

Range expansion of a habitat-modifying species leads to loss of taxonomic diversity: a new and impoverished reef state

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Abstract Global climate change is predicted to have major negative impacts on biodiversity, particularly if important habitat-modifying species undergo range shifts. The sea urchin *Centrostephanus rodgersii* (Diadematidae) has recently undergone poleward range expansion to relatively cool, macroalgal dominated rocky reefs of eastern Tasmania (southeast Australia). As in its historic environment, *C. rodgersii* in the extended range is now found in association with a simplified ‘barrens’ habitat grazed free of macroalgae. The new and important role of this habitat-modifier on reef structure and associated biodiversity was clearly demonstrated by completely removing *C. rodgersii* from incipient barrens patches at an eastern Tasmanian site and monitoring the macroalgal response relative to unmanipulated barrens patches. In barrens patches from which *C. rodgersii* was removed, there was a rapid proliferation of canopy-forming macroalgae (*Ecklonia radiata* and *Phyllospora comosa*), and within 24 months the algal community structure had converged with that of adjacent macroalgal beds where *C. rodgersii* grazing was absent. A notable scarcity of limpets on *C. rodgersii* barrens in eastern Tasmania (relative to the historic range) likely promotes rapid macroalgal recovery upon removal of the sea urchin. In the recovered macroalgal habitat, faunal composition redeveloped similar to that from adjacent

intact macroalgal beds in terms of total numbers of taxa, total individuals and Shannon diversity. In contrast, the faunal community of the barrens habitat is overwhelmingly impoverished. Of 296 individual floral/faunal taxa recorded, only 72 were present within incipient barrens, 253 were present in the recovered patches, and 221 were present within intact macroalgal beds. Grazing activity of *C. rodgersii* results in an estimated minimum net loss of approximately 150 taxa typically associated with Tasmanian macroalgal beds in this region. Such a disproportionate effect by a single range-expanding species demonstrates that climate change may lead to unexpectedly large impacts on marine biodiversity as key habitat-modifying species undergo range modification.

Keywords Biodiversity · *Centrostephanus rodgersii* · Climate change · Kelp beds · Sea urchin barrens

Introduction

Global climate change is predicted to have major negative consequences for marine biodiversity (reviewed by Rosenzweig et al. 2007). While impacts on species are widely anticipated to occur directly as a result of shifts in bioclimate envelopes (e.g. Hijmans and Graham 2006), ecosystem effects mediated by a range shift of key habitat-modifying species may result in disproportionately large impacts on marine biodiversity (e.g. Hughes 2000; Harley et al. 2006). If habitat-modifying species undergo range shift, the occurrence of ‘catastrophic shifts’ (Scheffer et al. 2001) in marine ecosystems are likely to become more common, with altered ecosystem states having major impacts on biodiversity (e.g. Elmquist et al. 2003; Folke et al. 2004; Hughes et al. 2005).

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Driven by increased poleward penetration of the warm East Australian Current (EAC, see Ridgway 2007), the sea urchin *Centrostephanus rodgersii* (Diadematidae) has recently undergone a southern range extension in temperate southeastern Australia (Edgar et al. 2004, 2005; Johnson et al. 2005; Ling et al. 2008). Extending its range from New South Wales (NSW) south to the Tasmanian coastline (Fig. 1), *C. rodgersii* is just one of many species observed to have undergone recent range extension in this region (Edgar 1997; reviewed by Poloczanska et al. 2007). However, it is the range extension of *C. rodgersii* that appears to be particularly important to the benthic community given the sea urchins' ability to eliminate macroalgal habitat and effect a catastrophic shift to an alternative sea urchin 'barrens' state (e.g. Fletcher 1987; Andrew 1991, 1993; Andrew and Underwood 1993; Hill et al. 2003). Such is the importance of this herbivore that within its historic NSW range approximately 50% of all near-shore rocky reef is urchin barrens as a result of grazing by this single sea urchin species (Andrew and O'Neill 2000).

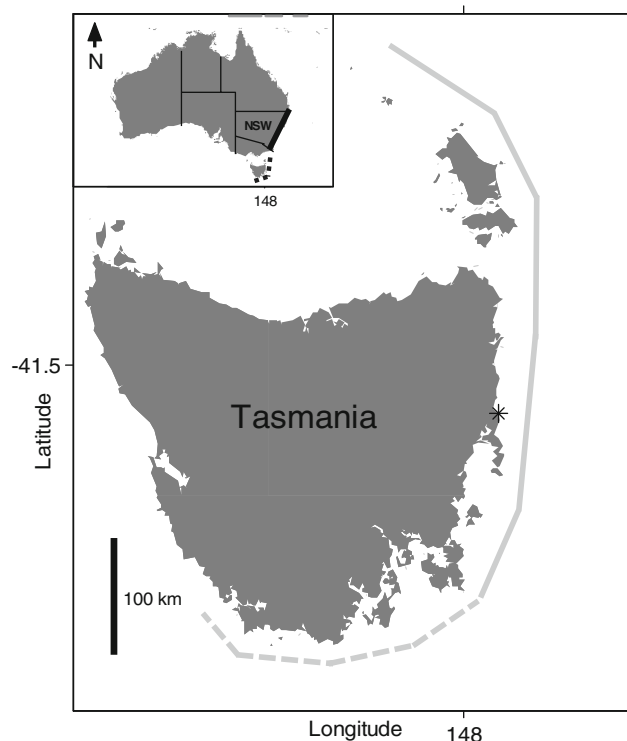


Fig. 1 Map of Tasmania showing the experimental site at Bicheno (asterisk). Inset indicates the distribution of *Centrostephanus rodgersii* in southeastern Australia, solid line indicates New South Wales range (after Andrew and Byrne 2001), broken line indicates range extension to Tasmania. On the main map of Tasmania, solid grey line indicates range over which barrens patches can be found, broken grey line indicates range where individuals, but not barrens patches, have been observed (after Johnson et al. 2005; J. Valentine, personal communication)

Since it was first detected off the Tasmanian mainland at St Helens in 1978, the abundance of *C. rodgersii* has increased, the range has moved further south and widespread barrens habitat (continuous across hundreds of metres) now occur in some locations (Johnson et al. 2005). While widespread barrens currently occur in relatively few places in eastern Tasmania, a major feature of *C. rodgersii* grazing on this coast is the occurrence of small incipient barrens patches (1–10 m in diameter) within dense and diverse macroalgal beds (Johnson et al. 2005). Given the anticipated positive effects of climate change on *C. rodgersii* dispersal and larval development within Tasmania (Ling et al. 2008; Ling, submitted), barrens habitat could potentially expand on this coastline to reflect patterns already observed in NSW (Johnson et al. 2005). Thus, *C. rodgersii* grazing in eastern Tasmania is considered to pose a major threat to the structure and functioning of the biologically diverse macroalgal-dominated rocky reefs (e.g. Edgar et al. 2004, Ling et al. 2008) and the important resources that they support (Johnson et al. 2005). The aim of this study was to explicitly examine the impact of this range-extending species on reef habitat structure and associated biodiversity within the extended range by using controlled sea urchin removals.

