

Thinning of kelp canopy modifies understory assemblages: the importance of canopy density

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ABSTRACT: Kelp forests in southeastern Australia form canopies that support complex understory assemblages. Predicted levels of climate change in this region are likely to impact the health and distribution of these forests, potentially resulting in large-scale reductions in canopy cover. This study determined the impacts of a permanent reduction in canopy cover of the dominant kelp in this region, *Ecklonia radiata*, on the structure of understory algal and sessile invertebrate community assemblages. Changes in assemblages were determined over 12 mo in 3 treatments: unmanipulated, 33% canopy reduction and 66% canopy reduction. Clearance treatments were maintained to simulate the predicted effects of long-term climate-driven canopy reduction. Thinning of *E. radiata* canopy (especially 66% loss) caused a shift towards a foliose algal-dominated understory, with an associated loss of sponges, bryozoans, and encrusting algae. Canopy loss homogenised existing patchiness in understory assemblages, and high recruitment of *E. radiata* occurred at both levels of thinning. A 66% reduction in kelp canopy increased understory community diversity, but did not affect species richness. Thus, changes to understory assemblages occurred in a density-dependent manner, with 66% canopy loss required to alter the structure of assemblages at the community scale. Changes at this scale were subtle but important (with stability attributed to a combination of biogeography and resistance to perturbation driven by high diversity), and indicate that partial loss of kelp canopy under future climate change scenarios will shift understory communities towards a foliose algal-dominated state, which has important implications for sessile invertebrates and potentially future recruitment of kelp.

KEY WORDS: *Ecklonia radiata* · Canopy disturbance · Understory assemblages · Kelp bed · Community ecology · Canopy density · Seaweeds · Community structure

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INTRODUCTION

Macroalgal beds are a dominant feature of temperate waters worldwide, and provide the ecological foundations of most temperate marine reef ecosystems (Steneck & Johnson 2013). The vertical structure of subtidal kelp forests creates a complex 3-dimensional habitat that modifies abiotic factors such as light (Gerard 1984, Reed & Foster 1984, Irving et al. 2004), hydrodynamics (Kennelly 1989, Duggins et al. 1990, Connell 2003) and sedimentation (Eckman et al. 1989, Wernberg et al. 2005), permitting the development of complex understory assemblages (Day-

ton et al. 1992, Clark et al. 2004). These communities are often characterised by high levels of biodiversity and endemism (Dayton 1985) and create an important food source and microhabitat for other reef-associated organisms (e.g. Andrew et al. 1998, Edgar et al. 2004).

An increasing threat to kelp and other canopy-forming macroalgae is increasing ocean temperatures driven by climate change processes (e.g. Dayton & Tegner 1984, Wernberg et al. 2010, 2011). Ocean warming, particularly when coupled with other (potentially synergistic) stressors such as nutrient depletion and/or eutrophication (Russell & Con-

nell 2007), ocean acidification (Wernberg et al. 2009), increased frequency of storm or El Niño events (Dayton & Tegner 1984) and strong grazing pressure (Vanderklift et al. 2009), is expected to erode the resilience of kelp beds via direct physiological effects (Wernberg et al. 2011) and reduction of successful recruitment (Mabin et al. 2013, Mohring et al. 2013). While kelp, as with most organisms, can undergo physiological and structural changes (acclimatise) to at least partially adapt to chronically warm environments (Staeher & Wernberg 2009), this comes at the ecological cost of reduced resilience which, in the context of sustained climate-driven warming, will ultimately lead to range contractions and decreased abundance of kelp as it approaches the limits of its physiological tolerance (Wernberg et al. 2010, Poloczanska et al. 2013).

Temperate reefs in southeastern Australia are dominated by the large brown kelp *Ecklonia radiata*. With a larger depth (4 to 50+ m) and latitudinal (27.5 to 43.5°S) range than any other canopy-former (Steinberg & Kendrick 1999), *E. radiata* is the most important habitat-forming seaweed in temperate Australia. The waters off southeastern Australia are warming at a rate of ~3.8 times the global average, and are predicted to establish as the most intense 'hotspot' of ocean warming in the southern hemisphere (Ridgway 2007). This increase in water temperature is driven by increased wind stress in the Southern Ocean, resulting in longer and stronger incursions of the warm East Australian Current (EAC) into waters off eastern Tasmania as a result of eddy propagation (Cai 2006, Ridgway 2007). Water temperatures in the southwest Tasman Sea have warmed by more than 2.2°C over the past century (Ridgway 2007) so that summer maxima now routinely reaches temperatures of ~18°C in southeastern Tasmania, which is nearing the upper thermal tolerance limits (~22°C) for successful reproduction of *E. radiata* in Tasmania (Mabin et al. 2013). Predicted levels of warming in this region over the next century (>3°C; Lough et al. 2012) are likely to impact the density and distribution of *E. radiata* via reduced growth (Hatcher et al. 1987), survival (Wernberg et al. 2013), success of microscopic stages (Mabin et al. 2013) and reproductive output (Mohring et al. 2013), which may ultimately result in widespread decline in density and thinning of adult canopies with concomitant impacts on associated understory assemblages.

The role of kelp in regulating understory communities has been demonstrated by canopy removal experiments (Johnson & Mann 1988, Valentine & Johnson 2005, Toohey et al. 2007), and by tracking

community responses to natural disturbances that create gaps in canopies through processes such as storms (Thomsen et al. 2004), herbivore grazing (Johnson & Mann 1993, Ling 2008), or localised warming events (Valentine & Johnson 2004, Smale & Wernberg 2013, Wernberg et al. 2013). In general, algal and invertebrate communities beneath kelp canopies are more diverse than those on reefs lacking a canopy (Dayton 1985, Watt & Scrosati 2013), which are typically dominated by few species of coralline algae (Melville & Connell 2001). Nonetheless, despite their importance in promoting biodiversity, canopy-forming seaweeds can also have a strong limiting effect on understory algae by reducing access to light and space (Goodsell & Connell 2005, Wernberg et al. 2005) and via mechanical abrasion of the benthos (Kennelly 1989, Connell 2003), all of which inhibit recruitment and post-recruitment survivorship (Toohey et al. 2007, Wernberg & Connell 2008). A partial reduction of canopy cover may therefore relax the competitive effects of the canopy-former (Dayton 1985, Kennelly 1987b, Edwards 1998), allowing the recruitment and proliferation of understory species (Kennelly 1989, Toohey et al. 2007).

