



## Assemblage turnover and taxonomic sufficiency of subtidal macroalgae at multiple spatial scales

Dan A. Smale<sup>a,\*</sup>, Gary A. Kendrick<sup>a</sup>, Thomas Wernberg<sup>a,b</sup>

<sup>a</sup> School of Plant Biology, University of Western Australia, Crawley, Western Australia, 6009, Australia

<sup>b</sup> Centre for Marine Ecosystems Research, Edith Cowan University, Joondalup, 6027 Western Australia, Australia

### ARTICLE INFO

#### Article history:

Received 21 September 2009

Received in revised form 19 November 2009

Accepted 23 November 2009

#### Keywords:

Kelp beds

Nearshore ecology

Nested designs

Southwest Australia

Spatial variability

### ABSTRACT

Spatial variability in the structure of subtidal macroalgal assemblages in southwest Australia was examined at multiple spatial scales using a three-factor hierarchical design. Spatial extents ranged from metres (between quadrats) to many hundreds of kilometres (between regions), and the study encompassed >2000 km of temperate coastline. In addition, the influence of taxonomic resolution, from species level data to class level, on spatial patterns was investigated to assess the potential evolutionary timescales of the pattern and for developing cost effective regionally applicable surrogates for biodiversity monitoring. Almost 300 species were identified from 14 sites, representing considerable biodiversity and a significant subset of the total benthic macroalgal diversity in the region (~1000 species). Multivariate variability was significant at all spatial scales examined, but most prominent at smallest spatial scales, regardless of taxonomic resolution. Assemblage and species turnover was pronounced at scales of metres to hundreds of metres. Generally, small scale patchiness was a ubiquitous pattern for all individual taxa examined, regardless of taxonomic resolution, while variability at the scale of 10s of km was less important. Even so, differences in spatial variability between taxa were observed, and ecological and historical reasons for such differences are proposed. Taxonomic aggregation to family level had minimal effect on spatial patterns, but aggregation to order level led to changes in some aspects of patterns of assemblage structure. The unique and speciose macroalgal assemblages on subtidal reefs in southwest Australia are shaped by a complex array of historical and contemporary processes that act at multiple spatial (and temporal) scales. Understanding the relative importance of these processes requires that further manipulative and correlative work is conducted across a range of ecologically-important spatial scales.

© 2009 Elsevier B.V. All rights reserved.

### 1. Introduction

The influence of spatial (and temporal) scale on ecological pattern, and the concept of taxonomic sufficiency and surrogacy for biodiversity monitoring have emerged as two key concepts in marine community ecology in recent decades (Hewitt et al., 2007; Magierowski and Johnson, 2006). The application of nested hierarchical sampling designs, conducted at spatial scales of <1 m to >1000 km, has led to a greater understanding of the importance of spatial scale on ecological pattern and process in marine habitats (Fraschetti et al., 2005). Fully nested sampling designs provide unbiased and independent assessments of variability at various spatial scales, which facilitates tests of structured hypotheses while maximising sampling efficiency (Underwood and Chapman, 1996; Underwood et al., 2000). In a recent review by Frascchetti et al. (2005), they reiterated that high variability at small

spatial scales (metres) is an almost ubiquitous pattern in benthic populations and assemblages, while variability at larger scales (kilometres) tends to differ more between habitats, locations and taxa. The authors also highlighted the relative lack of studies conducted in subtidal habitats and at regional scales of 1000 km or more.

With regard to biodiversity monitoring, a wide range of surrogates have been proposed for marine benthic communities. Surrogates for biodiversity are designed to be cost effective alternatives to species level data collection for entire assemblages, and usually involve either a measuring subset of species (or higher taxon) or quantifying complete assemblages at coarser taxonomic resolutions than species (e.g. Magierowski and Johnson, 2006; Olsgard et al., 2003). If a strong relationship exists between species level patterns (of richness or multivariate structure, for example) and surrogate patterns, the chosen surrogate may be a useful tool for ecological monitoring. However, a key assumption in the development of surrogates of biodiversity is that the relationship between the surrogate measure and actual biodiversity is constant in space and time (Colwell and Coddington, 1994). Previous work suggests that spatial patterns in marine benthic community structure at the genus and family levels are often sufficiently consistent

\* Corresponding author. Tel.: +61 8 64882219; fax: +61 8 64881108.  
E-mail address: [daniel.smale@uwa.edu.au](mailto:daniel.smale@uwa.edu.au) (D.A. Smale).

with species level patterns to serve as useful surrogates (Anderson et al., 2005a,b; Bates et al., 2007; Goldberg et al., 2006; Olsgard and Somerfield, 2000; Warwick, 1988). However, such consistencies have rarely been examined across multiple spatial scales, and the effect of taxonomic aggregation on patterns of community structure at the scale of regions to replicates clearly warrants further study.

