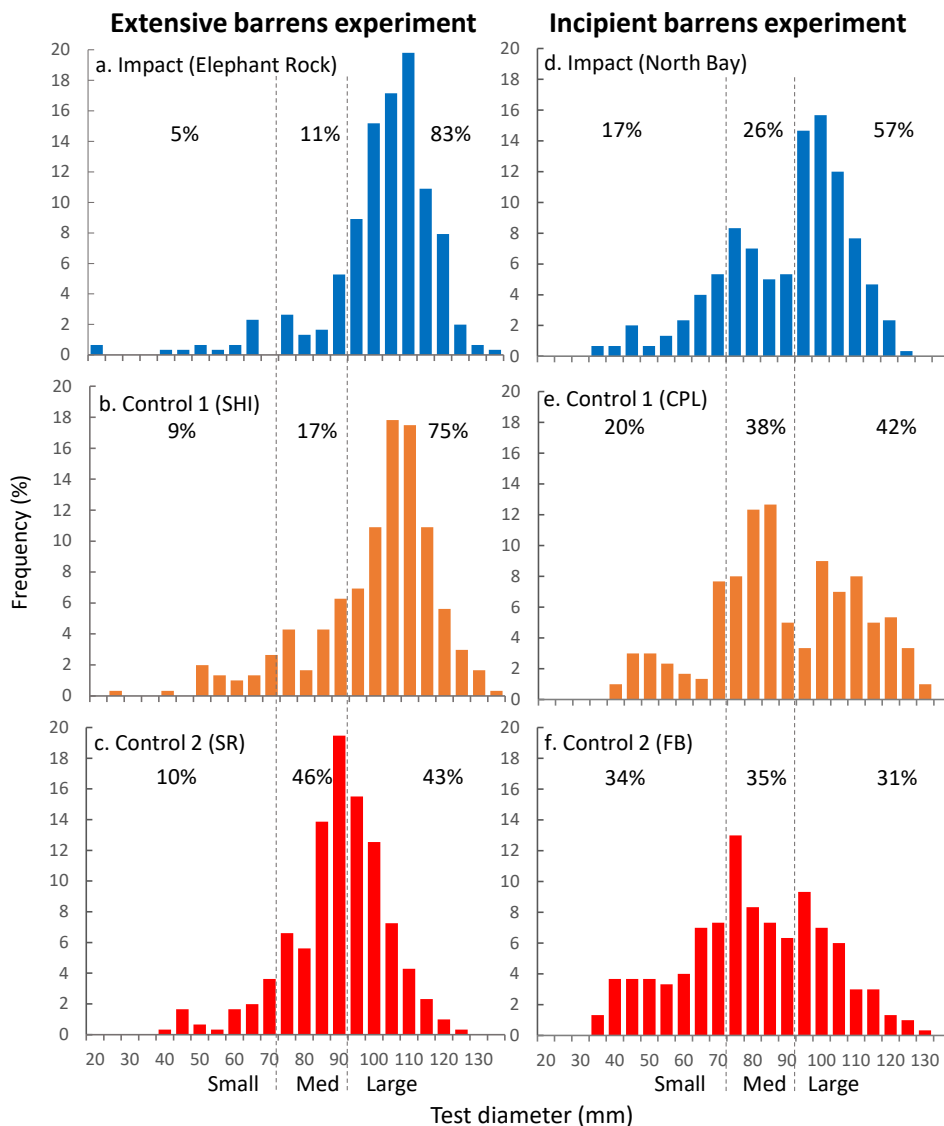


Figure 5. Size-frequency distributions of *Centrostephanus rodgersii* in 2020 at impact and control sites for the 'Extensive Barrens Experiment' (a-c, sampled October 2020) and the 'Incipient Barrens Experiment' (d-f, sampled January 2020), n=300 urchins per site. Dashed vertical lines indicate small (pre-emergent), medium (emergent) and large urchin size-classes.