Materials and methods

Experimental manipulation

Manipulations testing the effect of *C. rodgersii* grazing on the structure and biodiversity of rocky reefs within the extended range were undertaken at Bicheno on the east coast of Tasmania (Fig. 1). Six discrete incipient barrens patches, ranging in size from approx. 3 to 6 m in diameter, each supporting 8–116 resident *C. rodgersii* (density 1.3–3.6 m⁻²), were randomly assigned as complete *C. rodgersii* 'removal' or 'unmanipulated' control patches; no attempt was made to standardise urchin numbers across the naturally occurring patches. As described for NSW, *C. rodgersii* in Tasmania is highly nocturnal and displays a homing behaviour so that grazing is largely manifest as halos radiating from crevices used for daytime shelter (reviewed by Andrew and Byrne 2001). Typical of the Tasmanian east coast, the incipient *C. rodgersii* barrens investigated occurred deeper than 8 m where a combination of wave action and mechanical abrasion by macroalgae appears to determine the shallow limit of the barrens (Johnson et al. 2005) and also the passage by urchins between neighbouring patches.

The temporal response of the algal community following *C. rodgersii* removal was assessed using a non-destructive spatially nested sampling design consisting

of three replicate incipient barrens patches within each treatment (removal vs. unmanipulated control) and four replicate quadrats (0.25 m²) haphazardly sampled within each patch on each sampling occasion. Manipulations commenced in spring 2003 (19 November) with a single pair of barren patches (depth 9–10 m) randomly assigned as either urchin removal or unmanipulated control. The four additional barrens patches (approx. 150 m from original site in slightly deeper water, depth 14–15 m) were discovered 4 months later. To reduce possible bias of seasonal variability on algal recruitment on algal recovery, the additional barrens patches were manipulated during the following spring (24 November 2004). These patches were monitored over the preceding 8 months prior to random assignment of the urchin removal treatment to two of the patches. Thus, there was a total of three replicate urchin removal and three replicate control patches. Treatments were maintained and patches sampled approximately every 2 months for a period of about 36 months. The response of canopy-forming algal species was of a priori interest, and comparison among treatments was planned at 6, 12 and 24 months post-removal of *C. rodgersii*.

Reflecting the spatially circumscribed nature of patches, the limited movement of adult *C. rodgersii* and the apparent low recruitment of juveniles over the duration of the study, there was minimal re-invasion of patches from which urchins had been removed (i.e. fewer than ten individuals were required to be removed during routine maintenance of the urchin removal treatment as compared to a total of 169 urchins removed during the initial application of the treatment). Other large benthic herbivores present on the study reef included the sea urchin *Heliocidaris erythrogramma*, the lucrative blacklip abalone (*Haliotis rubra*), albeit rarely, and the herbivorous fish *Odax cyanomelas*. In particular, *H. erythrogramma* occurred commonly within barrens patches occupied by *C. rodgersii*; however, this endemic species is not known to form barrens at exposed sites in eastern Tasmania (Johnson et al. 2005). In notable contrast to sea urchin barrens within the historic NSW range, large limpets (>20 mm) were found to be absent on *C. rodgersii* barrens in eastern Tasmania. Benthic herbivores other than *C. rodgersii* were not manipulated as part of this study.

Monitoring algal response

On each sampling occasion, the four replicate 0.25-m² quadrats within each experimental patch were photographed to obtain a planar two dimensional (2D) image of the benthos. Reference to subsurface buoys ensured that sampling occurred only within the original boundaries of the barrens patches. Each quadrat was dissected by a grid of 10 × 10 equidistant lines, which enabled the percentage

cover of various taxa (and bare rock) to be estimated from the photographs by enumerating the taxa present at the 100 equidistant points defined by the intersecting lines. Taxa were identified to species level where possible; otherwise, functional groups were used, such as foliose red, filamentous red, filamentous brown and filamentous green algae. It was difficult to assess the cover of non-geniculate coralline algae due to the loss of pigmentation in some plants because it was generally unknown whether bleached areas were living or dead. Thus, for the purpose of this study, encrusting coralline algae included both bleached and pigmented components.

Habitat and faunal structure of ‘recovered’ macroalgal beds—destructive sampling

To assess the impact of *C. rodgersii* barrens on reef structure and associated fauna, all experimental patches were sampled destructively at the end of the experiment after the macroalgal canopy had re-established. On termination of the experiment in November 2006, the original urchin removal patch had experienced 36 months of recovery, whereas the additional manipulated patches had experienced 24 months post-removal of *C. rodgersii*. Thus, the destructive sampling design at the conclusion of the experiment captured both spatially and temporally variable components across patches nested within the urchin removal treatment. To enable a comparison of habitat and faunal structure between the urchin removal treatment and adjacent intact macroalgal beds of similar topography (boulder reef) and depth (9–15 m) but unaffected by *C. rodgersii* (i.e. where grazing had not been observed for at least 7 years), the nested experimental design was extended to include three adjacent ‘intact macroalgal bed’ patches. Selected by randomised fin kicks and compass directions, these patches were destructively sampled upon termination of the urchin removal experiment. Hence, the extended design included three levels of ‘treatment’ (unmanipulated barrens, sea urchin removal and unmanipulated intact macroalgal beds), three levels of ‘patch’ nested within ‘treatment’ and four quadrats within each ‘patch’, providing an estimate of error.