Macroalgal clearance studies examining understory community responses have typically focused on the effects of total canopy removal (Emmerson & Collings 1998, Edgar et al. 2004), particularly in the context of intense herbivory (Johnson & Mann 1993, Edgar et al. 2004, Ling 2008) or natural disturbances that effectively lead to total clearance of canopy-forming species (Valentine & Johnson 2004, Wernberg et al. 2013). In a climate change context, total canopy loss may only be realistic in situations such as El Niño (Dayton & Tegner 1984) or extreme warming events. For example, a recent warming event in Western Australia reduced *E. radiata* cover by almost 50% (Wernberg et al. 2013) and completely eliminated the fucoid *Scytothalia dorycarpa*, irreversibly reducing the northern extent of the latter species by ~100 km (Smale & Wernberg 2013). However, in areas that are not at the warm extreme of physiological tolerance for kelp, populations are more likely to be able to withstand periodic extreme warming by making physiological, structural, and metabolic adjustments (Wernberg et al. 2010); thus, a more realistic scenario is a gradual reduction in canopy extent. While a small number of partial clearance/disturbance experiments have been conducted (see Kennelly 1987b, Wernberg & Connell 2008, Araújo et al. 2012), these have focused on the recruitment of the disturbed species or on recovery of understory assemblages through time after a single manipula-

tion of the canopy. Importantly, we could not locate any previous studies that have applied and maintained a partial canopy clearance over a prolonged period of time. Understanding how understory algal and sessile invertebrate communities associated with kelp may respond to permanent canopy thinning is critical for predicting the impacts of future climate change-driven threats on temperate reef communities.

This work assesses the idea that climate change in southeastern Australia will impact the structure of understory community assemblages by reducing *E. radiata* canopy cover, but that the nature of this impact may vary depending on the extent of canopy loss. To simulate permanent climate change-driven reductions in kelp density, we thinned *E. radiata* canopy by 33 and 66% for 12 mo to determine (1) changes in understory algal and invertebrate community structure and (2) effects of canopy thinning on *E. radiata* recruitment. Although the ecological responses of understory communities to canopy removal may vary depending on both the identity of the canopy-forming species and the geographic context of the ecosystem (reviewed by Santelices & Ojeda 1984), this study provides an important first step in quantifying the effects of partial canopy loss in the context of climate-driven pressures on temperate reef communities.

MATERIALS AND METHODS

Study site and experimental setup

The effect of *Ecklonia radiata* canopy on the structure of understory communities was assessed in a canopy-thinning experiment undertaken on a shallow rocky reef in Fortescue Bay, Tasman Peninsula (43.123°S, 147.976°E) between 18 March 2011 and 16 March 2012. Fortescue Bay is characterised by moderate-relief boulder reef with extensive beds of *E. radiata* from a depth of ~6 m down to 15+ m where the reef–sand interface occurs. The study reef was chosen specifically for the homogeneity of its boulder substratum, moderate wave exposure and uniformity of depth. A total of 9 plots (5 × 5 m) were haphazardly placed within stands of well-developed *E. radiata* canopy at a depth of ~9 to 11 m. Treatment plots were separated from each other by ~5 to 10 m and positioned at least 1 m from any gaps in *E. radiata* canopy.

Three treatments were applied to experimental plots: control (0% canopy removal), low (one-third canopy removal, hereafter 33%), or high (two-thirds

canopy removal, hereafter 66%), with $n = 3$ plots for each treatment. This equated to densities of 8.9, 6.2 and 3.1 plants m^{-2} for control, 33 and 66% canopy-thinning treatments, respectively. No plots were totally cleared of *E. radiata*, as this is an unlikely outcome under predicted climate change scenarios in Tasmania. Treatments were ordered randomly across the 9 plots. Although the experimental plots were 5 × 5 m, response variables were only measured from the inner 3 × 3 m part of each plot, which was demarcated by 8 mm UV-resistant polypropylene rope, providing a 1 m treated buffer zone to minimise edge effects. Previous work with *E. radiata* has demonstrated that 2 × 2 m areas were sufficiently large to prevent shading of the centre of plots by surrounding canopies (Kennelly 1987b). Clearance treatments were administered by divers removing whole adult *E. radiata* plants (including stipes and holdfasts) by hand to reduce the density to 33 or 66% of the plot's original density. Plants were removed in a regular manner, i.e. 'every third plant' for 33% canopy thinning, or '2 of every 3 plants' for 66% thinning treatments. Plants were classified as adult only if they were deemed to contribute significantly to canopy shading, with a threshold of holdfast to blade tip length ≥ 50 cm used to distinguish (arbitrarily) between juvenile and adult plants. The density of mature *E. radiata* plants within each plot was assessed using 5 randomly placed 1 m² quadrats.

Surveys of algal community structure were conducted immediately prior to canopy thinning, and at 6 and 12 mo after administration of initial thinning treatment. Understory communities were assessed in 5 randomly placed 0.25 m² quadrats in each plot, and the cover of macroalgae, sessile invertebrates and bare substratum quantified using 49 regularly spaced points of intersecting wire. Large foliose understory alga that lay prostrate across the substrata were moved aside to determine the cover of smaller turfing algae, hence it was possible to arrive at a total percentage cover in a given plot greater than 100%. Where a species could not be accurately identified to at least family level (i.e. an immature or damaged specimen), it was allocated only to phylum or functional group. This made up <10% of species and <0.5% total cover on all occasions. Groups containing multiple morphologically indistinguishable species were classified into functional groups (e.g. encrusting red algae, filamentous red turfing algae, geniculate coralline algae; see Table 1). Adult *E. radiata* densities were quantified at ~2 mo intervals and adult thalli removed as necessary to maintain the appropriate canopy treatments. Any individuals of

the range-expanding diadematid grazing sea urchin *Centrostephanus rodgersii* were removed, as their presence was unrelated to canopy cover and their destructive grazing could mask effects of canopy-thinning treatments.

Data analyses

As we were not specifically interested in documenting seasonal changes in community structure, we focussed our analyses on similarities among treatments before (i.e. pre-manipulation) and after 12 mo of maintained canopy thinning. For this reason, and because we were *a priori* interested in determining similarity across treatment plots before the manipulations were undertaken, 'time' was not used as a factor in analyses. Instead, we ran separate tests for the start of the experimental period (pre-manipulation) and at the end of the monitoring period (following 12 mo of maintained canopy thinning). This approach avoids potential issues with seasonality in species abundances (Kennelly 1987b) because both sampling occasions are at the same time of year. While we could not negate the possibility of inter-annual variability in community structure, any such changes are likely to affect all treatments similarly.