DISCUSSION

Context-dependent impact of lobster-rebuilding on urchins and barrens

Results from this long-term study of the effectiveness of rebuilding predatory lobster populations as an option for controlling *Centrostephanus* has revealed that lobster-rebuilding can have significant mitigating effect on urchin abundance and risk of barrens formation. Conversely, rebuilding large lobsters to the same magnitude on extensive barrens had no detectable impact on urchin abundance or barrens coverage. That is, lobster-rebuilding on reef containing incipient barrens clearly increased the resilience of the kelp-dominated reef state but lobster-rebuilding, even over a 12-year period, had nil detectable effect in reducing urchins on extensive barrens towards the kelp recovery 'tipping-point' (i.e., <70 grams urchin m⁻², Ling et al. 2015). This result exemplifies the inherent hysteresis of *Centrostephanus* overgrazing, whereby urchin densities must be reduced to much lower densities than are required to create extensive barrens in the first place, i.e., the overgrazing 'tipping-point' of kelp bed collapse is approximately ten times higher at ~700 grams urchin m⁻², Ling et al. 2015).

Critically, while large lobsters can prey on urchins, results from the 12-years of monitoring indicate that increasing rock lobster numbers alone will not result in the recovery of extensive urchin barrens as revealed at the Elephant Rock lobster-rebuilding impact site relative to control sites. That is, over this time frame, lobsters were unable to build to a level where they could affect a significant reduction in urchin numbers on extensive barrens grounds to the kelp recovery tipping-point. Prior ecological modelling based on monitoring data from 2008-2011, predicted that ≥50-years will be required for lobster populations to impact urchin populations on extensive such that densities are reduced below the kelp recovery tipping-point (Johnson et al. 2013). In contrast, lobster-rebuilding was effective in limiting urchin populations within kelp beds with incipient barrens to minimise the risk of barrens formation in the first instance. Examination of the full time-series of data indicates this effect became apparent within the first 3-6 years of the 12-year study, indicating that a minimum of 3-years of closure to lobster fishing is required to locally rebuild ecologically meaningful size and abundance of predatory lobsters.

Extension and adoption

Results of this study demonstrate that management of the urchin problem requires proactive approaches due to the difficulty of removing sufficient urchins from extensive barren grounds once they are established. That is, given that "*an ounce of prevention is worth a ton of cure*", reefs with incipient barrens that are approaching the critical overgrazing tipping-point are logical targets for tactical lobster-rebuilding interventions. Towards 'curing' extensive barrens, the current study demonstrates that a very sizeable effort will be required to recover extensive barrens, which appears well beyond current capacity to accelerate natural predator rebuilding as an urchin control option within a short to medium timeframe. Given that control of urchins by natural predators is one of several identified approaches to urchin control, and that its effectiveness is context-dependent in space and time, a broader 'integrated pest management' approach utilizing multiple control methods will be essential for controlling *Centrostephanus*, especially for 'curing' extensive barrens. Direct human-driven mortality via intensive fishing, take-all harvesting and/or culling will be required if extensive barrens are to be recovered in short (years) or longer-term (decadal) time frames. Diver elimination of urchins has shown reef recovery within short 18-month timeframes, compared to projected multi-decadal time frames (>50 years) for recovery of extensive barrens via natural predation (Ling 2008; Johnson et al. 2013). Therefore, support and monitoring of the effects of the expanding *Centrostephanus* harvest industry in Tasmania, as well as

research to assess the comparative cost effectiveness and optimal allocation of culling and/or take-all size-class harvesting is warranted. Removal of urchins in deeper waters (18-35 m) to restore extensive barrens remains challenging, and alternate approaches, such as advanced dive techniques (decompression or rebreather) or the application of quicklime, will likely be required.