Because the routine photoquadrat monitoring provided only a 2D representation of the substratum, patterns in the total habitat structure (i.e. inclusive of macroalgal canopy, understory and basal substratum components) were examined in detail at the final assessment by sequentially photographing and then destructively sampling each stratum from top to bottom. The abundance and total length of individual canopy-forming macroalgae within each quadrat was also measured, and the total algal biomass of macroalgal canopy and understory strata was calculated from dry weights obtained by drying algal samples at 70°C for 48 h.

The cover of encrusting and structural invertebrates was estimated from photographs once the overlying algae had been removed. Associated benthic fauna were sampled from each quadrat by sealing underwater all excised macroalgal habitat and structural invertebrates in plastic bags, while the remaining benthic fauna were extracted from the substratum using a venturi suction sampler connected to 1-mm mesh bags (each quadrat was systematically suctioned for 3 min at a flow rate of 180 L min⁻¹). Fauna contained within algal habitat and/or benthic suction samples were extracted by thoroughly agitating samples in seawater before passing them through a 1-mm sieve. Faunal samples were then sorted and enumerated at the species level where possible. Where species could not be identified, individual specimens were assigned to taxonomic groups based on the finest taxonomic resolution possible.

Analysis

Univariate analyses The effects of *C. rodgersii* removal were analysed with a temporal series of one-way Model III nested analysis of variance (ANOVA) of factors ‘treatment’ (fixed effect) and ‘patch nested within treatment’ (random effect) at the pre-planned (a priori) times of interest of 0, 6, 12 and 24 months post-sea urchin removal. Data collected by destructive sampling at the conclusion of the experiment were analysed with the same nested ANOVA structure except for the addition of a third level of treatment, the ‘intact macroalgal bed’. All univariate statistical analyses were undertaken using SAS® (v. 6.12; SAS Institute, Cary NC), and data were checked for conformity to assumptions of homoscedasticity and normality. Where data were heteroscedastic, the transformation to stabilise variances was determined by the relationship between group standard deviations and means (Draper and Smith 1981). The appropriate transformation for each variable is expressed in terms of the untransformed variable *Y*. Where lower levels of nesting revealed non-significant results ($P > 0.25$, Winer et al. 1991), data at higher levels were pooled a posteriori to provide a more powerful test of lower order terms. Multiple range tests were conducted using the Ryan–Einot–Gabriel–Welsch (REGW) procedure. Size–frequency distributions of canopy-forming macroalgae, as assessed at the termination of the experiment, were compared between ‘urchin removal’ and ‘intact macroalgal beds’ using the Kolmogorov–Smirnov test.

Multivariate analyses Comparisons of communities were visualised using nMDS ordination, and the species contributing most to dissimilarity were revealed using the SIMPER software routine (PRIMER 5, ver. 5.2.9). Taxonomic diversity of each sample was calculated using the Shannon Diversity Index ($H' = -\sum_{i=1}^s p_i \log_e p_i$), where

p_i is the proportion of the community that belongs to the i th taxa. The significance of differences in assemblage structure was estimated using permutational multivariate analysis of variance (PERMANOVA; Anderson 2001, 2005; McArdle and Anderson 2001). All PERMANOVA tests were based on 9999 permutations of Bray–Curtis dissimilarity matrices generated from non-standardised fourth-root transformed data. Significant terms were investigated with a posteriori pairwise comparisons using the PERMANOVA t statistic based on distances of the correct permutable units. Corrections for type-I error rate were made using the Dunn–Sidak method.

Results

Recovery of macroalgal habitat

In all incipient barrens patches from which *C. rodgersii* was removed, a structurally complex assemblage of foliose algae developed that was ultimately dominated by the canopy-forming species *Ecklonia radiata* and *Phyllospora comosa* (Fig. 2). Filamentous algae and macroalgal sporophytes (height <20 mm) recruited to available space and began to overgrow the substratum within 1 month of the sea urchins being removed. Effects of *C. rodgersii* removal on the areal cover of canopy-forming macroalgae were statistically detectable at all pre-planned times (approx. 6, 12 and 24 months) after removal of the sea urchin (Table 1). The pattern of re-colonisation for *E. radiata* (by cover) occurred consistently across *C. rodgersii* removal patches, while significant between-patch variability was detected for *P. comosa* and total canopy cover (Table 1).

Assessment of benthic habitat structure by destructive sampling revealed that removal of *C. rodgersii* resulted in the replacement of the open barrens substratum with a structurally heterogeneous benthic habitat composed of a macroalgal canopy and accompanying understorey (Fig. 3). Nested ANOVA revealed significant differences in both canopy and understorey components between treatment groups, with pairwise comparisons revealing differences between urchin removal and unmanipulated barrens, but not between urchin removal and intact macroalgal beds (Fig. 3). Patterns in the cover of the basal substratum layer varied between treatment groups (Fig. 3), showing consistency across treatments in the cover of encrusting corallines but significantly higher cover of bare rock and filamentous algae on the unmanipulated barrens in comparison to the urchin removal and intact macroalgal treatments.

Canopy-forming macroalgae occurred at a higher abundance within the urchin removal treatment than on the barrens habitat or intact macroalgal beds; whereas in barrens patches there were low numbers of minute (length <50 mm)

Fig. 2 Response of incipient barren patches to the removal of *Centrostephanus rodgersii* showing percentage cover (mean $\pm$ SE) by canopy-forming macroalgae (**a**, **c**, **e**) and by the basal substratum layer (**b**, **d**, **f**). Urchin removal treatment (filled circles, $n = 3$) and unmanipulated ‘control’ patches (open circles, $n = 3$) are shown. Dashed vertical line in each column shows the timing of urchin removal; negative values on the X-axis represent months prior to removals, and vertical arrows indicate pre-planned times of interest for analysis of the urchin removal effect. Note: $n = 2$ for months prior to removals