Changes in understory community structure under different levels of canopy thinning were determined using multivariate analyses before and after 12 mo of the treatment being established. While adult *E. radiata* did not comprise part of the understory community and were not included in the community analyses, juvenile *E. radiata* were recorded in point intersect counts. We conducted 2 separate analyses with and without juvenile *E. radiata* to ascertain whether changes in understory community structure were due to *E. radiata* recruitment. Canonical analysis of principal coordinates (CAP) was used to distinguish differences in multivariate community structure using Bray-Curtis similarity matrices after data were square-root transformed (Clarke 1993). The 10 most influential taxa contributing to differences in assemblages across treatment groups, as identified by Spearman correlation coefficients, were examined graphically. Permutational multivariate analysis of variance (PERMANOVA) with pre-planned contrasts was used to test

Table 1. List of macroalgae and sessile benthic invertebrate taxa identified in understory assemblages beneath *Ecklonia radiata* canopy in Fortescue Bay, Tasmania

<p>Chlorophyta <i>Caulerpa flexilis</i> <i>Caulerpa geminata</i> <i>Caulerpa trifaria</i> <i>Codium fragile</i> <i>Ulva</i> spp.</p> <p>Phaeophyta <i>Acrocarpia paniculata</i> <i>Carpoglossum confluens</i> <i>Carpomitra costata</i> <i>Colpomenia</i> spp. <i>Cystophora</i> spp. <i>Dictyota</i> spp. <i>Ecklonia radiata</i> <i>Halopteris</i> spp. <i>Phyllospora comosa</i> <i>Sargassum</i> spp. <i>Seirococcus axillaris</i> <i>Xiphophora gladiata</i> <i>Zonaria/Lobophora</i> complex</p> <p>Rhodophyta <i>Ballia callitricha</i> <i>Callophyllis rangiferina</i> <i>Camontagnea oxyclada</i> <i>Carpopeltis phylophora</i> <i>Ceramium excellens</i> <i>Craspedocarpus ramentaceus</i> <i>Delisea plumosa</i> Encrusting red algae Filamentous turfing red algae <i>Gelidium asperum</i> Geniculate coralline algae <i>Gigartina pinnata</i></p>	<p>Rhodophyta (continued) <i>Glaphrymenia pustulosa</i> <i>Griffithsia elegans</i> <i>Halicnide similans</i> <i>Hemineura frondosa</i> <i>Hymenena</i> spp. <i>Hypnea racementacea</i> <i>Kuetzingia canaliculata</i> <i>Laurencia elata</i> <i>Lenormandia marginata</i> Non-geniculate coralline algae <i>Peyssonnelia novaehollandiae</i> <i>Phacelocarpus</i> spp. <i>Plocamium angustum</i> <i>Plocamium leptophyllum</i> <i>Polyopes constrictus</i> <i>Rhodophyllus multipartita</i> <i>Rhodophyllis</i> spp. (other) <i>Rhodymenia</i> sp. 1 <i>Rhodymenia</i> sp. 2 <i>Sarcothalia crassifolia</i> <i>Sonderopelta coriacea</i> <i>Thamnoclonium dichotomum</i></p> <p>Porifera Encrusting sponge</p> <p>Cnidaria Hydroid spp.</p> <p>Bryozoa Bryozoan spp.</p> <p>Chordata Ascidean</p>
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the null hypothesis that community assemblages did not differ among treatment groups at the commencement of the experiment, or after 12 mo of canopy manipulation. A nested PERMANOVA design was used at each of the 2 sampling occasions with the factors 'treatment', and 'plot' nested within 'treatment'.

The effects of canopy thinning on recruitment of *E. radiata*, and on understory community richness (algal and invertebrate species combined), Shannon-Wiener diversity (H') and maximum possible diversity (H_{max}) (Molles & Cahill 1999), evenness, understory algal cover, and total understory assemblage cover (i.e. non-bare areas of substratum, algal and invertebrate species combined) were examined using nested ANOVA, with the factors 'treatment' and 'plot' nested within 'treatment'. Two separate ANOVA were run for each dependent variable; one at the start, and one at the end of the experiment. All

data were first checked for conformity to the assumptions of homoscedasticity and normality, and transformations to stabilise variances (if required) were determined by the relationship between group SDs and means (Draper & Smith 1998). Tukey's HSD *a posteriori* multiple range tests were performed where significant differences were detected among treatments.

RESULTS

Understory assemblages were diverse in all canopy treatments, with a total of 52 algal species/taxa and 4 sessile invertebrate taxa identified (Table 1). The most abundant species at commencement of the experiment were *Sonderopelta coriacea* (15.3%) cover, *Rhodymenia* spp. (10.6%), non-geniculate corallines (10.2%), encrusting red algae (7.4%), and geniculate corallines (5.2%). Bryozoans (9.4%) and

sponges (7.9%) were also a prominent feature of assemblages. However, at the end of the experiment, invertebrates (sponges, bryozoans) and encrusting algal complexes had declined in the high-clearance treatment while certain terete and foliose species (*Griffithsia elegans*, *Hemineura frondosa*) increased in cover. This change was not observed in the low-clearance or control treatments (Fig. 1). *Halopteris* spp. and *Plocamium leptophyllum* cover also increased in plots subject to high-level canopy clearance, but abundance of these species was highly variable, both spatially and temporally.

Multivariate community structure

Community assemblages did not differ between treatment groups at the commencement of the experiment (Table 2, Fig. 2); however, after 12 mo of maintained canopy thinning, significant differences

