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The role of disturbance in maintaining diversity of benthic macroalgal assemblages in southwestern Australia

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SUMMARY

Temperate Western Australia (WA) is home with one of the most speciose macroalgal assemblages in the world. Species diversity in WA subtidal macroalgal assemblages is first described along 100 km of temperate coastline between Cape Leeuwin and Cape Naturaliste, southwestern Australia. A large amount of variation in the macroalgal assemblage was significantly related to whether the substratum was limestone or granite, depth was <10 m or 10-20 m, and whether the reef was high relief (>2 m), or low relief. Combined with the habitat driven differences in assemblage structure, macroalgal assemblages were also influenced by the presence of a canopy of *Ecklonia radiata* (C. Agardh) J. Agardh: species richness was reduced and assemblage composition altered under canopies of this kelp. A clearance experiment, to test whether changes in macroalgal assemblages were related to the presence of *E. radiata*, was performed at Hamelin Bay. Species richness in cleared treatments was double that under *E. radiata* canopy and there was a significant shift in assemblage composition towards a more speciose *Sargassum* spp. dominated assemblage. *Ecklonia radiata* canopy was shown to have a negative influence on species richness and assemblage structure of macroalgae in temperate southwestern Australia. Gap creation in *E. radiata* kelp beds resulted in high species diversity and small-scale species turnover. The contemporary process of physical disturbance and the subsequent gap creation in *E. radiata* beds is an important process in maintenance of contemporary diversity of marine macroalgae in temperate Western Australia.

Keywords: disturbance, diversity, *Ecklonia radiata*, habitat, Western Australia

INTRODUCTION

The South West corner of Australia is a region of high species diversity and endemism for marine macroalgae (Phillips 2001). High species richness in the region is attributed to the lack of mass extinction events associated with unfavorable environmental conditions, like glaciation, over recent geological past, and the moderating influence of the Leeuwin Current on the WA coastline since the Eocene (McGowran *et al.* 1997). High endemism is the product of long isolation of the marine flora as Australia has been separated from other land masses for the past 80 million years (Veevers 1991; Phillips 2001).

This paper first presents an analysis from a baseline survey of macroalgal diversity in the Cape Naturaliste to Cape Leeuwin region in southwestern Australia. The survey was designed to document how major geographical and geomorphological features influence macroalgal diversity. The survey was designed to assess differences in species assemblages (species diversity, species abundance, species turnover) from a small number of locations, habitats and depths that represent the range of reefs found within the region.

A strong relationship between the presence of the kelp *Ecklonia radiata* and decrease in species richness was observed from the survey of the Cape Naturaliste to Cape Leeuwin region (Kendrick *et al.* 1999a) as well as near Perth, Western Australia (Kendrick *et al.* 1999b). We hypothesize that the establishment of kelp canopy reduces total species richness in the macroalgal assemblage. The creation of gaps in the kelp canopy through physical disturbance by storm swells enhances species richness. Opportunistic species that are unable to colonize under the kelp canopy are capable of growing in the gaps. Kelp canopy rather than being a positive influence on species richness as stated by Phillips (2001), has a negative influence.

The links between high macroalgal diversity in the region and patch creation in *Ecklonia radiata* kelp beds was further investigated with a kelp canopy clearance experiment at Hamelin Bay, a location within the original survey area. The experimental results, that species richness is greatest in cleared patches within the kelp bed and least under kelp canopy, support the observations made during the regional survey.