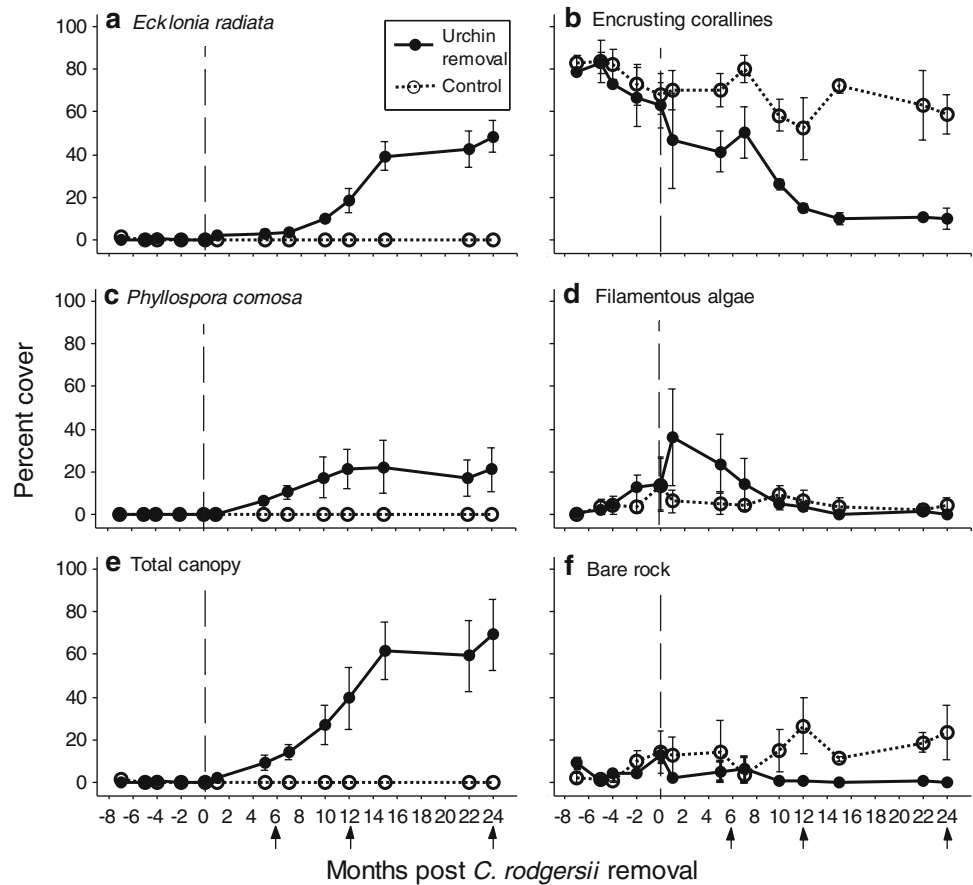


Table 1 Results of nested Model III ANOVA testing of the effect of *Centrostephanus rodgersii* removal on macroalgal cover at pre-planned months post-removal

Response variable (transformation 6, 12, 24 months)	Source	Orthogonal pre-planned comparisons		
		$T = \text{approx. 6 months}^a$	$T = 12 \text{ months}$	$T = 24 \text{ months}$
<i>Ecklonia radiata</i> [$\log(Y + 0.0001)$, $Y^{0.28}$, $Y^{0.24}$]	Treatment	$F_{1,22} = 53.15$ $P < 0.0001^*$	$F_{1,4} = 33.97$ $P = 0.0043^*$	$F_{1,22} = 80.22$ $P < 0.0001^*$
	Patch (treatment)	$F_{4,18} = 0.54$ $P = 0.7070$	$F_{4,18} = 2.28$ $P = 0.1006$	$F_{4,18} = 0.51$ $P = 0.7317$
<i>Phyllospora comosa</i> [$\log(Y + 0.0001)$, $Y^{0.45}$, $\log(Y + 0.0001)$]	Treatment	$F_{1,4} = 585.85$ $P < 0.0001^*$	$F = 7.87$ $P = 0.0485^*$	$F_{1,22} = 33.34$ $P < 0.0001^*$
	Patch (treatment)	$F_{4,18} = 5.19$ $P = 0.0059^*$	$F_{4,18} = 10.07$ $P = 0.0002^*$	$F_{4,18} = 0.68$ $P = 0.6133$
Total canopy macroalgae [, $Y^{0.67}$,]	Treatment	$F_{1,4} = 14.08$ $P = 0.0199^*$	$F_{1,4} = 10.07$ $P = 0.0338^*$	$F_{1,4} = 17.21$ $P = 0.0143^*$
	Patch (treatment)	$F_{4,18} = 5.89$ $P = 0.0033^*$	$F_{4,18} = 9.45$ $P = 0.0003^*$	$F_{4,18} = 15.35$ $P < 0.0001^*$

* Significant P values

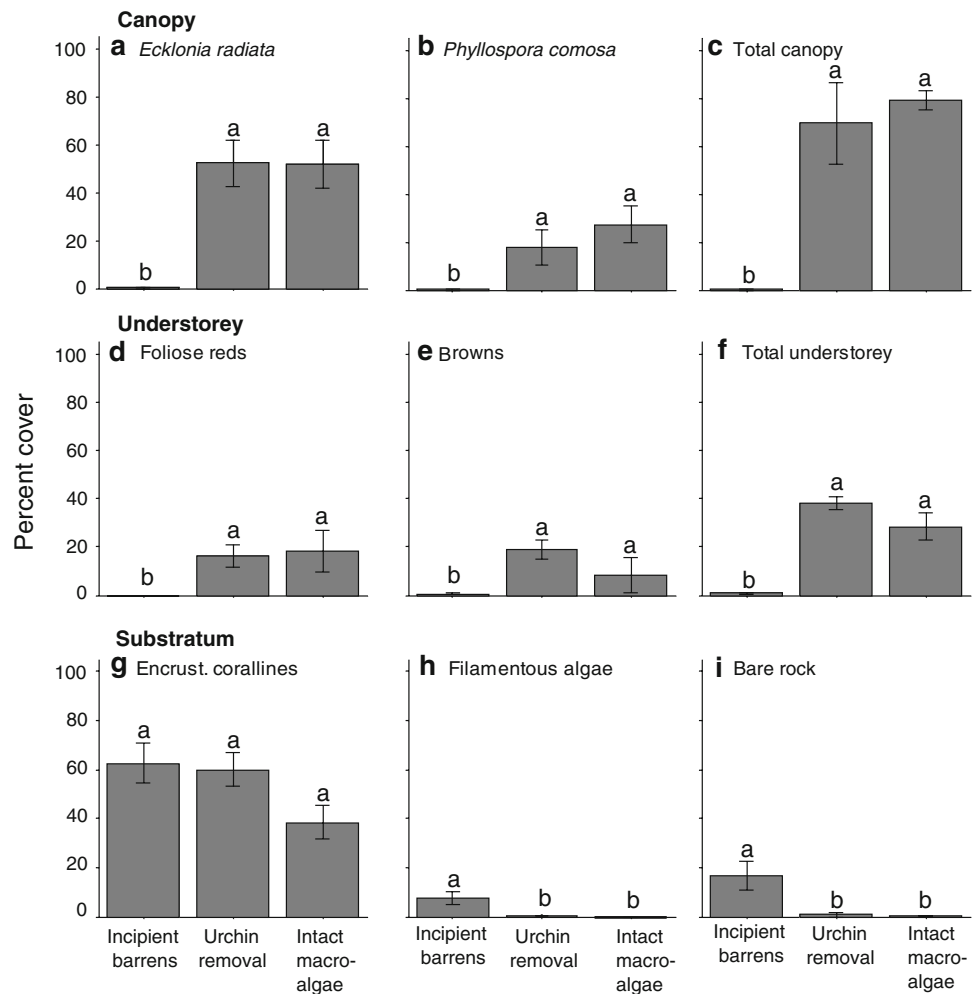
Note: prior to applying the *C. rodgersii* removal treatment, no differences in the cover of barrens substratum components were detected between incipient patches (encrusting corallines, $F_{1,4} = 0.1200$, $P = 0.7418$; bare rock [trans. = $Y^{0.22}$], $F_{1,4} = 0.1247$, $P = 0.8030$; filamentous algae, $F_{1,4} = 0.01$, $P = 0.9460$)

