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BIODIVERSITY RESEARCH

Regional differences in kelp-associated algal assemblages on temperate limestone reefs in south-western Australia

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Abstract. *Ecklonia radiata* (C. Agardh) J. Agardh kelp beds — a characteristic feature of the near-shore environment along the south-west Australian coastline — contribute significantly to the coastal biodiversity in temperate Australia, yet, little is known about the organization of these macroalgal assemblages.

By compiling existing and new data sets from habitat surveys, we have characterized and compared the structure of kelp-associated macroalgal assemblages in three regions (Marmion Lagoon, Hamelin Bay and the marine environment neighbouring the Fitzgerald River National Park) across more than 1000 kilometres of the south-west Australian coastline.

152 macroalgal taxa had been recognized within the three regions and this is in the range of species richness reported from other Australian and African kelp beds. The kelp-associated algal assemblages were regionally distinct, 66% of all taxa were only found in one region and only 17 taxa were found in all three regions. Adjacent regions shared an additional 13–15 taxa. The regional shifts in assemblage structure were evident in species composition of both canopy and understorey. The organization of assemblages followed a spatial hierarchy where differences in assemblage structure were larger among regions (hundreds of kilometres apart) than among sites within regions (kilometres apart) and differences among sites within region were larger than differences among quadrats within sites (metres apart). Despite this hierarchy each level of nesting contributed approximately the same to total variation in assemblage structure and these spatial patterns were stronger than temporal differences from seasons to 2–3 years. Our results suggest that local and small-scale processes contribute considerably to heterogeneity in macroalgal assemblages throughout south-western Australia, and, in particular, our results are consistent with *E. radiata* exerting a strong influence on macroalgal assemblage structure. Further, our study contradicts the existence of a general south-west Australian kelp assemblage, although a few species may form the core of *E. radiata* associations across regions.

Key words. Biogeography, *Ecklonia radiata*, kelp beds, macroalgal assemblage structure, regional, local and small-scale processes, Western Australia.

INTRODUCTION

Macroalgae and macroalgal habitats contribute significantly to the biodiversity of temperate coasts in Australasia (Schiel, 1990; O'Hara, 2001; Phillips, 2001; Kendrick *et al.*, 2003), Africa (Leliaert *et al.*, 2000) and in the northern hemisphere (Schiel and Foster, 1986), yet basic knowledge of species distributions and the processes structuring these patterns are lacking (Schiel, 1990; Underwood and Kennelly, 1990; Phillips, 1998). In particular, no study has compared algal assemblages across regions in temperate Western

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Australia and species-level studies are needed, not only to further our understanding of Australian kelp bed ecology, but also to understand larger-scale patterns in species diversity (Phillips, 2001).

Temperate limestone reefs in Western Australia

Nearshore limestone reefs are a prominent feature along more than 1600 kilometres of the south-west Australian coastline where they run almost unbroken from Shark Bay to Cape Leeuwin (Searle and Semeniuk, 1985) and mixed with granite reefs from Cape Leeuwin to Esperance (Kendrick, 1999). These reefs are linked through the dominant oceanographic feature influencing temperate Western Australia: the warm surface waters of the Leeuwin Current that flow south along the continental slope on the west coast and eastward on the continental shelf on the southern coast of Western Australia (Pearce, 1991). This current is strongest in austral winter and moderates winter seawater temperatures for the western and southern coasts of Western Australia (Fig. 1). The common kelp, *Ecklonia radiata* (C. Agardh) J. Agardh, which grows to a length of 1–2 meters (Wernberg *et al.*, 2003), is the dominant foliose alga on most nearshore limestone reefs (Phillips *et al.*, 1997; Kendrick *et al.*, 2003) where it forms a distinct habitat generally referred to as a kelp forest or a kelp bed (Steinberg and Kendrick, 1999).

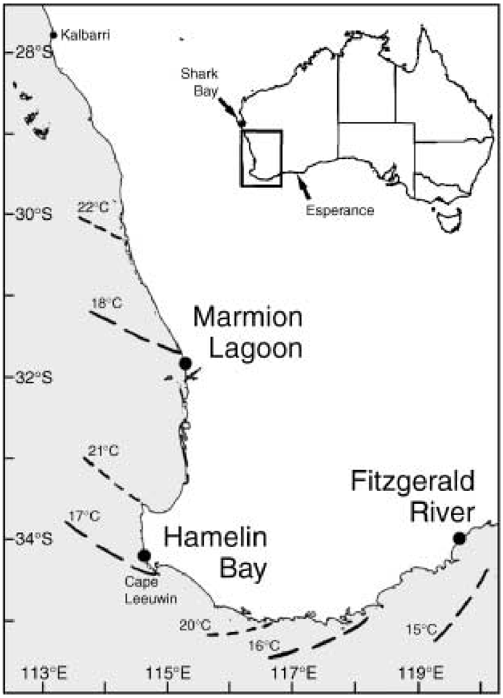

Fig. 1 Location of the three study regions: Marmion Lagoon, Hamelin Bay and Fitzgerald River along the Western Australian coastline. Short dashes are summer (February) and long dashes are Winter (August) isotherms (after Pearce, 1991).