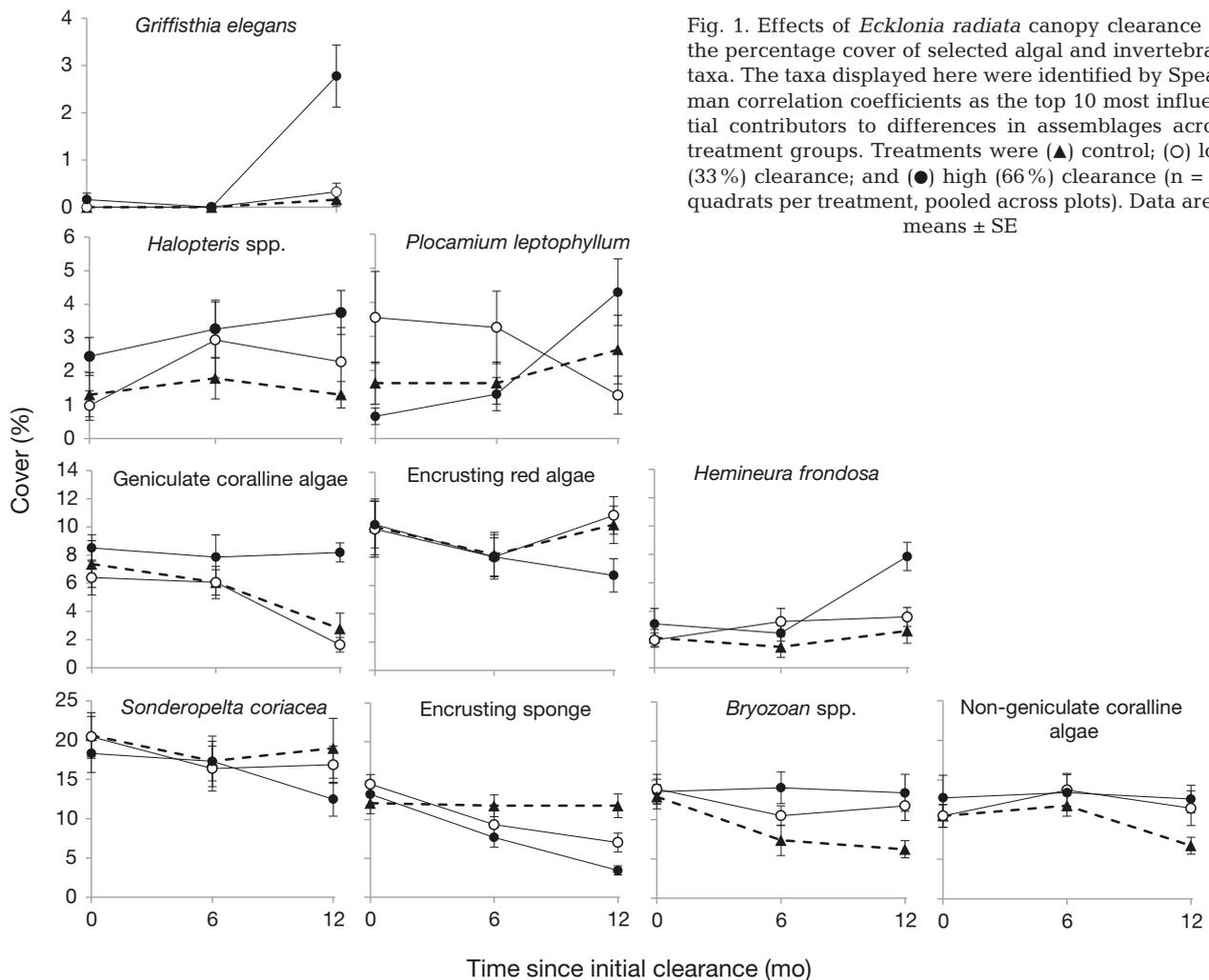


Fig. 1. Effects of *Ecklonia radiata* canopy clearance on the percentage cover of selected algal and invertebrate taxa. The taxa displayed here were identified by Spearman correlation coefficients as the top 10 most influential contributors to differences in assemblages across treatment groups. Treatments were (▲) control; (○) low (33%) clearance; and (●) high (66%) clearance (n = 15 quadrats per treatment, pooled across plots). Data are means \pm SE

Table 2. Nested PERMANOVA comparing among-canopy thinning treatments for understory community structure both excluding and including juvenile *Ecklonia radiata* (based on Bray-Curtis similarity of % cover using a square-root transformation). Factors are 'treatment' (3 levels of *E. radiata* canopy thinning: control, low, high) and 'plot' nested within 'treatment'. Significance is indicated in **bold**

Source	df	Start ($t = 0$ mo)			End ($t = 12$ mo)		
		MS	F	p	MS	F	p
Excluding							
Treatment	2	774	0.571	0.918	2725	2.201	0.029
Plot (Treat)	6	1355	1.540	0.008	1238	1.339	0.034
Res	36	881			925		
Including							
Treatment	2	778	0.569	0.928	3099	2.551	0.016
Plot (Treat)	6	1367	1.551	0.003	1215	1.330	0.043
Res	36	881			913		

in the structure of understory communities were detected among treatment groups (Table 2, Fig. 2). Initial CAP plots from all time periods represented on a single set of axes (data not shown) also indicated an overall shift in the structure of communities before clearance, and 12 mo after canopy manipulations. However, this affected all treatments equally (i.e. characterised reef-scale inter-annual variability), hence $t = 0$ and $t = 12$ mo data are presented on separate plots for clarity (Fig. 2). The separation of assemblages between manipulated (both low and high) and control plots was driven by changes in abundance of a number of different taxa ranging from coralline and encrusting algal species, to sessile invertebrates and erect foliose algae (Fig. 1). Pairwise tests could not identify which treatments differed (control vs. high, $p = 0.089$; control vs. low,

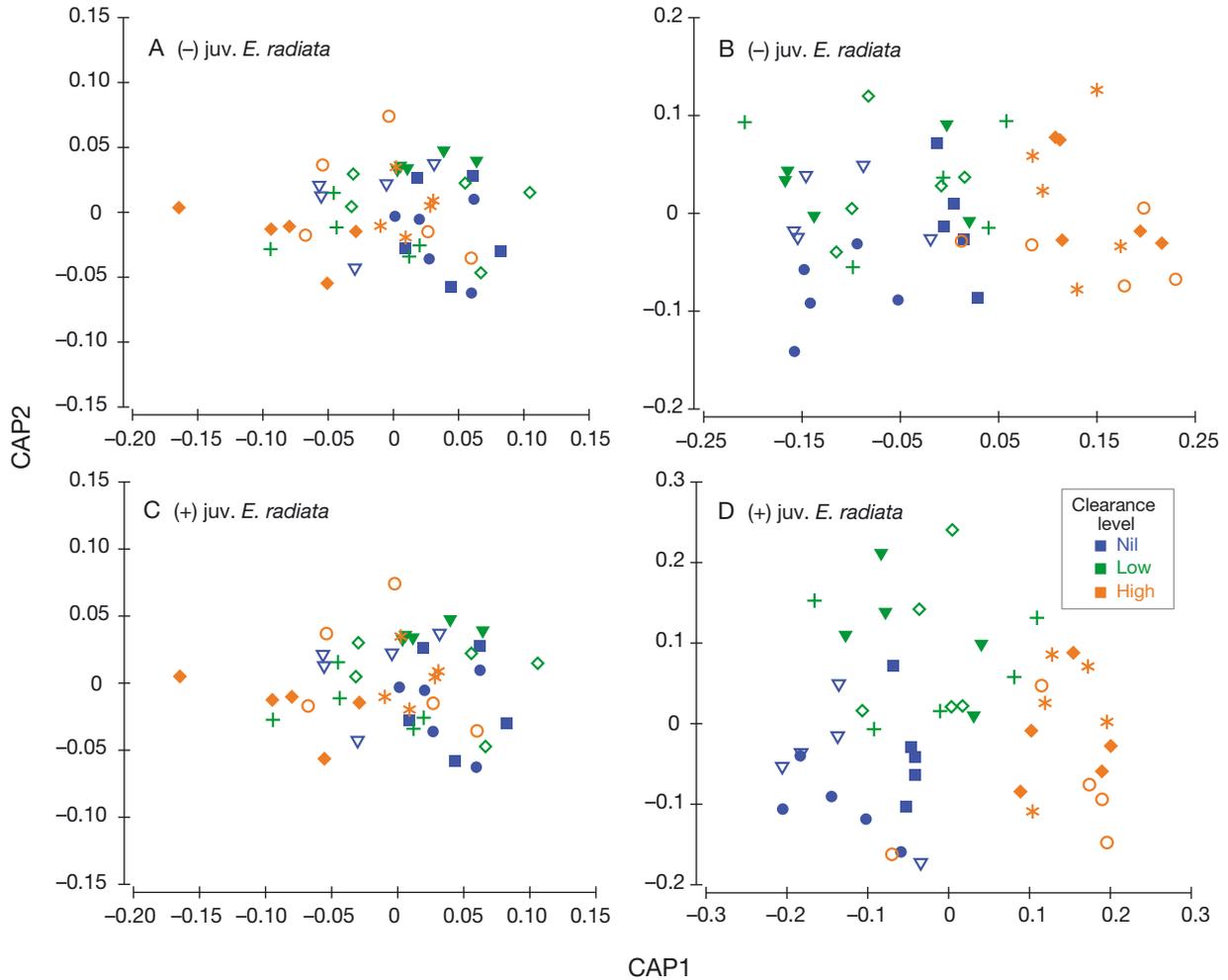


Fig. 2. Structure of understory algal and sessile invertebrate community assemblages (A,C) before, and (B,D) after 12 mo of maintained *Ecklonia radiata* canopy thinning. Canonical analysis of principal coordinates of assemblages (% cover data) (A,B) excluding (-) and (C,D) including (+) juvenile *E. radiata*. Symbols identify individual plots ($n = 3$), with each point representing a quadrat subsampled within that plot (5 quadrats plot⁻¹). Canopy manipulation treatments were nil: no clearance; low: 33% clearance; high: 66% clearance ($n = 15$)