Summary of management implications

- Implementing management responses to prevent formation of extensive *Centrostephanus* barrens is far more achievable than rehabilitating extensive barrens once they form. Once extensive barrens form, reef restoration will likely be in the order of many decades (if at all) if rebuilding populations of large predatory lobsters is the only management response.
- Reducing the likelihood of incipient barrens developing into extensive barrens in the first instance is far more achievable by managing lobster populations within largely intact kelp beds (providing natural predatory control is the sole management measure). This research also indicates that rebuilding of lobster stocks has been uneven along the coast which emphasises the need for detailed information on progress in east coast lobster stock rebuilding, plus consideration of strategies to increase rebuilding in more accessible areas.
- Integrating lobster-rebuilding and urchin harvesting and/or culling within kelp beds with emerging incipient barrens will augment sources of urchin mortality and reduce the risk of urchin populations building to point at which extensive barrens are formed. Therefore, ongoing spatial targeting of urchins within kelp beds approaching the tipping-point of urchin overgrazing needs to be prioritized (e.g., lobster translocation release sites and directed dive operations).
- Despite extensive barrens supporting the rebuilding of large predatory capable lobsters, recovery of kelp beds on extensive barrens in the near-term will require additional intervention such as intensive harvesting, culling, or the use of quicklime.
- Providing urchin density can be sufficiently reduced to allow kelp bed recovery on extensive barrens, rebuilding the size and abundance of lobsters as natural predators will be important for reducing risk of transition back to barrens (if natural predatory control is the sole management measure).



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APPENDICES

Appendix I.

'Extensive barrens experiment' analysis of change *Before* (2008) vs *After* (2020) for *Controls* vs *Impact*. Data analysed is the change ('*After*' minus '*Before*') for pre-planned contrasts between impact and controls. Response variables are (a.) change in *Centrostephanus rogersii* abundance, (b.) change in urchin barrens, (c.) change in *Heliocidaris erythrogramma*, and (d.) change in abalone (*Haliotis rubra*). Refer to Fig. 3 (a,c,e,g) for trends from 2008 to 2020.

<i>a. Centrostephanus</i>	Transformation	Source	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Impact vs Control (SHI)	log(y+6.9)	treatment	1	0.10	0.10	0.06	0.81
		Residuals	10	15.35	1.54		
Impact vs Control (SR)		treatment	1	0.85	0.85	0.23	0.64
		Residuals	10	37.35	3.74		
Control (SHI) vs Control (SR)	log(y+6.9)	treatment	1	0.23	0.23	0.15	0.71
		Residuals	10	15.74	1.57		
Impact vs Control (pooled)	log(y+6.9)	treatment	1	0.01	0.01	0.01	0.94
		Residuals	16	16.84	1.05		

<i>b. Barrens</i>			Df	Sum Sq	Mean Sq	F value	Pr(>F)
Impact vs Control (SHI)	log(y+36.5)	treatment	1	5.33	5.33	1.53	0.24
		Residuals	10	34.76	3.48		
Impact vs Control (SR)	log(y+36.5)	treatment	1	4.49	4.49	1.28	0.28
		Residuals	10	35.08	3.51		
Control (SHI) vs Control (SR)		treatment	1	0.84	0.84	1.22	0.30
		Residuals	10	6.88	0.69		
Impact vs Control (pooled)	log(y+36.5)	treatment	1	6.53	6.54	2.98	0.10
		Residuals	16	35.13	2.20		

<i>c. Heliocidaris</i>			Df	Sum Sq	Mean Sq	F value	Pr(>F)
Impact vs Control (SHI)	log(y+2.4)	treatment	1	1.10	1.10	1.42	0.26
		Residuals	10	7.80	0.78		
Impact vs Control (SR)	log(y+2.4)	treatment	1	0.97	0.97	1.24	0.29
		Residuals	10	7.81	0.78		
Control (SHI) vs Control (SR)	log(y+0.6)	treatment	1	0.29	0.29	0.49	0.50
		Residuals	10	6.03	0.60		
Impact vs Control (pooled)	log(y+2.4)	treatment	1	1.38	1.38	2.82	0.11
		Residuals	16	7.85	0.49		

<i>d. Abalone</i>			Df	Sum Sq	Mean Sq	F value	Pr(>F)
Impact vs Control (SHI)	log(y+0.3)	treatment	1	0.14	0.14	0.42	0.53
		Residuals	10	3.42	0.34		
Impact vs Control (SR)	log(y+0.1)	treatment	1	0.04	0.04	0.14	0.72
		Residuals	10	2.86	0.29		
Control (SHI) vs Control (SR)	log(y+0.3)	treatment	1	0.26	0.26	0.66	0.44
		Residuals	10	3.88	0.39		
Impact vs Control (pooled)	log(y+0.3)	treatment	1	0.02	0.02	0.08	0.78
		Residuals	16	4.28	0.27		

Appendix II.