^a The approx. 6-month sample was only attainable at 7 months post manipulation

individuals, macroalgae in the urchin removal patches were dominated by small individuals tailing to large-sized classes, and in the intact macroalgal habitat, there were fewer but

relatively more larger individuals (Fig. 4). A comparison of macroalgal size–frequency distribution between urchin removal and intact macroalgal beds revealed significantly

Fig. 3 Percentage cover (mean $\pm$ SE) of unmanipulated barrens (incipient barrens), barrens with urchin removal and intact macroalgal beds for canopy (a, b, c), understorey (d, e, f) and substratum (g, h, i) components of benthic habitat structure. Bars with identical letters indicate Ryan–Einot–Gabriel–Welsch (REGW) groupings of treatments for each response variable. $\alpha = 0.05$



different size distributions (Kolmogorov–Smirnov, $P < 0.0001$). For urchin removal patches, total algal biomass m^{-2} (canopy plus understorey species, excluding encrusting corallines) was not statistically different to that of intact macroalgal beds, but it was much greater than for the barrens habitat [total algal biomass for urchin removal patches = 845.68 ± 451.81 (SE) g m^{-2} , for intact macroalgal beds = 844.22 ± 127.45 g m^{-2} , for unmanipulated barrens = 0.20 ± 0.04 g m^{-2} , nested Model III ANOVA; trans. = $(\log(Y + 0.0001))$, treatment, $F_{(2,6)} = 84.07$, $P < 0.0001$; patch (treatment), $F_{(6,27)} = 1.98$, $P = 0.1035$]. Other benthic structural components, namely sessile encrusting and erect invertebrates, contributed to the physical structure of recovered macroalgal and intact macroalgal habitats, but they contributed little to the barrens habitat (Fig. 5).

Effect of barrens on taxonomic diversity

Recovery of canopy-forming macroalgae within *C. rodgersii* removal patches (Fig. 6a) resulted in an associated

re-colonisation of this habitat by a benthic faunal assemblage vastly different to that of the barrens, but not different to that observed in intact macroalgal beds (Fig. 6b; see Table 2 for PERMANOVA summaries). The removal of *C. rodgersii* clearly increased taxonomic richness, total abundance and Shannon diversity of benthic fauna (independent of structure-forming invertebrates); however, there was little difference in the composition of benthic faunal communities between urchin removal and intact macroalgal bed treatments (Fig. 7). The taxa contributing most to dissimilarity in faunal abundance between macroalgal bed and barrens habitats were Amphipoda (38.2%); Polychaeta (8.76%); Isopoda (6.91%); Gastropoda (6.16%); Tanaidacea (3.95%); Hirudinea (3.59%); Bivalvia (3.47%); Echinodermata (3.06%); Mysidaceae (2.66%); Serpulidae (2.65%); Decapoda (2.05%); Brachiopoda (1.80%); Terebellidae (1.68%); Oligochaeta (1.51%). Graphical examination of whole benthic communities (flora and fauna), based on the presence/absence of all described taxa (including structure-forming invertebrates) revealed overwhelmingly different benthic communities in the presence of *C. rodgersii* grazing

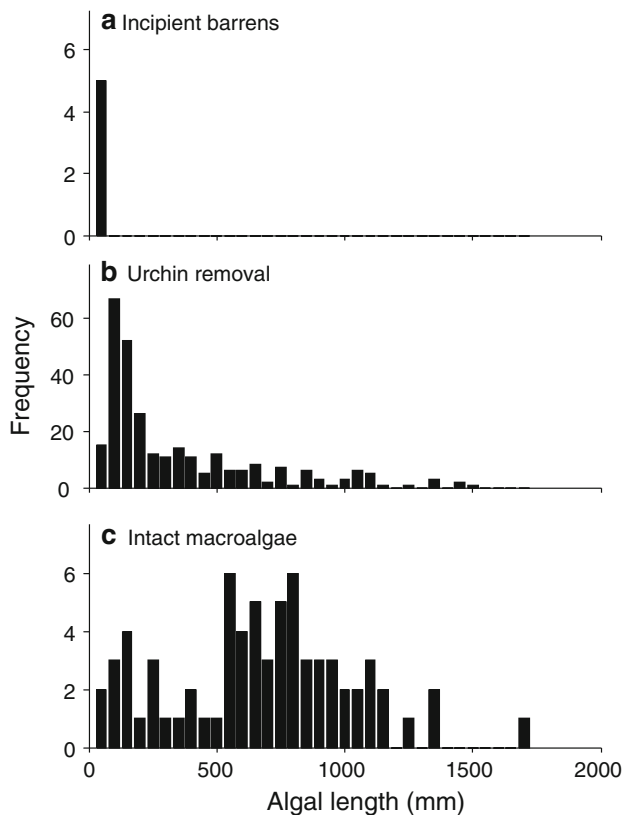


Fig. 4 Size–frequency distributions of canopy-forming macroalgal species (*Ecklonia radiata* and *Phyllospora comosa*) at termination of the experiment in incipient barrens patches (**a**; $n = 5$), *Centrostephanus rodgersii* removal patches (**b**; $n = 287$), intact macroalgal beds (**c**; $n = 70$). Note different scales for the Y-axis

(Fig. 6c; see Table 2 for PERMANOVA summary). Of the 296 individual floral and faunal taxa recorded, only 72 were present within incipient barrens, 253 were present in the urchin removal patches and 221 were recorded within intact macroalgal beds (see Appendix 1 of the Electronic Supplementary Material). Thus, the formation of barrens by *C. rodgersii* is estimated to result in a minimum localised loss of approximately 150 taxa from with eastern Tasmanian macroalgal beds.