$p = 0.999$; low vs. high, $p = 0.090$), but the effect of treatment was clearly driven predominantly by a separation between high-clearance plots and low-clearance/control plots (Fig. 2B). When juvenile *Ecklonia radiata* were also considered as a component of the understory community, low-clearance plots became distinguishably different from controls but were still separated from high-clearance treatments in CAP space (Fig. 2D), although as with the previous analysis, pairwise tests could not determine significance because of the plot within treatment effects ($p = 0.043$, Table 2B).

The significant plot within treatment effect (Table 2) indicated spatial variability in understory community structure occurred on a scale of 10^0 to 10^1 m. Examination of individual subsamples in CAP plots at the commencement of the experiment (Fig. 2A,C) revealed significant 'clumping' of subsamples within plots, demonstrating the small spatial scale of patchiness in community structure. After 12 mo of maintained canopy thinning (low and high), subsamples became more similar across replicate plots within each treatment group, and this homogeneity increased with increasing levels of clearance (Fig. 2B,D).

Univariate parameters

There was no initial difference in total assemblage cover, algal cover, species richness or Shannon-Wiener diversity indices among treatment groups before the canopy clearances were applied ($p > 0.08$ for all parameters; analyses not shown; Fig. 3). The 12 mo of sustained canopy thinning had no effect on species richness or H_{\max} ; however, it did result in a significant increase in overall algal cover, H' , and evenness (Table 3). In a similar pattern to that observed in multivariate space, high-clearance treatments had significantly higher levels of both H' ($p =$

0.007) and evenness ($p = 0.015$) than either low-clearance or control treatments (Table 3, Fig. 3C,D). The percentage cover of understory algae was elevated in both high- and low-clearance treatments relative to control plots ($p = 0.009$), experiencing an 11 and 15% increase to 93 and 101% cover, respectively (Table 3, Fig 3G). This was due to a shift from sessile invertebrate to algal cover (Fig. 3G, see also Fig. 1), as absolute cover of combined invertebrate and algal assemblages remained high and unchanged across all treatment groups for the duration of the experiment (~93 to 98% at all times, Fig. 3F). In general, plots of these parameters over time show a clear divergence of communities in high-clearance treatments from low-clearance and control treatments (for H' and evenness) after 12 mo of maintained thinning (Fig. 3C,D).

Kelp recruitment

Both low- and high-clearance treatments resulted in a significant increase in recruitment of juvenile *E. radiata* (Table 3, Fig. 3A). A strong recruitment pulse occurred within the first 6 mo of canopy thinning in both low- and high-clearance plots. This elevated level of recruitment continued for the following 6 mo despite an increasing proportion of these 'early' recruits being classified as adults at the time of the 12 mo surveys (Fig. 3A). The increased frequency of clearance of 'adult' *E. radiata* necessary to maintain canopy density at appropriate levels from 6 to 12 mo is further evidence for elevated recruitment (Fig. 4). Unlike whole community structure, there was no small-scale patchiness observed in *E. radiata* recruitment between plots ($p > 0.3$; Table 3), indicating that recruitment either occurred relatively homogeneously on this spatial scale, or that any patchiness in recruitment was at too small (<3 m) or too large (>10s of m) a scale to be detected by our sampling.

Table 3. Nested ANOVAs comparing among-canopy thinning treatments (control, low, high) for 7 parameters relating to understory algal and invertebrate community structure: the density of juvenile *Ecklonia radiata*, understory community richness and diversity (3 indices: Shannon-Wiener H' , H_{\max} , evenness); algal cover (3-dimensional); and total cover (non-bare areas occupied by invertebrate and algal assemblages). * $p < 0.05$; ** $p < 0.01$

Source of variation	df	Density juv. <i>E. radiata</i>		Species richness		Diversity (H')		H_{\max}		Evenness		% algal cover (3-D)		% total cover (2-D)	
		MS	F	MS	F	MS	F	MS	F	MS	F	MS	F	MS	F
Treatment	2	172.4	6.847**	14.96	2.876	0.264	5.782**	0.089	3.225	0.0086	4.713*	0.0581	5.394**	0.000287	0.477
Plot (Treat)	6	31.5	1.251	7.67	1.474	0.099	2.169	0.044	1.600	0.0024	1.305	0.0118	0.387	0.000990	1.646
Res	36			5.20		0.046		0.028		0.0018		0.0108		0.000602	