METHODS

Survey of Macroalgae Diversity

Marine macroalgae were surveyed from subtidal benthic marine habitats at 17 locations along 100 km of coastline

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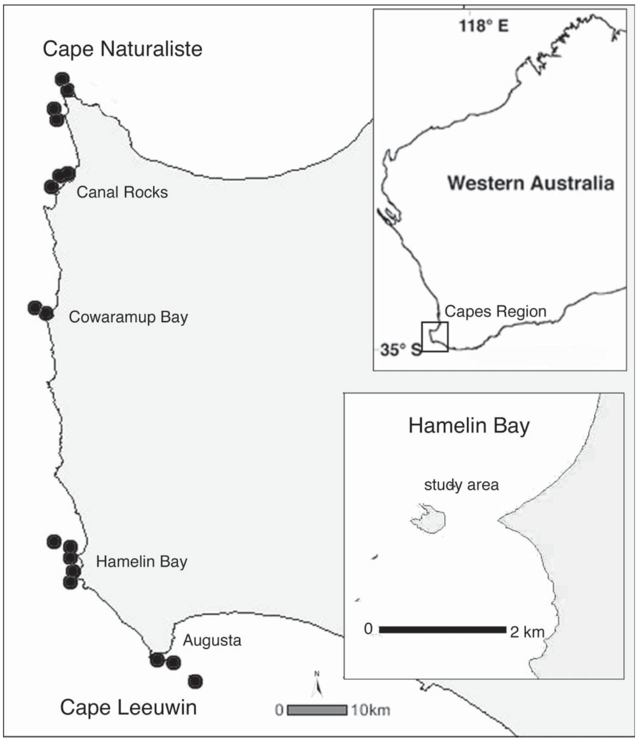

Fig. 1. Map of Capes Region showing sampling locations (∑) from the baseline survey between Cape Naturaliste and Cape Leeuwin conducted in 1999, and in the insert, detail of Hamelin Bay showing the study area for the clearing experiment conducted between April 2001 and February 2002.

between Cape Leeuwin (34˚22.78'S, 115˚08.86'E) and Cape Naturaliste (33˚31.95'S, 115˚01.06'E), on the southwest coast of Western Australia between 28th January and 8th February 1999 (Fig. 1). The survey design incorporated: 2 geographical regions: Southern and Western shores; 2 substrata: Limestone and Granite; 2 levels of relief of reefs: high and low relief high (>2 m and <2 m vertical relief, respectively); and 2 depths : <10 m, 10-20 m

The sampling design was not fully orthogonal as in some locations, combinations of substratum, relief and depth were difficult to locate. For example, limestone reef was restricted to the southwest portion of the study area and mostly occurred in shallow waters less than 10m deep.

At each location, divers collected macroalgae within six 0.25 m^2 quadrats placed randomly within a single substratum, relief and depth combination. Five quadrats were sampled at St. Alouarn Island and two quadrats at Sugarloaf, these two locations were undersampled because of deteriorating weather. Sampling was stratified such that only quadrats that fell on horizontal surfaces were sampled. Samples were sorted, and a species list compiled for each quadrat shortly after collection. Voucher specimens were prepared for each species and were accessioned in the Herbarium at the Botany Department, The University of Western Australia.

Differences in species composition of marine algae between regions, habitats and depths were analyzed using multivariate analysis of similarities (ANOSIM) on a Bray-Curtis similarity matrix constructed from 4th root transformed data. Clarkes Global R and significant probabilities were determined from 5,000 random permutations (Clark and Warwick 2001).

Single one-way ANOSIMs were used to address four specific null hypotheses:

H_{01}: There is no significant difference in assemblages of macroalgae between shallow (<10m) and deep (10-20 m) granite reefs.

H_{02}: There is no significant difference in assemblages of macroalgae between shallow limestone and shallow granite reefs.

H_{03}: There is no significant difference in assemblages of macroalgae between low and high relief granite reefs at deep locations (10-20 m).

H_{04}: There is no significant difference in assemblages of macroalgae between low and high relief limestone reefs at shallow locations (<10 m).

The relationship between the presence, density and biomass of the canopy forming kelp, *E. radiata* and species richness was investigated. Species richness was calculated for each sampling location and biomass and density of adult kelps recorded. Spatial patterns in the occurrence of algae species among sampling locations in the presence and absence of *E. radiata* were examined using 3 dimensional non-metric multidimensional scaling based on a Bray-Curtis dissimilarity matrix (Belbin 1993).