Heterogeneity in Australian kelp beds

The dominance of *Ecklonia radiata* creates an impression of a homogeneous habitat across a range of spatial extents from metres to hundreds of kilometres or more. Even so, numerous studies over the past two decades have emphasized how community structure (i.e. the relative species composition, Foster, 1990) of *E. radiata* beds is variable over multiple temporal and spatial scales (Hatcher, 1989; Underwood *et al.*, 1991; Kennelly and Underwood, 1992, 1993; Phillips *et al.*, 1997; Kendrick *et al.*, 1999a, 2003; Andrew and O'Neill, 2000; Fowler-Walker and Connell, 2002). The processes behind this heterogeneity include direct and indirect interactions among macroalgae (Kennelly, 1987a, 1989), grazing (Andrew and Jones, 1990; Andrew, 1993; Andrew and O'Neill, 2000), hydrodynamic gradients (Hatcher, 1989; Phillips *et al.*, 1997) and large-scale environmental clines and biogeography (Huisman *et al.*, 1998; Phillips, 2001). Despite this large research effort the organization (i.e. causes of structure, Foster, 1990) of these kelp beds appears complex and remains poorly understood. Therefore, only limited generalizations about the spatio-temporal variability of communities in these subtidal habitats have been possible (Schiel, 1990; Underwood and Kennelly, 1990; Kennelly and Underwood, 1992; Fowler-Walker and Connell, 2002). Indeed, the answer to a fundamental question remains ambiguous: are kelp beds just loose associations of species with no consistent patterns other than the presence of kelp (Kennelly and Underwood, 1992) or are they organized habitats with predictable patterns of community structure (Melville and Connell, 2001; Fowler-Walker and Connell, 2002)?

Identifying spatial scales of significant variation is a primary step in generating hypotheses about spatial organization for experimental testing (Underwood and Petraitis, 1993). For example, on scales of regions hundreds of kilometres apart, variation in kelp-associated macroalgal assemblages may be caused by geographical clines in the contemporary environment (Anderson *et al.*, 1997; Middelboe *et al.*, 1997; Huisman *et al.*, 1998; Leliaert *et al.*, 2000; Phillips, 2001) or historical constraints on biogeography (Phillips, 2001). Local variation, among sites separated by kilometres, may originate from differences in geology (Wells *et al.*, 1989; O'Hara, 2001; Harman *et al.*, 2003a) or exposure to waves (Shepherd and Womersley, 1970; Phillips *et al.*, 1997; Collings and Chesire, 1998; Leliaert *et al.*, 2000). Small-scale variation, i.e. among quadrats separated by metres, may be caused by differences in kelp canopy cover (Kennelly, 1989; Kendrick *et al.*, 1999a, 2003; Melville and Connell, 2001) or the grazing activity of fish and invertebrates (Andrew and Jones, 1990; Andrew, 1993). Estimating the relative importance of variation at each of these spatial scales may therefore provide information on the relative importance of the different processes structuring kelp beds in Western Australia and give a point of comparison to other temperate *Ecklonia radiata* kelp beds in Australia, New Zealand and Africa.

Aim and predictions

The aim of this study was to characterize regional patterns in species richness and composition of macroalgal assemblages associated with kelp beds in south-western Australia, and to identify the relative importance of regional, local and small-scale processes in the organization of these assemblages.

We tested three competing models (Cleland, 2001) of macroalgal assemblage organization on limestone reefs in Western Australia. We do not consider these models mutually exclusive, but use them as a heuristic tool: regional scale organization of assemblage structure predicts large differences among regions, and relatively small differences among smaller spatial scales, because assemblages change gradually over hundreds of kilometres without being markedly affected by local or small-scale processes. Local-scale control of assemblage structure predicts large differences among sites within regions as assemblages respond to broad (kilometres) environmental conditions, and small-scale assemblage organization predicts large variation among quadrats metres apart because many ecological processes such as canopy — understorey interactions takes place on these spatial scales (Kennelly, 1989; Kendrick *et al.*, 1999a, 2003; Connell, 2003; Wernberg, 2003).

To test these predictions we collated and compared data on algal assemblage structure in *Ecklonia radiata* kelp beds from surveys of the limestone reefs in three regions of temperate south-western Australia (Table 1). The surveys were made in different years (1996, 1998 and 1999) and at slightly different times of the year. As a consequence of this weakness in the analysis we also estimated the potentially confounding effects of interannual and seasonal differences (Underwood and Petraitis, 1993) from within two of the regions.

METHODS

Study sites

The data presented in this study were collected from Marmion Lagoon (31°50′S, 115°42′E), Hamelin Bay (34°14′S, 115°01′E) and the marine environment neighbouring the Fitzgerald River National Park (hereafter referred to as Fitzgerald River; 33°56′S, 120°07′E). These three regions are distributed along more than 1000 kilometres of coastline around the south-western corner of Australia (Fig. 1) and cover two-thirds of the distribution range of temperate limestone reefs in south-west Australia (Searle and Semeniuk, 1985).