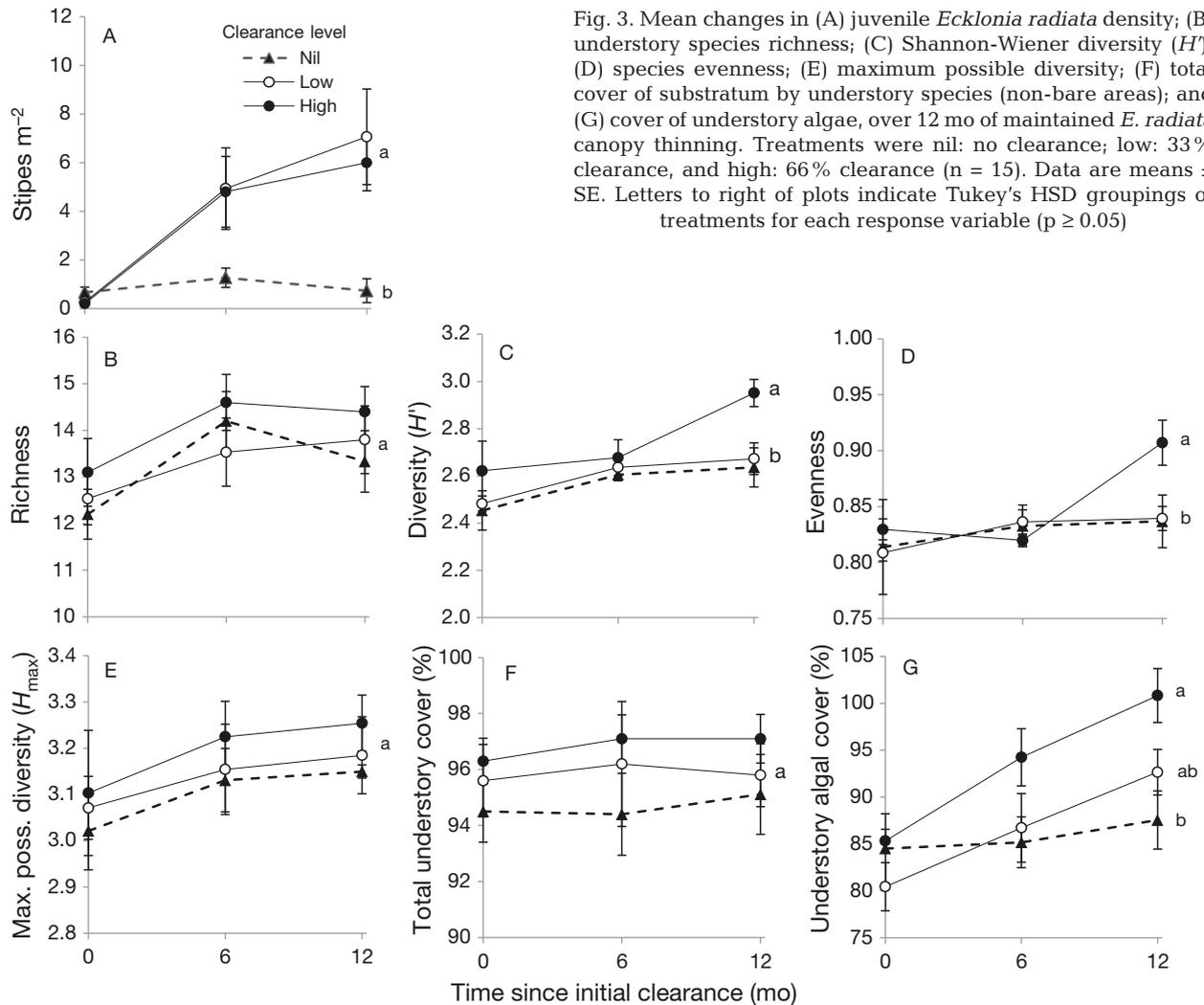


Fig. 3. Mean changes in (A) juvenile *Ecklonia radiata* density; (B) understory species richness; (C) Shannon-Wiener diversity (H'); (D) species evenness; (E) maximum possible diversity; (F) total cover of substratum by understory species (non-bare areas); and (G) cover of understory algae, over 12 mo of maintained *E. radiata* canopy thinning. Treatments were nil: no clearance; low: 33% clearance, and high: 66% clearance ($n = 15$). Data are means \pm SE. Letters to right of plots indicate Tukey's HSD groupings of treatments for each response variable ($p \geq 0.05$)

DISCUSSION

Density-dependent effects of canopy reduction, and nonlinearities in community responses

A reduction in the cover of *Ecklonia radiata* canopy resulted in significant changes in the structure of understory community assemblages, and elevated recruitment of kelp. The shift in overall community structure between cleared and control treatments was driven predominantly by an increase in filamentous and foliose algae such as *Hemineura frondosa*, *Halopteris* spp. and *Griffithsia elegans*; and a concomitant loss of sponges, bryozoans and encrusting and calcareous algae. Although high levels of patchiness occurred in understory communities on the scale of 10^0 to 10^1 m, analysis of individual species responses suggested that community structure typically varied little between control and low canopy-

thinning treatments, with high (66%) levels of canopy thinning required to cause a significant change in the structure of understory assemblages.

Perhaps the most dramatic effect of macroalgal canopy on the understory environment occurs via shading, with estimates of light absorbance by kelp canopies ranging from ~75% (Edwards 1998) to >95% (Reed & Foster 1984, Kennelly 1989, Wernberg et al. 2005). Wernberg et al. (2005) demonstrated that kelp canopies reduce irradiance in a nonlinear manner, with irradiance decreasing up to a density of 2 sporophytes 0.25 m^{-2} , beyond which denser canopies caused no further reduction in light at the understory level. A similar nonlinear effect of *E. radiata* canopy density on understory irradiance occurs at our site, with photosynthetically active radiation (PAR) levels beneath the canopy subject to high levels of thinning (mean daily irradiance \pm SE of 2.17 ± 0.16 and $0.50 \pm 0.03 \text{ mol photons m}^{-2} \text{ d}^{-1}$ for

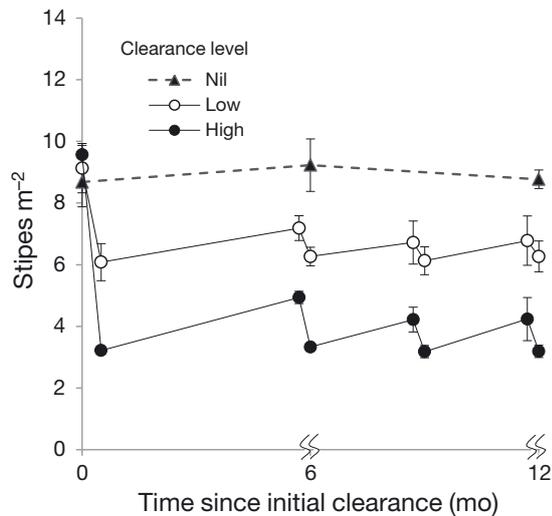


Fig. 4. Mean changes in the density of adult *Ecklonia radiata* over 12 mo of *E. radiata* canopy thinning. Treatments were nil: no clearance; low: 33% clearance, and high: 66% clearance ($n = 15$). Data are means \pm SE. Decreases in low and high clearance treatments at ~6, 9 and 12 mo indicate where canopy has been thinned by divers to maintain clearance treatments. Axis breaks are used to show kelp density before and after thinning treatment was applied on each occasion

January and June, respectively); consistently greater than those beneath low clearance (1.04 ± 0.12 and 0.32 ± 0.19 mol photons $m^{-2} d^{-1}$) and unmanipulated (0.84 ± 0.12 and 0.34 ± 0.02 mol photons $m^{-2} d^{-1}$) canopy, which were indistinguishable and ~70% less than in areas completely cleared of kelp (7.44 ± 0.43 and 0.75 ± 0.04 mol photons $m^{-2} d^{-1}$; M. Tatsumi unpubl. data). A consequence of nonlinearities in the physical environment with varying levels of canopy cover may be nonlinearities in the response of understory communities. The fact that high levels of canopy thinning were required to effect significant change in the structure of understory assemblages suggests that, under low levels of canopy thinning, the density of the remaining canopy is sufficient to maintain a similar light (Gerard 1984, Reed & Foster 1984, Irving et al. 2004, Wernberg et al. 2005), hydrodynamic (Kennelly 1989, Duggins et al. 1990, Connell 2003) and sediment (Eckman et al. 1989, Wernberg et al. 2005) environment to that beneath intact canopies.