Hamelin Bay Clearance Experiment

The relationship between *Ecklonia radiata* canopy and macroalgal diversity was further investigated in a canopy clearance experiment in Hamelin Bay (34˚13.08'S, 115˚00.88'E), in the southwest part of the Cape Leeuwin to Cape Naturaliste study area. Prior to clearing (February, 2001) we surveyed high (>2 m vertical relief) and low relief (<2 m vertical relief) limestone reefs from Hamelin Bay and found significant differences in macroalgal assemblages between substrata (ANOSIM: Clarkes R = 0.253; $p < 0.001$, 5,000 permutations). The larger canopy species dominated low relief reef (*Ecklonia radiata, Scytothalia doryocarpa* (Turner) Greville , *Sargassum* spp.) whereas high relief reef had higher species richness and more even contributions of species (*E. radiata*, *Sargassum* spp., *Platythalia quercifolia* (R. Brown ex. Turner) Sonder, *Pterocladia lucida* (Turner) J. Agardh, *Amphiroa anceps* (Lamarck) Decaisne, *Metagoniolithon radiatum* (Lamarck) Ducker, *Metamastophora flabellata* (Lamarck) Ducker, *Caulerpa* spp.). Therefore, high and low relief reef was treated as separate habitats for the canopy clearance experiment. During April 2001 (autumn), 18 plots (9 on high and 9 on low relief reef) were cleared of kelp and other large macrophytes to a 10 m circle (314 m^2 cleared). Eighteen similar control plots were left uncleared. Here we describe the differences between cleared

Table 1. Results of ANOSIMs testing influence of reef type (limestone, granite), depth (<10 m, 10 - 20 m) and relief (>2 m, <2 m) on macroalgal assemblages.

HABITAT	Clarke's R	p value
H_{01}: Shallow vs Deep Granite	0.476	<0.001
H_{02}: Shallow Limestone vs Granite	0.458	<0.001
H_{03}: Low vs High Relief Deep Granite	0.101	0.031
H_{04}: Low vs High Relief Shallow Limestone	0.288	0.020

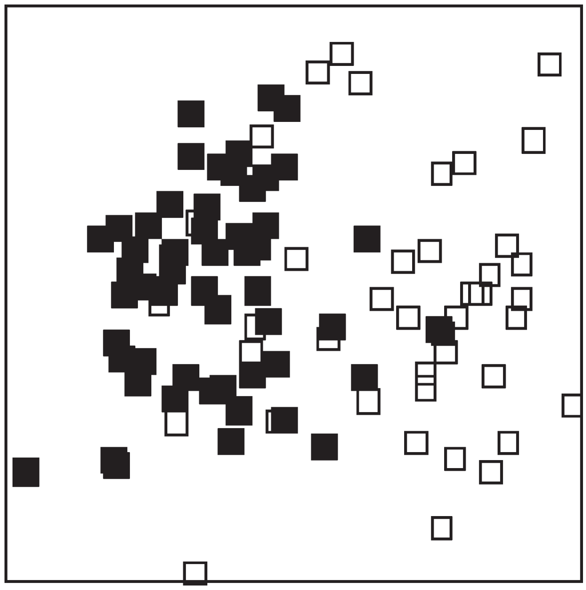

Fig. 2. Non-metric MDS plot of macroalgal assemblages in quadrats from the 1999 Cape Leeuwin to Cape Naturaliste survey (3D nMDS: axes 1 and 2 shown: stress = 0.18). Filled squares are quadrats with *E. radiata* and open squares are quadrats without *E. radiata*.

and uncleared plots in February 2002, 10 months after the clearings were established. Two-way fixed-factor non-parametric multivariate analysis of variance (NPMANOVA: Anderson, 2001) was performed on Bray-Curtis dissimilarities. This statistic allowed us to evaluate multivariate interactions. The fixed factors were relief (high, low) and clearance (cleared, uncleared). Influential species were further investigated using a similarity percentage procedure (SIMPER: Clark and Warwick 2001).