Discussion

Effect of sea urchin range expansion on reef habitat

Climate change is leading to a re-distribution of marine species and altering ecosystem dynamics (e.g. Harley et al. 2006; Rosenzweig et al. 2007). Within the newly extended eastern Tasmanian range of *Centrostephanus rodgersii*, this sea urchin now deconstructs the macroalgal habitat and maintains a simplistic and homogeneous benthic habitat typical of barrens described from its endemic range (e.g.

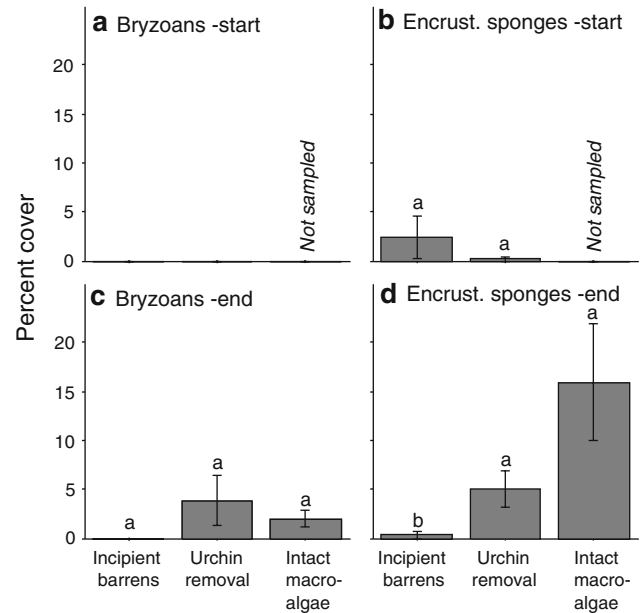


Fig. 5 Effect of *Centrostephanus rodgersii* on the cover of habitat-forming bryzoans (**a**, **c**) and encrusting sponges (**b**, **d**) for incipient barrens, urchin removal and intact macroalgal patches. Start of the experiment prior to sea urchin removal, bryzoans absent; sponge cover (nested Model III ANOVA; trans. = $Y^{0.69}$, 'treatment', $F_{(1,5)} = 1.09$, $P = 0.3548$; 'patch (treatment)', $F_{(4,18)} = 24.09$, $P < 0.0001$). End of experiment, bryzoans (trans. = $\log(Y + 0.0001)$, 'treatment', $F_{(2,6)} = 3.23$, $P = 0.1116$; 'patch (treatment)', $F_{(6,27)} = 6.02$, $P = 0.0004$); sponges (nested Model III ANOVA; trans. = $\log(Y + 0.0001)$, 'treatment', $F_{(2,33)} = 11.05$, $P = 0.0002$; 'patch (treatment)', $F_{(6,27)} = 0.85$, $P = 0.5423$). Bars with identical letters indicate REGW groupings of treatments within each sampling period, $\alpha = 0.05$

Andrew and Byrne 2001) and broadly typical of sea urchin 'coralline' barrens throughout the world (reviewed by Pinnegar et al. 2000). The removal of *C. rodgersii* from barrens patches in eastern Tasmania resulted in a rapid replacement of the flat structurally homogeneous substratum of the initial urchin barrens with a structurally heterogeneous 3D benthic habitat complete with macroalgal canopy, diverse algal understory and structural basal invertebrates. Indeed, the dramatic and consistent pattern of algal recovery across all urchin removal patches indicated that the timing of urchin removals from barrens patches (September 2003 as opposed to September 2004) was unimportant. While patterns in canopy cover and algal biomass clearly converged on that observed for intact macroalgal beds, recovering patches were still biased towards smaller and yet more abundant plants, indicating that effects of previous grazing on community succession were still detectable >24 months after removal of the sea urchin. Most importantly, however, return to the macroalgal-dominated ecosystem state (macroalgal canopy cover >50%) was achieved rapidly (within approx. 15 months) after urchin removal (for comparison of algal

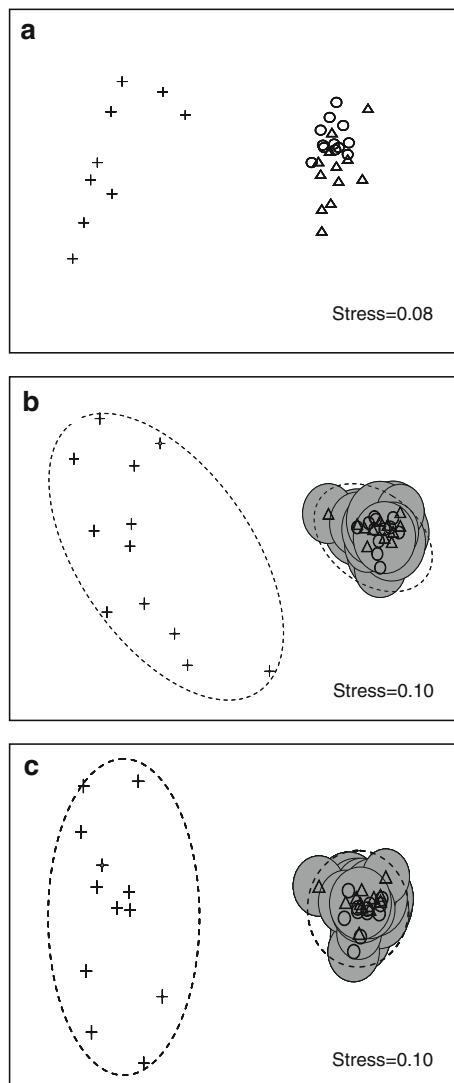


Fig. 6 Ordinations (nMDS) showing the effect of *Centrostephanus rodgersii* on benthic algal assemblages (a), benthic faunal assemblages (b) and entire benthic assemblages (flora plus fauna) (c) at termination of experiment. Symbols represent individual quadrats nested within replicate barrens patches (crosses), urchin removal patches (triangles) and intact macroalgal beds (circles). Ordinations are based on Bray–Curtis similarity matrices obtained from fourth-root transformed percentage cover data for algae, from abundance data for faunal assemblages and from the presence/absence data for whole benthic assemblages. Faunal and whole assemblage ordinations are overlaid with a bubbleplot (grey) representing macroalgal canopy cover (largest bubbles represent 100% macroalgal canopy cover); dashed ellipses encompass the space occupied by the alternative assemblages of barrens and macroalgal ecosystem states

recovery in other systems, see Duggins 1980; Himmelman et al. 1983; Keats et al. 1990; Johnson and Mann 1993; Leinass and Christie 1996).