All three regions are characterized by a series of limestone reefs, were approximately the same depth and similar range of wave exposures. Marmion Lagoon is characterized by a series of three high relief (> 2 m) limestone ridges that run parallel to the shore onshore, 3 and 5 kilometres offshore, but low relief reef platforms are also abundant (Phillips *et al.*, 1997). The main reef system is approximately 15 kilometres long and most reefs are found within 3–10 m depth. The region has its name from the sheltered waters behind the innermost reef line, but the majority of reefs are located outside of this. In Hamelin Bay the reef system is dominated by several small limestone islands and granitic outcrops (Harman *et al.*, 2003a). Both limestone and granite reefs

Table 1 Sampling statistics for the data sets included in the analyses. Sites and quadrats were separated by 1–3 km and 1–10 m, respectively. A 0.25-m^2 quadrat was used in all data sets

Data set	Used in analysis	Time of sampling	No. of Sites	No. of Quadrats	Sampling design published in	Collected by and/or published in
Marmion Lagoon						
MAR1	R	Apr–May 1996	9	90	Haphazard allocation of 10 quadrats within 3 sites nested within 3 wave exposure levels. Algae harvested and identified.	Phillips *et al.* (1997), Kendrick *et al.* (1999a)
MAR2	T_1	Nov 2000	6	18	Haphazard allocation of 3 quadrats within 3 sites nested within 2 wave exposure levels. Sites selected as > 60% kelp canopy cover. Algae identified *in situ* by G.A. Kendrick	T. Wernberg and G.A. Kendrick
MAR3	T_1	Nov 2001	6	18	As for MAR2.	As MAR2
MAR4	T_3	May 1999–Apr 2001	1	85	Haphazard allocation of 5 quadrats within 1 site at each of 17 monthly sampling times. Algae harvested and identified.	T. Wernberg
Hamelin Bay						
HAM1	R, T_2	Jan–Feb 1999	6	35	Haphazard allocation of 5–6 quadrats within sites evenly distributed across the region to sample a range of physical environments. Algae harvested and identified.	Kendrick *et al.* (1999b)
HAM2	T_2	Feb 2000	3	36	Haphazard allocation of 6 quadrats within high and low relief limestone reefs nested within sites. Algae harvested and WW determined.	G.A. Kendrick and N. Harman
HAM3	T_2	Feb 2001	3	54	As for HAM2, number of quadrats increased to 9 per site.	G.A. Kendrick and N. Harman
Fitzgerald River						
FIT	R	Feb–Mar 1998	8	84	8–10 quadrats located at 10 m intervals along a transect within sites distributed across major physical habitats. Algae identified *in situ*. Large data set subsampled to only include samples from limestone reefs collected by G.A. Kendrick to minimize observer bias.	Kendrick in Bancroft and Davidson (2000)

R = regional comparison, T = Temporal comparison 1, 2 or 3.

Table 2 Species richness, observed and estimated, of each data set. No. of species max is the parameter estimate (± SE) for the asymptote of a hyperbolic function fitted to the species-sample data, r^2 is the correlation coefficient for the hyperbolic regression model

Data set	No. of species found	No. of species max	Saturation (% found of max)
MAR1	67	80.1 ± 0.8 ($r^2 = 0.99$)	83.6
MAR2	43	49.9 ± 0.5 ($r^2 = 0.99$)	86.2
MAR3	40	47.4 ± 0.9 ($r^2 = 0.98$)	84.4
MAR4	94	99.3 ± 0.5 ($r^2 = 0.99$)	94.7
HAM1	66 (63*)	81.2 ± 1.2 ($r^2 = 0.99$)	81.3
HAM2	45	56.3 ± 0.8 ($r^2 = 0.98$)	79.0
HAM3	56	68.2 ± 0.8 ($r^2 = 0.99$)	82.1
FIT	87	97.5 ± 0.5 ($r^2 = 0.99$)	89.2

* when standardized with HAM2 and HAM3 for the temporal comparison. MAR = Marmion Lagoon, HAM = Hamelin Bay, FIT = Fitzgerald River.

are found in the region, which extends from Hamelin Bay itself southward 10 km into the adjacent Foul Bay. Most reefs are found in depths less than 15 m, but offshore reefs continue beyond 30 m. The limestone reefs in Fitzgerald River occur as a series of offshore ridges much like Marmion Lagoon. They occur from Hopetoun to Starvation Boat Harbour, approximately 30 km to the east, and consist mainly of narrow platforms parallel to the coastline at depths of 3–15 m. Granitic islands and outcrops are also common offshore and to the west of the study area.

Assemblage data

We define ‘assemblage’ as the macroalgae of temperate limestone reefs in Western Australia (Fauth *et al*., 1996). Assemblage data were collected from a number of sites in each of the three regions (Table 1). All sites included were limestone reefs in the depth range 7–10 m. Large (> ~1 centimetre) epilithic macroalgae were sampled within 0.25 m^2 quadrats by SCUBA diving and either harvested for identification in the laboratory or identified *in situ*; in the latter case reference material was brought back for further identification. Assemblage data were standardized for analyses among the relevant data sets (Table 1) by grouping all lower taxa under their highest common taxon (usually genus) whenever there were inconsistent levels of identification. This has been demonstrated to have little effect on the overall assessment of patterns of diversity in south-western Australian algal assemblages (Harman *et al*., 2003b). Unidentified groups of encrusting algae (e.g. ‘corallines and crust’, ‘brown crusts’ and ‘red crusts’) were not used in multivariate analyses. Algal taxonomic nomenclature followed. Womersley (1984, 1987, 1994, 1996, 1998), Huisman and Walker (1990) and Huisman (2000). A complete list of taxa can be found as an online appendix at the journal website.