RESULTS

Exploratory data analysis

Macroalgal diversity was linked to habitat diversity. One hundred and fifty four taxa of marine macroalgae were identified from the Cape Leeuwin to Cape Naturaliste region. Approximately 75.5% of taxa occurred in 5 or less locations during the survey. Significant differences in macroalgal assemblages were observed between shallow and deep granite (reject H_{01}), limestone and granite reefs in shallow waters (reject H_{02}), high (>2 m) and low (< 2 m) relief deep granite (reject H_{03}) and high and low relief shallow limestone reefs (reject H_{04}) (Table 1).

Locations where *Ecklonia radiata* canopy was dominant had the lowest species richness (e.g. 20 taxa: Hamelin Bay). Locations that were characterized by granite substrata in shallow water (>10m depth) and that lacked a canopy of *E. radiata*, had highest numbers of taxa of benthic macroalgae (Foul Bay: 40 taxa; Canal Rocks: 50 taxa). The canopy in these areas was fucalean algae, either *Cystophora* spp or *Platythalia* spp. *E. radiata* and *Scytothalia doryocarpa* were the only canopy-forming species that occurred at greater than 50% of the survey locations. Of the 20 most commonly occurring understory taxa, 6 were coralline red algae (crustose corallines, *Haliptilon roseum* (Lamarck) Garbary & Johansen, *Amphiroa anceps*, *Metamastophora flabellata* , *Metagoniolithon radiatum*, *Jania pulchella* (Harvey) Johansen & Womersley, *Rhodopeltis australis* Harvey). Other abundant species included *Zonaria turneriana* J. Agardh and *Lobophora variegata* (Lamouroux) Womersley. Juveniles of *Scytothalia doryocarpa* and *E. radiata* were also common components of the understory. A nMDS plot of quadrats sampled during the survey indicated a difference in assemblage structure between those quadrats with *E. radiata* present and those without (Fig. 2). This difference was driven by numbers of species present in each quadrat, with fewer species of macroalgae in quadrats with *E. radiata*. Also, species richness of macroalgae at locations decreased as density and biomass of adult kelps increased (Fig. 3). As *E. radiata* increased in biomass (Fig. 3A) and density (Fig. 3B) the variability in species richness at any single biomass or density also increased dramatically.

Experimental Clearance in Hamelin Bay

Ten months after clearing (February, 2002) the macroalgal assemblages in areas where *Ecklonia radiata* canopy was cleared were significantly different from areas with *E. radiata* canopy (Table 2). The interaction between clearing and relief was not significantly different, suggesting the process of canopy loss through clearing had a similar influence on both high and low relief reef (Table 2). Species richness in areas where *E. radiata* canopy was cleared (28 ± 1, mean ± SE, n=18) was almost double that of areas with the *E. radiata* canopy intact (15 ± 1, mean ± SE, *n* = 18). Those species of macroalgae that contributed most to the differences in assemblage structure were canopy species that also contributed the most biomass to the macroalgae assemblage (e.g. *E. radiata*, *Scytothalia doryocarpa*, *Platythalia quercifolia*, *Cystophora retorta* (Mertens) J. Agardh and *Sargassum* spp.; Table 3). High relief reef contained larger numbers of species contributing to the differences between uncleared and cleared areas. *Ecklonia radiata* canopy was replaced by *Sargassum* spp. canopy in those areas that were cleared. *Sargassum* spp. increased in biomass over 185% between 6 and 10 months after canopy clearing, suggesting that *Sargassum* spp. are still in the process of establishment.