It has yet to be determined (due to a paucity of studies on the effects of partial canopy removal) whether the reduction in kelp canopy required to effect a community-scale change depends on the proportion of existing canopy removed (i.e. relative change), or whether an absolute threshold of canopy

cover exists below which understory assemblages will be affected. Regardless, the effects of kelp canopy removal is likely to depend on the initial density of adult kelp on a reef, which can be highly spatially variable (Schiel & Foster 1986, Kendrick et al. 1999) depending on local environmental factors (e.g. Wernberg & Thomsen 2005, Fowler-Walker et al. 2006). Indeed, encrusting coralline algae appear to be affected by kelp clearance in a nonlinear manner depending on the initial kelp density, with responses to experimental clearance occurring in different directions depending on the initial cover of kelp (Melville & Connell 2001). Moreover, the initial composition of understory assemblages likely also plays an important role in community-scale resistance to canopy perturbation. For example, Kennelly (1987b) found some understory species responded to a 25% thinning of canopy, while others were unaffected by canopy reductions less than 50%. Clearly, further research on the density-dependent effects of canopy thinning is required; however, in the context of predicted climate change-driven reductions in *E. radiata* canopy, it appears that the response of understory assemblages will depend strongly on the extent to which canopy is reduced, and thus on how well *E. radiata* can acclimate and adapt to a changing environment (Wernberg et al. 2010).

Effects of canopy loss on the diversity and structure of understory communities

Natural disturbance to kelp forests or canopy clearance experiments have previously demonstrated large understory community-scale transformations (e.g. Kennelly & Underwood 1993, Melville & Connell 2001, Toohy et al. 2007, Wernberg et al. 2013). A frequently reported effect of canopy clearance is a dramatic increase in species richness that is thought to be due to increases in light and space resources (e.g. Kennelly 1989, Toohy et al. 2004, 2007, Wernberg et al. 2005). While we observed an increase in diversity (Shannon-Wiener H' index) after 12 mo of high-level canopy thinning, this was driven primarily by a reduction in abundance of dominant taxa rather than increased richness. Specifically, a reduction in cover of sessile invertebrates and encrusting algae (which were abundant at the start of the experiment) increased the evenness of the community without affecting species richness. We cannot isolate whether this assemblage shift was driven by a decrease in sessile invertebrates and encrusting algae because the loss of canopy created an unfavourable environ-

ment for these taxa, or by the competitive dominance of foliose algal species upon release of light and space resources. Wernberg et al. (2013) suggest a combination of both these effects, proposing that a reduction in kelp canopy facilitates proliferation of understory algae but also causes a decline in encrusting invertebrates that are associated with kelp (see also Wernberg & Connell 2008).

The marked decrease in the abundance of sessile invertebrates and encrusting red algae with increasing levels of *E. radiata* canopy thinning are consistent with the observations of Kennelly (1989) and Wernberg & Connell (2008). In the present study, the abundant encrusting algae *Sonderopelta coriacea* decreased with increasing canopy loss similar to the declines in *Peyssonelia* spp. observed by Kennelly (1989). These taxa are structurally and functionally very similar, and species in this family often co-occur in shaded environments on the reef matrix due to their obligate low light requirements (Häder et al. 1998). Similarly, many sponges host photosynthetic symbionts which are sensitive to elevated light levels (Lemloh et al. 2009). Kelp canopies are known to reduce sedimentation on understory communities by trapping sediment 'rain' and scouring sediment from the substrata (Kennelly 1989, Wernberg et al. 2005). Organisms that we observed to decline following canopy clearance (particularly the filter-feeding bryozoans and ascidians) may be susceptible to a synergy of increased sediment loading and light, as the end stage of many invertebrate larvae is photonegative (Thorson 1964) and their developmental success is reduced by sedimentation (Irving & Connell 2002). While Connell (2003) demonstrated that the negative effects of macroalgal canopy abrasion can outweigh the positive effects of reduced light and sedimentation for sessile invertebrates, we found invertebrate assemblages to be a dominant (>25% cover) component of communities beneath unmanipulated canopy, and their observed decline (to <10% cover) under high levels of canopy thinning suggests a climate-driven loss of canopy will likely reduce the abundance and biodiversity of these taxa.

Relative stability of understory communities

A previous study across multiple sites in this region reported no significant change in understory community structure following *E. radiata* canopy clearance (Edgar et al. 2004). The authors proposed that the lack of community-scale responses may be due to the high diversity and density of understory species; both

of which were similar to values observed in our experiment. Given the magnitude of community-scale changes following canopy reduction reported elsewhere (often a halving of species richness or a complete shift from foliose- to encrusting coralline alga-dominated communities; Melville & Connell 2001), the shifts we observed here were relatively modest. As proposed by Edgar et al. (2004), the apparent stability of assemblages in southeastern Tasmania may be driven (at least in part) by high diversity, which is known to enhance community resistance to perturbation and recovery from disturbance (e.g. Johnson et al. 1996, Tilman 1996, Aquilino & Stachowicz 2012). Indeed, the high species richness of 12 to 16 species 0.25 m⁻² quadrat in the present study is similar to that reported by Sánchez & Fernández (2005) on intertidal assemblages in Spain and by Toohey et al. (2007) in Western Australia, and is typical of the speciose nature of reef systems around southern Australia (Bolton 1994, Kerswell 2006). Although we observed only subtle community-level changes following canopy reduction, they were important nonetheless and contrast with the absence of community effects observed by Edgar et al. (2004). This may be due to the depth of our study site (~10 m) where sponges and bryozoans were an abundant (13.3 and 13.7% of initial plot cover, respectively) component of assemblages and strongly influential in separating the structure of communities beneath thinned vs. unmanipulated canopy, whereas sessile invertebrates are less abundant at 3 to 6 m and were not recorded by Edgar et al. (2004). Furthermore, only administering a single clearance treatment (100% canopy loss) once at the commencement of the experiment may not allow relaxation of *E. radiata* competitive-dominance, thereby reducing the opportunity for understory species to utilise available light resources (Dayton 1985, Kennelly 1987b).

Importance of biogeography, scale, and localised patchiness in determining the effects of canopy thinning

Recent work by Wernberg et al. (2013) reports on changes in community assemblages following an opportunistic thinning of *E. radiata* canopy resulting from an extreme warming event in Western Australia (WA). Loss of kelp canopy in this context appeared to represent an irreversible change, and Wernberg et al. (2013) reported a dramatic shift to an ecologically depauperate state of simple algal turf mats. Russell & Connell (2005) also observed a similar response in

South Australia (SA) with a proliferation of turf-forming algae in the absence of *E. radiata* canopy, although they linked the final composition of algal assemblages to an interaction between nutrient levels and the presence of grazers. In these systems, the establishment of turfs facilitated by canopy loss effectively excludes all other species by inhibiting the further recruitment of canopy-formers (Kennelly 1987b, Russell & Connell 2005). However, dense turf mats do not appear to develop following canopy removal in eastern Tasmania (Edgar et al. 2004, Valentine & Johnson 2005) in the same manner as occurs in WA and SA, highlighting the importance of biogeographic context in determining community responses to canopy loss. The shifts in community structure we observed are likely to be conservative in that they represent a response to manipulation of a single species in the community matrix, whereas multiple understory species are likely to be directly affected by climate change via warming water temperatures in addition to the indirect effects of canopy loss (which may act synergistically). In this sense, the observations of Wernberg et al. (2013) are particularly important because they provide observations on multiple species affected by a warming event. However, it is also important to note that many of these species were on the threshold of their physiological tolerance and hence caution must be exercised in extrapolating the observed effects to higher latitudes away from range margins.