To estimate how well each data set described the assemblage it sampled, species-sample curves showing the increase in new species detected as the number of samples (quadrats) increased, were generated by permutation of the species-sample matrix (Primer ver. 5.2.0, Clarke and Gorley, 2001). A hyperbolic function was found to model the data accurately ($r^2 > 0.98$; Table 2) and was fitted to each species-sample curve (Sigmaplot ver. 4.01). The asymptote was used as an estimate of the maximum number of detectable species in the assemblage. Saturation was calculated as the total number of species found relative to the estimated maximum number of detectable species. The estimate of maximum detectable species is specific to the sampling method and the saturation is a measure of adequacy of sampling effort (number of quadrats) given the limitations of the method. The relationship between sampling effort and species richness was analysed with Pearson’s Product — Moment Correlation (Zar, 1996).

Multivariate analyses

All multivariate analyses, except nonparametric multivariate analysis of variance (NP-MANOVA), were conducted in Primer version 5.2.0 (Clarke and Gorley, 2001). Bray-Curtis dissimilarities (Bray and Curtis, 1957) were calculated using species presence-absence data between all quadrat pairs for each set of analyses.

Differences among and within regions were evaluated from three data sets (MAR1, HAM1, FIT; Table 1). Summary statistics on species richness were calculated to describe the distribution of taxa among these three regions. Three-dimensional nonmetric multidimensional scaling (nMDS) was used to graphically depict the relationship among samples but only the most informative plot, subjectively selected in terms of apparent groupings, is presented. Analysis of similarities (Anosim: Clarke, 1993), with sites nested within regions, followed by *post hoc* pairwise comparisons, was performed to test the degree of difference among regions. To identify which taxa most influenced the observed patterns by exhibiting consistent differences among groups, percentages of similarities (Simper: Clarke, 1993) were used to calculate the relative contribution of each taxon towards the total dissimilarity between two samples. Assemblage heterogeneity among regions, among sites nested within regions and among quadrats within sites was compared by averaging the mean dissimilarity among samples within each of these levels of nesting. In addition, nested NP-MANOVA (Anderson, 2000, 2001) was performed on a data set reduced by randomly deleting samples to balance the number of sites and quadrats among regions. This analysis is analogous to a nested analysis of variance (Anderson, 2001) and partitions the total multivariate variation into the contributions from each spatial component in the sums of squares (SS). The percentage contribution to the total variation can then be calculated for each level of nesting and this provides a direct measure of their relative importance to assemblage heterogeneity in the data set (Welden and Slauson, 1986).

The temporal variation of algal assemblages was addressed to estimate the bias of using data sets collected at different times for the spatial analyses. Three tests of temporal variation were performed; three data sets collected in Hamelin Bay each February from 1999 to 2001 (HAM1, HAM2, HAM3; Table 1), two data sets from Marmion Lagoon collected in November 2000 and 2001 (MAR2 and MAR3), and a data set from Marmion Lagoon (MAR4) where the assemblage was sampled approximately every month from May 1999 to April 2001. In this data set samples were grouped into seasons (Autumn: March, April, May; Winter: June, July, August; Spring: September, October, November and Summer: December, January, February) for analysis. Differences in assemblage structure among sampling times were tested with one-way ANOSIM (Clarke and Green, 1988).

RESULTS

Species-sample relationships

Between 40 and 94 macroalgal taxa were recognized in each of the eight data sets included in this study, and across all data sets there was a significant correlation ($R = 0.85$, $P = 0.008$, $n = 8$) between the number of quadrats sampled and the species richness found. Each data set described the assemblage relatively well as the species-sample curves indicated that more than 80% of the maximum detectable species were picked up in all data sets (Table 2).

Regional differences in algal assemblages

A total of 152 algal taxa were recognized in the three regions (Fig. 2) and the number of taxa was of the same order of magnitude within each region. Only 17 of the 152 taxa (11%) were found in all three regions whereas 101 (66%) taxa were found only in one region. Marmion Lagoon, Hamelin Bay and Fitzgerald River had 31, 21 and 49 unique taxa, respectively (46%, 56% and 32% of the regional algal flora). Hamelin Bay, located midway between Marmion Lagoon and Fitzgerald River, shared more than twice as many taxa with each of these two regions as the two other regions did with each other.