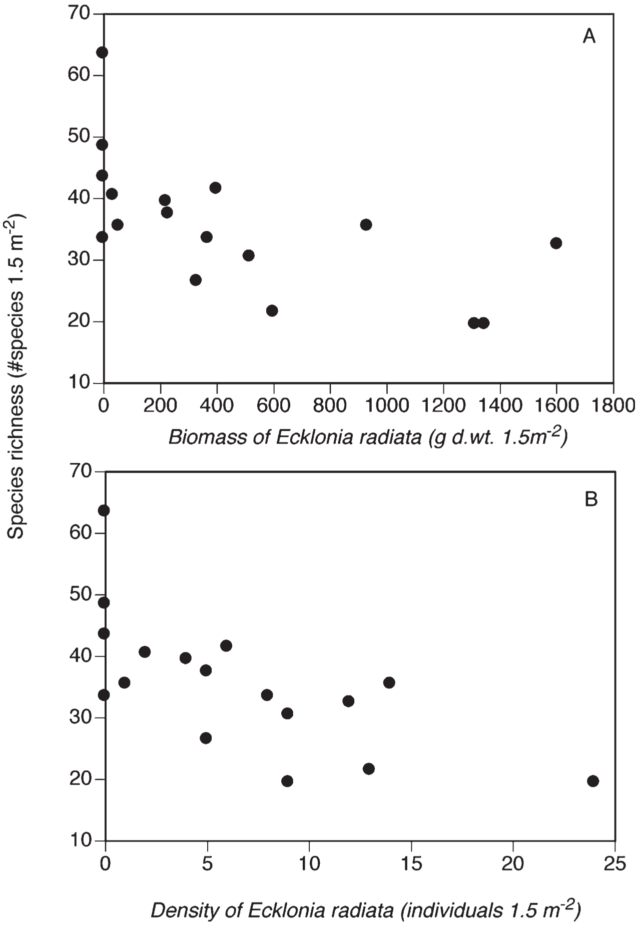

Fig. 3. Decrease in species richness with increase in total (A) biomass (g. dwt. 1.5 m^{-2}) and (B) density of adult *Ecklonia radiata* (individuals1.5 m^{-2}) for locations surveyed from the Cape Naturaliste to Cape Leeuwin region.

Table 2. Non-parametric Multivariate Analysis of Variance with Relief (High, Low) and Clearance (Uncleared, Cleared) as fixed factors. Data were square-root transformed. Analysis was based on Bray-Curtis dissimilarities with 5000 permutations.

Source	df	MS	F	P
Relief (R)	1	6803	4.32	0.0040
Clearance (C)	1	36555	23.23	0.0002
R x C	1	2394	1.52	0.1540
Residual	32	1573		
Total	35			

DISCUSSION

Diversity of macroalgae related to diversity of habitat

Diversity of marine macroalgae in southwestern Australia is in part linked to diversity of habitats of different rock types at different depths and to the presence of *Ecklonia radiata* canopy. Similarly, O'Hara (2001) found habitats supported unique macroalgal and faunal assemblages over 10˚ of latitude in Victoria, Australia. Assemblages of marine algae varied across the study region and were significantly different between granite and limestone reefs and between depths <10 m and 10-20 m.

Algal assemblages on deeper granite reefs offshore were significantly different to shallow onshore reefs and boulder fields. *Ecklonia radiata* and, *Scytothalia doryocarpa* were the dominant canopy on deeper granite reefs. The understory assemblage was depauperate, with the foliose red alga *Dictyomenia sonderi* Harvey and the bladed brown alga *Lobophora variegat*a recorded in patches with little or no kelp canopies. Shallow granite reef and boulder fields had species-rich canopies of *E. radiata*, *Sargassum*, *Cystophora*, *Platythalia* and *Scytothalia*. Understory assemblages were also more diverse, with high species turnover between replicate quadrats within locations.