In contrast to the rapid and consistent pattern of macroalgal recovery observed in the current study, experimental removals of *C. rodgersii* in NSW have resulted in a less predictable transition to assemblages of

foliose algae and often slower or less complete recovery of canopy-forming species, a result consistently attributed to patterns in propagule supply (Fletcher 1987; Andrew 1991, 1993, 1998; Hill et al. 2003). A notable difference in the barrens assemblage across eastern Tasmania is the general lack of limpet ‘mesograzers’ that occur in high abundances on *C. rodgersii* barrens in NSW and which are capable of delaying macroalgal recovery following *C. rodgersii* removal (Fletcher 1987). Thus, the functional redundancy of the grazer group on barrens throughout eastern Tasmania would likely be enhanced if limpets were to establish at high densities. While regional differences in macroalgal growth rates and grazer interactions are likely, experiments on NSW reefs have in general been undertaken on, or near, widespread barrens habitat. Conversely, I manipulated small incipient barrens patches (scale of metres) surrounded by reef dominated by dense macroalgal habitat, which likely provided a saturating supply of algal propagules at this scale. Therefore, direct scaling-up of these results is likely to lead to over-expectations of macroalgal recovery rates for larger scale barrens (10^2 – 10^3 m) where algal propagule supply may become limiting (reviewed by Dayton 1985). Unlike the dynamic recovery of macroalgal habitat following *C. rodgersii* removal, un-manipulated barrens patches displayed a high stability over the 3-year duration of the study. In combination with in situ observations at several sites over >8 years (author, personal observations), *C. rodgersii* barrens in eastern Tasmania appear to constitute a truly alternative and persistent state, as also reported for conspecific barrens in NSW (reviewed by Andrew and Byrne 2001).

Effect of sea urchin grazing on taxonomic diversity within the expanded range

Examination of the benthic fauna in barrens patches confirmed the major effects of *C. rodgersii* grazing that extend to the entire benthic community. While *C. rodgersii* is known to be omnivorous, consuming encrusting and structure-forming invertebrates as well as algae (A. Pile, personal communication; author, personal observation), the greatest faunal impacts by *C. rodgersii* appear to be those caused by the loss of macroalgal habitat due to intense herbivory. Indeed, the barrens state is characterised by an impoverished benthic community, with approximately 150 taxa fewer than adjacent macroalgal beds (also see Himmelman et al. 1983; Bodkin 1988; Graham 2004). When the potential number of species that are either directly consumed by sea urchins or simply associated with the macroalgal habitat (e.g. Graham 2004) are considered, the total number of taxa potentially impacted by *C. rodgersii* grazing in eastern Tasmania may increase dramatically. As an example, intensive grazing by *C. rodgersii* eliminates

Table 2 PERMANOVA testing the effect of *Centrostephanus rodgersii* on algal, faunal and entire benthic assemblages at the conclusion of the experiment

PERMANOVA		Algal assemblage		Faunal assemblage		Whole benthic assemblage	
Source	df	F	P (perm)	F	P (perm)	F	P (perm)
Treatment	2	15.87	0.0129*	6.41	0.0096*	7.33	0.0076*
Patch (treatment)	6	2.76	0.0071*	1.69	0.0130*	1.70	0.0186*
Residual	27						
Total	35						
Tests among 'treatment'							
Groups	Unique perm.	t	P (MC)	t	P (MC)	t	P (MC)
Barrens vs. removal	10	4.46	0.0015*	2.80	0.0097*	3.02	0.0055*
Barrens vs. intact	10	5.34	0.0009*	2.71	0.0098*	2.93	0.0081*
Removal vs. intact	10	1.02	0.3996	1.12	0.3170	1.13	0.3207
Average Bray–Curtis percentage dissimilarities within and between treatments: macroalgal, faunal and whole assemblages							
	Barrens	Removal	Intact				
Barrens	21.88; 46.98; 43.90						
Removal	64.85; 69.48; 67.95	25.38; 25.00; 23.72					
Intact	65.31; 68.92; 68.44	21.06; 27.05; 26.32	18.21; 27.21; 26.69				

*Significant values. Pair-wise a posteriori comparisons were made after adjusting the type I error rate, $\alpha = 0.017$

Results are given for one-way mixed model nested PERMANOVA, tests among treatments and dissimilarities within and between treatments. For the pair-wise tests, Monte Carlo (MC) asymptotic *P* values were used given the small number of unique permutations (after Anderson 2005)

almost all algal species, of which there are an estimated 373 species in Tasmanian coastal waters alone (reviewed by Sanderson 1997). Thus, one may expect that the rate of species accumulation with increasing sampling area (the species–area curve) is likely to be much greater for heterogeneous macroalgal habitat relative to homogenous barrens where a consistent community containing relatively few species is observed.