The three regions had significantly different, although overlapping, algal assemblages (Fig. 3, Table 3, Table 4). Generally, there were low contributions to assemblage dissimilarity from individual species in pairwise comparisons among regions (Table 5). The contributions of individual

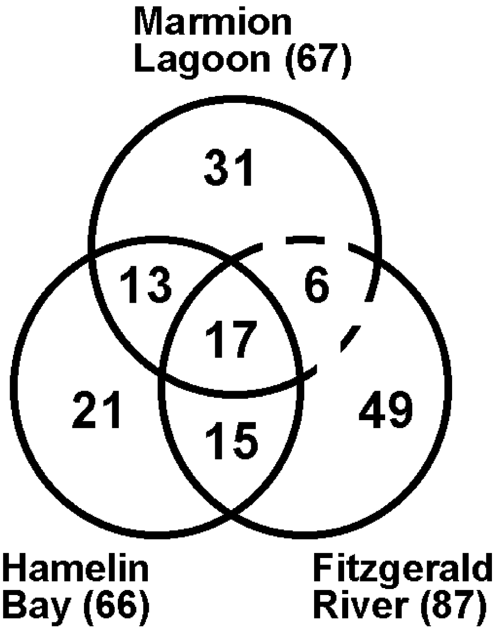

Fig. 2 Venn-diagram of the distribution of macroalgal taxa among the three regions. Numbers in parentheses are total numbers of species found within a region. The broken lines between Marmion Lagoon and Fitzgerald River indicate that these regions are geographically disjunct.

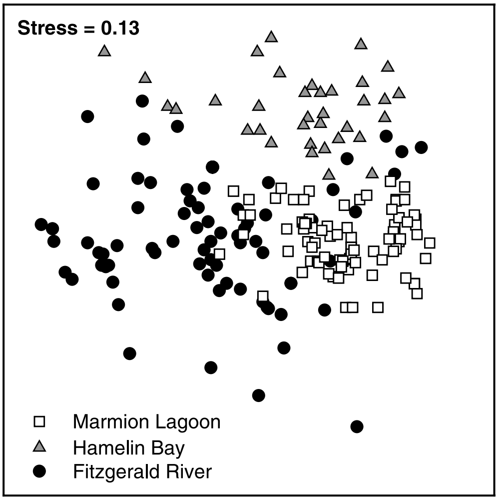

Fig. 3 Three-dimensional nMDS plot of samples of macroalgal presence-absence in Marmion Lagoon, Hamelin Bay and Fitzgerald River. Only dimension 1 (*X*-axis) and dimension 3 (*Y*-axis) are shown.

Table 3 Results from the two-way nested ANOSIM among regions and *post hoc* pairwise comparisons, based on 999 permutations

	Clarke's *R*
Global test	
Regions	0.582
Sites (regions)	0.632
Pairwise comparisons	
FIT vs. HAM1	0.535
FIT vs. MAR1	0.678
HAM1 vs. MAR1	0.808

$P \leq 0.003$; MAR = Marmion Lagoon, HAM = Hamelin Bay, FIT = Fitzgerald River.

species to dissimilarity were also not consistent between pairwise comparisons. Changes in algal assemblage structure were associated with changes in both canopy and understorey algae (Table 5). The importance of *Ecklonia radiata* as a canopy species was gradually replaced by Fucalean algae (e.g. *Sargassum* spp., *Cystophora* sp. and *Scytothalia doryocarpa* (Turner) Greville) from Marmion Lagoon to Fitzgerald River and the species richness of the canopy increased three-fold (Fig. 4). Of the 20 species with the highest contribution to within-region similarity, only five were common to all three regions (Table 6).

There were significant differences in assemblage structure among sites nested within regions (Table 3, Table 4). Dissimilarities in assemblage structure were hierarchical with regions > sites > quadrats (Fig. 5). However, the relative contribution of each level of nesting to the total multivariate variation indicated that each level of nesting contributed roughly the same (30–35%; Table 4) to heterogeneity in assemblage structure.

Temporal variation of algal assemblages

The assemblage structure was barely separable ($R < 0.25$, Clarke and Gorley, 2001) among sampling times within both Marmion Lagoon and Hamelin Bay (Table 7). The differences in assemblage structure were as small among seasons as they were among consecutive years.

Table 4 Results from NP-MANOVA. 49 999 out of > 10^{10} possible permutations were used to calculate the *P*-values

Source of variation	D.f.	SS	*F*	*P*	% of multivariate variation
Region	2	69 892	6.47	< 0.001	29.9
Sites (region)	15	81 030	4.71	< 0.001	34.7
Quadrats (sites)	72	82 584			35.4
Total	89	233 506			100

SS = Percent of multivariate variation is equivalent of percentage Sum of Squares.

Table 5 The 10 algal species with the highest contribution towards dissimilarity among Marmion Lagoon (MAR1), Hamelin Bay (HAM1) and Fitzgerald River (FIT)