Limestone reefs had similar dominant understory species to those observed in Marmion Lagoon, near Perth Western Australia (Hatcher 1989; Phillips *et al.* 1997; Kendrick *et al.* 1999b). *Amphiroa anceps*, *Jania pulchella*, *Callophyllis* sp. and *Pterocladia lucida* are abundant understory species under kelp-dominated limestone reefs from near Hamelin Bay to Augusta. The species, *A. anceps*, *Jania* sp. and *P. lucida* also characterize understory species in kelp forests on limestone reefs in Marmion Lagoon (Phillips *et al.* 1997; Kendrick *et al.* 1999b).

Local variability in species composition within habitats

Species composition was variable and species turnover was high between replicate quadrats within habitats. Algal assemblages in the study area were species rich (154 species) with many rare species. Similarly, from Marmion Lagoon, eighty two taxa of red, brown and green algae were found associated with *Ecklonia radiata* (Phillips *et al.* 1997). Many of these taxa were rare: only 18 occurred in >10% of samples and 13 taxa in 5-10%.

The negative influence of the kelp Ecklonia radiata

The contemporary process of physical disturbance and the subsequent gap creation in *E. radiata* beds is an important process in maintenance of contemporary diversity of marine macroalgae in temperate Western Australia. *Ecklonia radiata* canopies exerted a negative influence on diversity of marine macroalgae. In the presence of *E. radiata*, macroalgal assemblages are species poor. Local diversity in marine macroalgae are maintained through the physical removal of canopy species by swells during storms and the colonisation of those cleared gaps by a range of ephemeral, opportunistic species, including other canopy species like *Sargassum* spp. Most locations within *E. radiata* beds have a mosaic of *E. radiata* dominated canopy and gaps occupied by more species-rich macroalgal assemblages with canopies of *Sargassum*, *Cystophora* and *Platythalia*. These local scale patterns reflect the interaction between local disturbance and colonization history, localized dispersal and

Table 3. Mean percent dissimilarity between macroalgal assemblages in cleared treatments (Cleared) and uncleared *E. radiata* dominated canopy (Uncleared) calculated from SIMPER, and most influential species (species that contributed to 90% of overall dissimilarity).

	Mean % dissimilarity	Uncleared	Cleared
Low relief reef	94.2	*Sargassum paradoxum* (R. Brown ex. Turner) Hooker & Harvey	*Ecklonia radiata*
		Codium duthiae Silva	*Scytothalia doryocarpa*
High relief reef	96.1	*Sargassum paradoxum*	*Ecklonia radiata*
		Sargassum distichum Sonder	*Scytothalia doryocarpa*
		Sargassum podocanthum Sonder	*Platythalia quercifolia*
		Lobospira bicuspidata Areschoug	*Cystophora retorta*
		Glossophora nigricans (J. Agardh) Womersley	
		Pterocladia lucida	
		Codium duthiae	

recruitment in macroalgae, and patchiness in grazing (Kendrick *et al.* 1999b).

A canopy clearance experiment on high and low relief limestone reef supported our observations that gap creation in *Ecklonia radiata* canopies maintained diversity of benthic macroalgae. The influence of local interactions between *E. radiata* and other benthic macroalgae has a large and statistically significant influence on diversity of the macroalgal assemblage within any habitat. The scale of canopy influence on diversity is similar in size to differences in macroalgae assemblages between habitats. Similarly, in clearing experiments in eastern Australia, a range of species of filamentous and foliose turfing algae dominated substrata after kelps were removed (Kennelly 1987). The turf persisted and kelps did not recruit back into these areas. Kennelly (1987) proposed that turfs were an alternative state to the *E. radiata* canopy, but warned that this was heavily influenced by the spatial and temporal scales being studied and the timing of clearances.

What drives this process of reduction in macroalgae species under kelp canopies? We have tested a range of factors that could influence macroalgae under canopies and have found the reduction in light under canopies to be the major factor in southwestern Australia (Wernberg and Kendrick, unpublished data). Other factors, like sand inundation and canopy scour, have been shown to have an influence on understory algae and animals in other temperate locations in Australia (Melville and Connell 2001).

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