'Incipient barrens experiment' analysis of change *Before* (2008) vs *After* (2020) for *Controls* vs *Impact*. Data analysed is the change ('*After*' minus '*Before*') for pre-planned contrasts between impact and controls. Response variables are (a.) change in *Centrostephanus rodgersii* abundance, (b.) change in urchin barrens, (c.) change in *Heliocidaris erythrogramma*, and (d.) change in abalone (*Haliotis rubra*). Refer to Fig. 3 (b,d,f,h) for trends from 2008 to 2020. Significant effects at $\alpha=0.05$ are highlighted in bold.

a. <i>Centrostephanus</i>		Transformation	Source	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Impact vs Control (FB)	sqrt(y+1)	treatment	1	1.29	1.29	6.23	0.032	*
			Residuals	10	2.08	0.21		
Impact vs Control (CPL)	sqrt(y+1)	treatment	1	1.23	1.23	6.40	0.030	*
			Residuals	10	1.92	0.19		
Control (FB) vs Control (CPL)	sqrt(y+1)	treatment	1	0.00	0.00	0.00	0.96	
			Residuals	10	3.19	0.32		
Impact vs Control (pooled)	sqrt(y+1)	treatment	1	1.68	1.68	7.49	0.015	*
			Residuals	16	3.59	0.22		

b. Barrens			Df	Sum Sq	Mean Sq	F value	Pr(>F)	
Impact vs Control (FB)	(y+2.8)^{0.25}	treatment	1	1.27	1.27	10.94	0.008	**
			Residuals	10	1.16	0.12		
Impact vs Control (CPL)	sqrt(y+1)	treatment	1	0.59	0.59	7.84	0.019	*
			Residuals	10	0.76	0.08		
Control (FB) vs Control (CPL)		treatment	1	0.13	0.13	1.61	0.23	
			Residuals	10	0.79	0.08		
Impact vs Control (pooled)	(y+2.8)^{0.25}	treatment	1	1.20	1.20	12.96	0.002	**
			Residuals	16	1.48	0.09		

c. <i>Heliocidaris</i>			Df	Sum Sq	Mean Sq	F value	Pr(>F)	
Impact vs Control (FB)	(y+7.5)^{0.75}	treatment	1	26.22	26.22	25.99	<0.001	***
			Residuals	10	10.09	1.01		
Impact vs Control (CPL)	(y+7.5)^{0.75}	treatment	1	11.53	11.53	9.91	0.010	*
			Residuals	10	11.63	1.16		
Control (FB) vs Control (CPL)	log(y+6.2)	treatment	1	2.04	2.04	1.454	0.26	
			Residuals	10	14.00	1.40		
Impact vs Control (pooled)	(y+7.5)^{0.5}	treatment	1	5.79	5.79	18.08	<0.001	***
			Residuals	16	5.12	0.32		

d. Abalone			Df	Sum Sq	Mean Sq	F value	Pr(>F)	
Impact vs Control (FB)	sqrt(y+0.7)	treatment	1	0.07	0.07	1.64	0.23	
			Residuals	10	0.41	0.04		
Impact vs Control (CPL)	sqrt(y+0.7)	treatment	1	0.50	0.50	10.59	0.009	**
			Residuals	10	0.47	0.05		
Control (FB) vs Control (CPL)	sqrt(y+0.7)	treatment	1	0.93	0.93	20.05	0.001	**
			Residuals	10	0.47	0.05		
Impact vs Control (pooled)	(y+0.7) ^{0.25}	treatment	1	0.01	0.01	0.44	0.52	
			Residuals	16	0.53	0.03		

Appendix III.