	Abundance (% of quadrats)		Contribution to dissim. among regions (%)	Consistency of contribution (mean dissim./SD)
Species	MAR1	HAM1	mean dissimilarity = 73.7	
Metamastophora flabellata (U)	1	60	4.6	1.12
Callophyllis sp. (U)	11	63	4.5	1.13
Peyssonnelia rubra (U)	0	54	4.4	0.94
Scytothalia doryocarpa (C)	3	60	4.4	1.11
Pterocladia lucida (U)	87	51	4.1	0.86
Amphiroa anceps (U)	24	51	4.0	0.92
Sargassum spp. (C)	54	20	3.9	0.97
Lobophora variegata (U)	16	40	3.6	0.76
Jania sp. (U)	7	49	3.6	0.94
Curdiea obesa (U)	12	40	2.3	0.90
	MAR1	**FIT**	**mean dissimilarity = 83.3**	
Pterocladia lucida (U)	87	4	6.8	1.54
Unidentified red sp. 1 (U)	0	75	5.9	1.25
Rhodymenia sonderi (U)	87	30	5.4	1.15
Sargassum spp. (C)	54	55	3.9	0.89
Lobophora variegata (U)	16	58	3.9	1.00
Ecklonia radiata (C)	99	58	3.5	0.75
Amphiroa anceps (U)	24	44	3.3	0.83
Chauviniella coriifolia (U)	38	19	2.8	0.79
Sargassum tristichum (C)	3	39	2.5	0.73
Laurencia spp. (U)	16	27	2.4	0.68
	HAM1	**FIT**	**mean dissimilarity = 84.5**	
Unidentified red sp. 1 (U)	0	75	4.5	1.34
Rhodymenia sonderi (U)	80	30	3.8	1.17
Callophyllis sp. (U)	63	1	3.6	1.17
Metamastophora flabellata (U)	60	0	3.5	1.10
Peyssonnelia rubra (U)	54	0	3.4	0.93
Scytothalia doryocarpa (C)	60	25	3.3	0.98
Lobophora variegata (U)	40	58	3.1	0.88
Amphiroa anceps (U)	51	44	3.1	0.90
Sargassum spp. (C)	20	55	3.0	0.93
Pterocladia lucida (U)	51	4	2.9	0.95

C = canopy species, U = understorey species; determined from SIMPER.

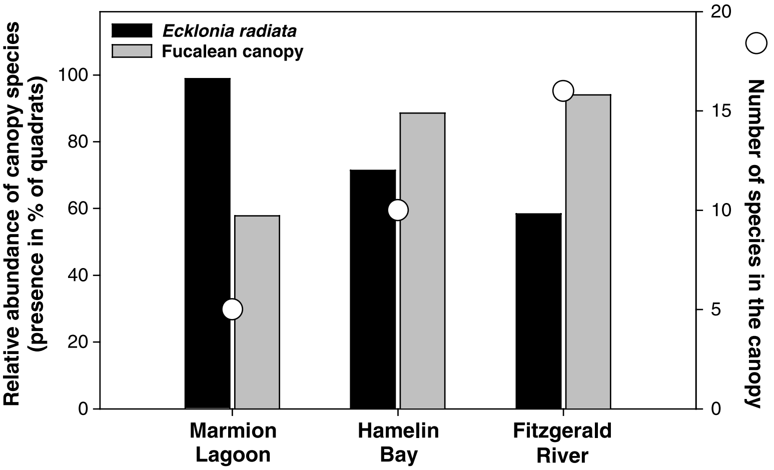

Fig. 4 The relative importance of *Ecklonia radiata* and Fucalean macroalgae (e.g. *Sargassum* spp., *Cystophora* spp. and *Scytothalia doryocarpa*) as canopy species, and the number of taxa in the canopy, across regions.

Table 6 Main contributors to similarity within regions, common to all three regions, among the 20 most influential species in each data set. Rank indicate the species' contribution to within-region similarity and abundance gives its frequency of occurrence in the quadrats sampled

	Marmion Lagoon		Hamelin Bay		Fitzgerald River	
	Rank	Abundance	Rank	Abundance	Rank	Abundance
Canopy						
Ecklonia radiata	1	99%	2	71%	2	58%
Sargassum spp.	4	54%	19	20%	4	55%
Understorey						
Rhodymenia sonderi	3	87%	1	80%	9	30%
Amphiroa anceps	7	24%	7	51%	5	44%
Lobophora variegata	12	16%	10	40%	3	58%

DISCUSSION

The study area is located well within the broad transition zone between the tropical Damperian and temperate Flindersian macroalgal provinces (Huisman *et al*., 1998). To our knowledge, this floristic gradient has previously only been described qualitatively in compilations of species lists. The structure of algal assemblages associated with *Ecklonia radiata* kelp beds within this overlap zone demonstrated regional, local and small scale organization. Spatial patterns in assemblage structure were consistent with a strong influence from a large-scale geographical cline, despite the ubiquitous distribution of the dominant and influential canopy species *E. radiata*. However, variation in assemblage structure at local and small spatial scales were of similar magnitude and suggest that processes such as differences in wave exposure and habitat modification by kelp, are very important to the organization of these habitats within regions. Our outcomes support the additive spatial model of algal assemblage organization proposed by Kendrick *et al*. (1999a) where organizational processes acting across scales of metres to kilometres result in variable algal assemblage structures at all spatial scales.

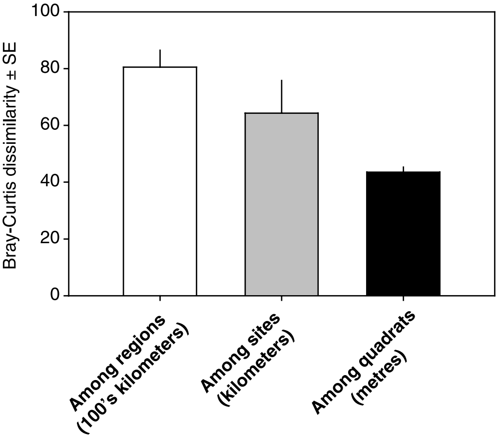

Fig. 5 Levels of dissimilarity among regions (Marmion Lagoon, Hamelin Bay and Fitzgerald River) separated by hundreds of kilometres, among sites separated by kilometres and among quadrats separated by metres. The dissimilarity among regions is the average of three pairwise comparisons, dissimilarities among sites and quadrats are averages across regions (i.e. $n = 3$).