The scale of canopy clearance is an important factor determining the nature of detectable community responses (Kennelly & Underwood 1993, Kendrick 1994, Emmerson & Collings 1998). For example, larger clearances involve a greater proportion of the total pool of available species and are more likely to detect changes in communities at the reef scale, but most studies focus on relatively small (several m²) areas of clearance (e.g. Kennelly & Underwood 1993, Emmerson & Collings 1998, Sánchez & Fernández 2005), as this is a common size of naturally-occurring clearances caused by storms or grazers. In the context of long-term climate change, canopy thinning would be expected to occur over 10s to 100s of km, but ongoing maintenance of experimental treatments at this scale is clearly unfeasible. Importantly, we were able to detect patchiness within communities at the scale of 10⁰ to 10¹ m, with quadrats within plots sharing more similar community structure than those in adjacent plots. A similar effect was reported by Kendrick et al. (2004) and Toohey et al. (2007), and may be due to variability in the scale of disturbances (e.g. selective removal of individual plants by grazers vs.

extensive canopy denudation in storm events), timing of disturbances in relation to phenology and spatial extent of spore dispersal (Dayton 1985). Although the reef we selected for this study was relatively homogeneous, differences in the size of boulders and degree of shading would cause microhabitat heterogeneity (e.g. in local hydrodynamics and the light environment) among plots. However, this patchiness appears not to alter the nature of the community response to canopy thinning, and the thinning itself actually homogenises this spatial variability. Thus, canopy thinning appears to reduce small-scale patchiness in community structure at the 'plot' scale, effectively removing the effects of past disturbance history.

The ecological responses of communities to canopy removal will not necessarily be geographically consistent, as demonstrated by the varying responses of understory assemblages to total canopy removal experiments in southern Chile and the North Pacific (Santelices & Ojeda 1984). Moreover, the effects of canopy clearance are likely to depend on the identity of the dominant canopy-forming species in a region, as this influences the initial composition of understory assemblages (e.g. see differences in assemblage composition between Reed & Foster 1984, Santelices & Ojeda 1984, Kennelly 1987b, Kendrick et al. 1999, Clark et al. 2004, Araújo et al. 2012). The treatments applied in this study were not spatially replicated across multiple sites, as the degree of within-site replication and fine scale at which we assessed understory assemblages made replication across multiple sites and/or regions unfeasible. Edgar et al. (2004) identified this issue of scaling and applied a broad level of spatial replication (over 50 km) to their *E. radiata* canopy manipulation study, and found that variation in macroalgal assemblages between sites was much greater than that associated with experimental treatments, and that the nature of canopy clearance effects had a minimal, but spatially consistent effect. Moreover, Kennelly & Underwood (1993) demonstrated geographic consistencies in the effects of *E. radiata* canopy disturbance on understory community structure in New South Wales across a range of different spatial scales. Thus, while we recognise that a lack of site replication does restrict the general applicability of results obtained here and that caution must be exercised in extrapolating results to other regions dominated by *E. radiata* (or indeed other canopy forming species), the patterns we observed are unlikely to be unique to southeastern Australia. Clearly, spatial replication of sustained 'pressure'-type (partial) canopy clearance experiments is required across a broad geographic scale, and we recommend the de-

velopment of standardised methodology to assist with comparing the outcomes of such studies.

Effects of canopy removal on kelp recruitment

The high recruitment by *E. radiata* following a reduction in canopy cover supports the findings of previous studies on *E. radiata* and other kelp (e.g. Johnson & Mann 1988, Kennelly & Underwood 1993, Kendrick 1994, Emmerson & Collings 1998). In general, canopy removal is associated with enhanced survival, settlement and growth of recruits, but the timing of clearances (both seasonal and in relation to species phenology) has been highlighted as important in influencing survival of new recruits (Kennelly 1987a, Kennelly & Underwood 1993). We observed elevated levels of recruitment throughout both summer and winter, and although plots contained a dense foliose-dominated understory, these assemblages did not appear to inhibit growth of *E. radiata* sporophytes in the same manner as turfing algae (Emmerson & Collings 1998, Russell & Connell 2005).

The enhanced kelp recruitment we observed may have been due to increased settlement success, or recruits may have been present prior to canopy manipulations (as dormant/seed bank stages) and simply experienced rapid growth upon opening of canopy gaps. Regardless, it suggests that the competitive ability of juvenile *E. radiata* when light resources are released may be particularly strong in southeastern Tasmania, potentially as a compensatory mechanism to facilitate growth in a low light climate. While Valentine & Johnson (2005) observed very little recovery of *E. radiata* in eastern Tasmania following removal of a competitively dominant invasive kelp, their site was characterised by high sediment loading which is known to inhibit recruitment success (Devlin & Volse 1978, Eriksson & Johansson 2003). Here, we observed a proliferation of juvenile *E. radiata* at both levels of clearance, indicating that a small reduction in canopy cover is sufficient to allow large increases in zoospore settlement and/or gametophytic growth, or possibly a release of microscopic stages from developmental dormancy that can occur when conditions are unfavourable for growth (e.g. Hoffmann & Santelices 1991, Carney & Edwards 2006, 2010). This finding does not necessarily imply equal or greater recruitment under scenarios of total canopy clearance, as environmental conditions in the absence of canopy (high light and sedimentation, reduced hydrodynamic dampening) can be unfavourable for seaweed recruitment (Wernberg &

Connell 2008). Moreover, canopy clearance may indirectly affect kelp recruitment by altering the abundance of invertebrate grazers (positively or negatively; see Konar & Estes 2003, Christie et al. 2009), which can have complex effects on kelp microscopic stages and recruitment success (e.g. Henríquez et al. 2011). Finally, total canopy loss may result in proliferation of turf-forming algae in place of diverse foliose-dominated communities (although this may depend on biogeography, as previously discussed), which can strongly negatively affect growth and/or settlement success of microscopic stages (Emmerson & Collings 1998, Russell & Connell 2005).

CONCLUSIONS

We have demonstrated that a reduction in cover of *Ecklonia radiata* canopy causes subtle but important changes to the structure of understory community assemblages. If future climate change causes significant thinning of the *E. radiata* canopy, understory communities may shift towards a more foliose, algal-dominated state with fewer sponges, bryozoans and encrusting/calcareous red algae. Moreover, we have shown that the understory communities associated with *E. radiata* vary in a density-dependent and non-linear manner. However, the specific way in which a community will respond to canopy thinning is likely to depend on the initial composition of the community (including the individual species' physiological tolerances to elevated light and sediment), the biogeographic context of the system, and the extent of canopy thinning. Given the high species diversity and spatial coverage of assemblages documented in this study, we suggest that community assemblages beneath monospecific *E. radiata* stands in southeastern Tasmania are very resistant to external perturbations. Future work should focus on spatial replication of sustained canopy thinning across the latitudinal range of *E. radiata*, and examining the effects of varying levels of canopy reduction to identify potential critical thresholds of canopy loss and nonlinearities in community responses.

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