In a similar study by Vance (1979) in California, overgrazing of the macroalgal habitat by the congeneric *Centrostephanus coronatus* also dramatically decreased local taxonomic diversity. Interestingly, the author considered that a patchwork of grazed patches among macroalgal habitat may have the net effect of increasing the diversity of the community as a whole because localised barrens patches may provide a habitat for grazer resistant taxa that were otherwise rarely observed. While there were few taxa (less than six) that were unique to the barrens patches studied in eastern Tasmania (other than *C. rodgersii* itself; see Appendix I of the Electronic Supplementary Material), it is clearly the catastrophic shift to widespread barrens (10^2 – 10^3 m), via the coalescence of incipient barrens patches, that will lead to the loss of taxonomic diversity across increasingly large and ecologically important spatial scales. Furthermore, the formation of *C. rodgersii* barrens may also be expected to

result in negative impacts for nektonic species that associate with macroalgal habitat either as a result of direct habitat loss or the loss of an abundance of prey items associated with vegetated habitats (e.g. Edgar and Shaw 1995). While the spatial grain of the current study can be considered to be too small for an adequate examination of the effects of *C. rodgersii* barrens on fish assemblages (reef fish in Tasmania typically possess home ranges >2000 m²; Barrett 1995), of the few small cryptic fishes (length <100 mm) sampled from the benthos (a total of 15 individuals in seven taxonomic groups), none were recorded from the barrens.

Effects of barrens on ecosystem functioning

As evidenced by the dramatic recovery of standing stocks in algal biomass and associated benthic fauna, vast changes in the physical and community structure of rocky reefs occur with the transition from macroalgal beds to *C. rodgersii* barrens. What remains less clear is how such shifts impact ecosystem functioning. However, given that epifauna are known to be major contributors to the flux of materials in macroalgal dominated reef habitats (e.g. Taylor 1998), the loss of fauna on barrens implies major functional differences between alternative macroalgal and barrens states. Ultimately, the conversion of macroalgal

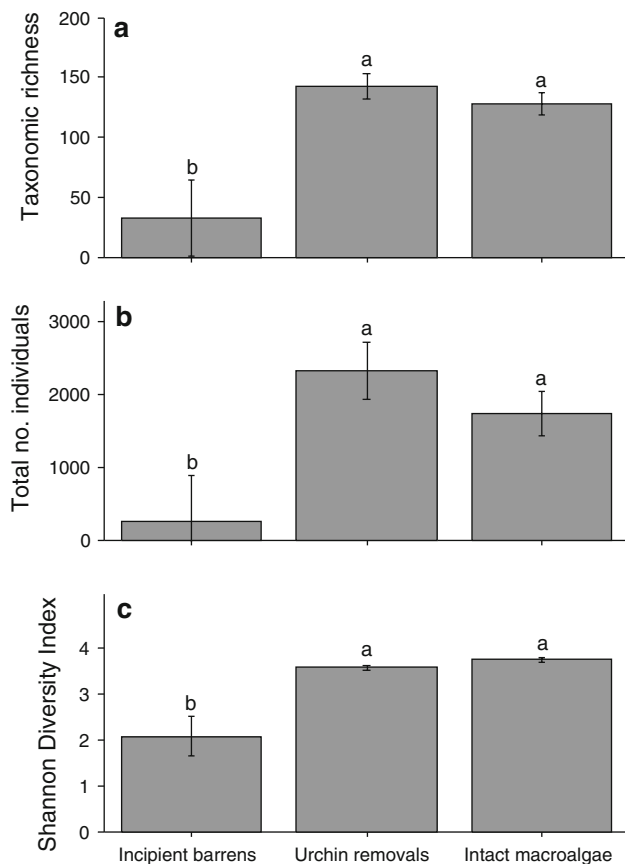


Fig. 7 Effect of *Centrostephanus rodgersii* on benthic faunal diversity assessed at the end of the experiment on incipient barren patches, urchin removal patches and intact macroalgal beds. Data shown are means per square metre $\pm$ SE and do not include habitat-forming invertebrates. **a** Taxonomic richness, i.e. total number of taxa (Model III one-way nested ANOVA; trans. = $Y^{0.5}$, Treatment, $F_{(2,6)} = 125.47$, $P < 0.0001$; patch (treatment), $F_{(6,27)} = 1.71$, $P = 0.1575$). **b** Total number of individuals (trans. = $Y^{0.22}$, treatment, $F_{(2,27)} = 57.45$, $P < 0.0001$; patch (treatment), $F_{(6,27)} = 1.34$, $P = 0.2728$). **c** Shannon diversity index (treatment, $F_{(2,33)} = 123.42$, $P < 0.0001$; patch (treatment), $F_{(6,27)} = 0.56$, $P = 0.7589$). Note that the index was calculated using $\log_e$. Bars with identical letters indicate REGW groupings, $\alpha = 0.05$

beds to widespread *C. rodgersii* barrens within the extended Tasmanian range is anticipated to reduce benthic primary (after Chapman 1981; Babcock et al. 1999) and secondary productivity (e.g. Duggins et al. 1989), with flow-on effects to many species, including species of commercial importance (Andrew and Underwood 1992; Andrew et al. 1998; Johnson et al. 2005).

Habitat loss coupled with changing climate

The results presented here demonstrate that disproportionately large impacts on marine biodiversity may occur as a result of range shifts of key habitat-modifying organisms. Furthermore, climate change also acts

independently on individual species within a community (e.g. Parmesan and Yohe 2003). Thus, the loss of local habitat as a result of range extension by habitat-modifying organisms coupled with large-scale shifts in the suitable ‘climate envelope’ (e.g. Hijmans and Graham 2006) may be particularly devastating for some populations, particularly those with contracted ranges to begin with. These kinds of interactions are acutely relevant in places such as Tasmania where poleward range retreat is prevented by a lack of contiguous poleward land mass. Indeed, the large-scale decline of the giant kelp *Macrocystis pyrifera* in eastern Tasmania over the past 50 years appears to be the result of the new regime of warm, nutrient-poor water on this coast (e.g. Edgar et al. 2005; see also Ridgway 2007). While *C. rodgersii* grazing does not appear to be responsible for the decline of this macroalga over large scales, localised barrens formation may prevent the recovery of this alga at some sites even if poor nutrient conditions for plant growth were temporally reversed. Moreover, because further strengthening of the EAC and greater thermal stratification are predicted for southeastern Australia under global climate change (Cai et al. 2005), coastal waters off eastern Tasmania appear to be committed to a warm and oligotrophic trajectory (reviewed by Poloczanska et al. 2007). This trend will have a positive effect on the reproductive success of *C. rodgersii* (Ling et al. 2008) but will negatively influence macroalgal growth and likely result in more frequent dieback events (e.g. Valentine and Johnson 2004). Thus, the warming climate of this coast appears poised to tilt macroalgal–urchin dynamics in favour of further sea urchin grazing and disproportionately large effects on reef biodiversity.

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