Table 7 Results from one-way ANOSIMs of temporal differences in assemblage structure in Hamelin Bay and Marmion Lagoon. Autumn is March, April, May; Winter is June, July, August; Spring is September, October, November; and Summer is December, January, February; based on 999 permutations. $P \leq 0.02$

	R
Hamelin Bay	
February 99 vs. February 00 vs. February 01	0.197
Marmion Lagoon	
November 00 vs. November 01	0.109
Seasons (May 99–March 02)	0.142

Species distributions

South-western Australian kelp beds appear to be similar to other Australian and African kelp beds in terms of total species richness of the algal assemblage. May and Larkum (1981; Jervis Bay) and van der Velde and King (1984; Botany Bay) found 89 and 69 macroalgal species, respectively, in *Ecklonia radiata* kelp beds off New South Wales. O'Hara (2001) found a total of 169 algal species among a diverse range of subtidal habitats in Victoria (including kelp beds) while Shepherd and Womersley (1970) found 132 algal species among many subtidal habitat types around West Island in South Australia. Similarly, in South Africa, Leliaert *et al.* (2000) found 142 macroalgal taxa in the kelp beds around the Cape Peninsula.

The distribution of species was consistent with distinct regional algal assemblages with some overlap between adjacent regions. All regions had a high proportion of unique taxa, although Hamelin Bay had fewer than Marmion Lagoon and Fitzgerald River. Moreover, Hamelin Bay shared more species with Marmion Lagoon and Fitzgerald River than these regions did with each other. The southern Australian algal flora has the highest proportion of endemic species in the world (Bolton, 1994) and to a large degree this has been attributed to the region being relatively stable since the Eocene and the historical and contemporary influence of the Leeuwin Current (Phillips, 2001). Contrary to all other eastern boundary currents in the southern hemisphere the Leeuwin Current flows south (Pearce, 1991), bringing warm water down along the west coast, around the capes and onto the south coast. The transition zone between tropical and temperate algal floras is therefore very large unlike that found around the South African Cape (Bolton, 1986; Anderson *et al.*, 1997; Leliaert *et al.*, 2000), but similar to that described by Schiel (1990) from New Zealand.

In the Capes region, where Hamelin Bay is located, a cold summer inshore current called the Capes Current moves northwards counter to the Leeuwin Current (Gersbach *et al.*, 1999; Pearce and Pattiaratchi, 1999). The Capes Current may obstruct southward dispersal along the coast, isolating Hamelin Bay from Marmion Lagoon and increasing the effective dispersal distance between the west and the south coast. As most macroalgae have very limited long-range dispersal properties (van den Hoek, 1987) this could have implications for the exchange of species among regions.

Seventeen taxa of macroalgae were found in all three regions but only four of these (*Sargassum* spp., *Rhodymenia sonderi* P. Silva, *Amphiroa anceps* (Lamarck) Decaisne and *Lobophora variegata* (Lamouroux) Womersley ex. Oliveira), other than *E. radiata*, contributed markedly to similarity in assemblage structure within all regions. These species are also common components of *E. radiata* kelp beds in other parts of Australia (May and Larkum, 1981; van der Velde and King, 1984; Kennelly and Underwood, 1992), and while there appear to be no broad associations of algae justifying the definition of a universal kelp bed assemblage in Australia, there may be a core group of widely distributed algae which are often found in association. Interestingly, these species do not appear to be adapted to live in the biogenically modified environment under the kelp but rather in the low-kelp density gaps of the canopy (Kendrick *et al*., 1999a), suggesting that the association may be a response to similar environmental conditions rather than an association with kelp *per se*. As such, the positive interactions (Callaway, 1998) apparent across large spatial scales may represent a release from negative interactions on smaller spatial scales.

The kelp *Ecklonia radiata* decreases in importance as a canopy species from Marmion Lagoon to Fitzgerald River. This outcome is consistent with studies from the south coast showing a predominance of Fucalean algae in many places (e.g. Shepherd and Womersley, 1970; Collings and Cheshire, 1998; Goodsell *et al*., 2003). Causes for the change in canopy dominance requires further study, although the decrease in water temperature may play a major organizing role (see Hatcher *et al*., 1987 for *E. radiata* and Womersley, 1987 for Fucalean algae).

Assemblage organization

Heterogeneity in macroalgal assemblage structure appears to be organized by a hierarchy of processes where the relative importance of each process intergrades with changing spatial scales (Levin, 2000) such that the effect of kelp, and factors affecting the distribution of kelp, are superimposed on a larger geographical cline. Because of their obviously large influence on algal assemblage structure, understanding canopy–understorey interactions may be the key to deciphering the small-scale 'noise' clouding larger-scale patterns in assemblage structure and biodiversity (Kendrick *et al*., 1999a).