Incipient barrens experiment analysis of change in (a.) barrens patch size, (b.) abundance of incipient barrens patches, and (c.) individually marked barrens *Before* (2008) vs *After* (2020) for impact vs control sites. Data analysed is the change ('*After*' minus '*Before*') for pre-planned 1-way ANOVA contrasts between impact and controls. Data for Control 1 & 2 was compared and pooled if non-significant for an overall test of the impact. Significant effects at alpha=0.05 are highlighted in bold.

a. Change in size	Transformation	Source	Df	Sum	Mean	F value	Pr(>F)	
Impact vs Control (CPL)	log(y)	treatment	1	1.05	1.05	1.669	0.33	
		Residuals	2	1.26	0.63			
Impact vs Control (FB)		treatment	1	16.67	16.67	0.51	0.55	
		Residuals	2	65.37	32.69			
Control (CPL) vs Control (FB)		treatment	1	22.69	22.69	0.69	0.49	
		Residuals	2	65.67	32.84			
Impact vs Control (pooled)		treatment	1	3.86	3.86	0.175	0.697	
		Residuals	4	88.38	22.1			

b. Change in abundance	Transformation	Source	Df	Sum	Mean	F value	Pr(>F)	
Impact vs Control (CPL)	log(y)	treatment	1	1.15	1.16	26.23	0.04	*
		Residuals	2	0.09	0.04			
Impact vs Control (FB)	log(y)	treatment	1	0.96	0.96	7.426	0.11	
		Residuals	2	0.26	0.13			
Control (CPL) vs Control (FB)	log(y)	treatment	1	0.01	0.01	0.09	0.79	
		Residuals	2	0.20	0.10			
Impact vs Control (pooled)		treatment	1	11.54	11.54	11.55	0.03	*
		Residuals	4	4.00	1.00			

c. Change in marked patches	Transformation	Source	Df	Sum	Mean	F value	Pr(>F)	
Impact vs Control (CPL)	(y+0.01)^{0.25}	treatment	1	4.07	4.07	16.77	<0.001	***
		Residuals	26	6.31	0.24			
Impact vs Control (FB)		treatment	1	3.31	3.31	14.73	<0.001	***
		Residuals	26	5.85	0.23			
Control (CPL) vs Control (FB)	(y+0.01) ^{0.25}	treatment	1	0.53	0.53	2.05	0.17	
		Residuals	18	4.63	0.26			
Impact vs Control (pooled)	(y+0.01)^{0.25}	treatment	1	3.34	3.34	13.53	<0.001	***
		Residuals	36	8.89	0.25			

Appendix IV. Summary of size-distribution analysis. (a., b.) Pre-planned Kolmogorov-Smirnoff comparisons of *Centrostephanus rodgersii* size-distributions, and (c.) 1-way ANOVA table of the proportions of vulnerable medium-sized urchins compared between impact and control sites for the extensive barrens and incipient barrens experiments as measured in 2020.

a. Extensive Barrens		
	D	p-value
Impact (ER) vs Control 1 (SHI)	0.12	0.0308
Impact (ER) vs Control 2 (SR)	0.48	<0.001
Control 1 (SHI) vs Control 2 (SR)	0.43	<0.001

b. Incipient Barrens		
	D	p-value
Impact (NB) vs Control 1 (CPL)	0.16	<0.001
Impact (NB) vs Control 2 (FB)	0.26	<0.001
Control 1 (CPL) vs Control 2 (FB)	0.19	<0.001

c. Medium-urchin proportion	Transformation	Source	Df	Sum Sq	Mean	F value	Pr(>F)
Impact vs Control	log(y)	treatment	1	0.54	0.54	2.30	0.20
		Residuals	4	0.94	0.23		
Control (Ext. Barrens) vs Control (Incip. Barrens)	log(y)	treatment	1	0.07	0.07	0.28	0.65
		Residuals	2	0.50	0.25		