Differences among sites within regions, and, in particular, among quadrats within sites, were smaller albeit of the same magnitude as differences from region to region, suggesting that small-scale processes are equally important determinants of algal assemblage structure. Specifically, the canopy density of *Ecklonia radiata* varies at this spatial scale (Kendrick *et al*., 1999a; Wernberg, 2003), and *E. radiata* exerts a strong influence on macroalgal assemblage structure through modification of light and the physical environment (Kennelly, 1987b; Daume *et al*., 1999; Kendrick *et al*., 1999a, 2003; Melville and Connell, 2001). Grazing, a process often attributed to patterns at smaller spatial scales (Andrew and Jones, 1990; Jones, 1992; Andrew, 1993), does not appear to be a major factor in determining algal assemblage structure in Western Australia and abundances of the main invertebrate grazers, urchins (*Heliocidaris erythrogramma*, *Phyllacanthus irregularis* and *Centrostephanus tenuispinus*) and gastropods (*Turbo torquatus*, *Australium squamifera* and *Haliotis scalaris*) are generally very low (Fowler-Walker and Connell, 2002; Vanderklift, 2002). This is in contrast to the east coast of Australia (Andrew and Jones, 1990; Andrew, 1993; Fowler-Walker and Connell, 2002), northern New Zealand (Schiel, 1990) and east of Cape Point in South Africa (Anderson *et al*., 1997; Leliaert *et al*., 2000), but similar to observations from South Australia (Fowler-Walker and Connell, 2002), the South Island of New Zealand (Schiel, 1990) and west of Cape Point in South Africa (Anderson *et al*., 1997; Leliaert *et al*., 2000). We believe absence of macroinvertebrate grazers partly explains the predominance of foliose algae in the kelp understory in south-west Australia.

Macroalgal assemblage structure was relatively consistent on temporal scales from months to a few years in both Hamelin Bay and in Marmion Lagoon. Interannual and seasonal differences in macroalgal assemblages were 2–3 times less than differences reported from the regional study. The relatively small temporal variation in macroalgal assemblage structure, which probably reflects a dominance of perennial species, is consistent with observations from elsewhere in Australia. Both Shepherd and Womersley (1970; West Island, South Australia) and May and Larkum (1981; Jervis Bay, New South Wales) found the majority of species to be present in the macroalgal assemblage year round with only few species showing distinct seasonal patterns.

Limitations of compiled data: sampling biases

A mensurative experiment designed to test specific hypotheses about spatial patterns would have been more powerful than the 'meta-analysis' approach taken here. However, often logistics and funding precludes such large-scale experiments. Differences in sampling design and methods were the major inconsistencies among the data sets included in this study. For instance, some data sets were sampled by *in situ* identification of taxa, whereas sampling in others involved harvesting and laboratory identification. The former method tended to underestimate rare and small species and thus total species numbers and occurrences. Not all taxa could be identified to species but this is unlikely to affect our assemblage comparisons. Patterns of species composition have been shown to be consistent at genus and higher taxonomic levels in south-western Australia, because in many genera there are low numbers of species, and species within genera tend to have the same ecological requirements (Harman *et al*., 2003b). The positive correlation between regional species richness and the number of quadrats sampled is also a potentially serious bias. This relationship is confounded by total area and the diversity of subhabitats (i.e. number of sites) sampled, both of which are known to influence the number of detected species (Huston, 1994).

These methodological differences are important, but we think they are of lesser significance in the current regional comparison because any bias would contribute to an underestimation of the difference among assemblages: only Fitzgerald River (FIT), which was the most species rich data set, used *in situ* identification. All regions had similar saturation of species-sample curves despite different numbers of quadrats sampled. In conclusion, algal assemblages associated with kelp beds on limestone reefs in south-western Australia are distinct over spatial scales of hundreds of kilometres. The differences among algal assemblages over spatial scales of metres to kilometres however, have similar magnitudes as differences among regions, and these spatial patterns are stronger than temporal differences from seasons to a few years. Our results suggest that local (kilometre) and small-scale (metre) processes contribute considerably to heterogeneity in macroalgal assemblages and, in particular, our results are consistent with *E. radiata* exerting a strong influence on macroalgal assemblage structure on spatial scales of metres.

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SUPPLEMENTARY MATERIAL

The following material is available from: http://blackwellpublishing.com/products/journals/suppmat/DDI/DDI048/DDI048sm.htm

Table S1. Presence-absence of macroalgae in the data sets used in the geographical (MAR1, HAM1, FIT) and temporal (MAR2, MAR3; MAR4; HAM1, HAM2, HAM3) analyses of heterogeneity in macroalgal assemblages in south-western Western Australia. Numbers are quadrats with the taxon registered. Time of collection varied among data sets. Marmion Lagoon: MAR1 Apr–May 1996, MAR2 Nov 2000, MAR3 Nov 2001, MAR4 May 1999–Apr 2001. Hamelin Bay: HAM1 Jan–Feb 1999, HAM2 Feb 2000, HAM3 Feb 2001. The marine environment neighbouring the Fitzgerald River National Park: FIT Feb–Mar 1998. Au (autumn) = Mar, Apr, May; Wi (winter) = Jun, Jul, Aug; Sp (spring) = Sep, Oct, Nov; Su (summer) = Dec, Jan. Feb.

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