Here, we examine variability in assemblage structure of subtidal macroalgae at multiple spatial scales, along >2000 km of temperate coastline in southwest Australia. Furthermore, we assess shifts in assemblage structure through space at different taxonomic resolutions, to determine taxonomic sufficiency at small to large spatial scales for ecological monitoring of a unique and speciose flora.

The temperate macroalgal flora of Australia is highly diverse and endemic (Kerswell, 2006; Phillips, 2001). Around 1000 species of benthic macroalgae have been recorded from southern Australia, with over 50% of all genera endemic to the bioregion (Phillips, 2001). Such high richness and endemism has been attributed to fluctuating environmental conditions, abundant rocky substrata and considerable habitat heterogeneity, coupled with a long period of isolation and a lack of mass extinction events (see Phillips, 2001 for review). It is clear that complex evolutionary and ecological processes have shaped the contemporary flora over the last 160 million years.

At large spatial scales, a major driver of ecological pattern along the southwest Australian coastline is the Leeuwin Current (LC). The LC originates in the Indo-Pacific and flows polewards along the coast of WA, before deviating eastwards into the Great Australian Bight (Pearce, 1991; Smith et al., 1991). During winter, the LC transports tropical (and subtropical) dispersal stages and nutrient-poor water polewards, which enhances north to south mixing of species and effectively raises winter water temperatures (Ayvazian and Hyndes, 1995; Caputi et al., 1996; Smale and Wernberg, 2009). Its influence is geographically extensive; its effects are detectable from northwest Australia to Tasmania, and it is therefore thought to be a structural force acting on benthic communities at regional scales. Crucially, the LC originated ~40 Mya following the separation of Australia and Antarctica, and has had a major influence in shaping the marine flora of the region since its formation (McGowran et al., 1997). Thus, the flora has evolved largely in isolation, remained free from glaciation, and experienced stable warm waters and poleward winter flow for millions of years.

At small spatial scales, canopy-understorey interactions, habitat heterogeneity and provision of space by wave disturbance influence assemblage structure. Kelp beds are dominated by *Ecklonia radiata* in temperate WA, which forms large monospecific stands and may reduce small scale richness through competitive exclusion (Kendrick et al., 1999; Wernberg et al., 2005). However, removal of the kelp canopy by wave disturbance and substantial habitat heterogeneity on subtidal reefs promote and maintain local assemblage richness and structure in space and time (Toohey and Kendrick, 2008; Toohey et al., 2007; Wernberg and Goldberg, 2008).

For these systems, the few explicit tests of spatial variability in assemblage structure have demonstrated high patchiness at small spatial scales (metres), which is superimposed onto large scale biogeographic shifts between regions (1000s of km) (Kendrick et al., 1999; Wernberg et al., 2003). Furthermore, the only explicit test of taxonomic sufficiency (Goldberg et al., 2006), showed that aggregation to family level does not, in most instances, lead to unacceptable loss of ecological pattern, although this study was spatially restricted. In the present study, we used a database of quantitative samples (quadrats) that contain both presence and absence data for over 500 samples, comprising of almost 300 species, to expand on these studies by testing the following hypotheses:

1. Multivariate variation in macroalgal assemblage structure will be significant at multiple spatial scales, but variability at small spatial scales will be the greatest contributor to overall variance.
2. Taxonomic aggregation from species to genus and family levels will result in similar spatial patterns, but ecological pattern will differ at coarser taxonomic levels than family.
3. Key taxa will vary significantly at multiple spatial scales, but the relative importance of variance components (or pseudo variance components in the multivariate sense) will differ between taxa.

## 2. Methods

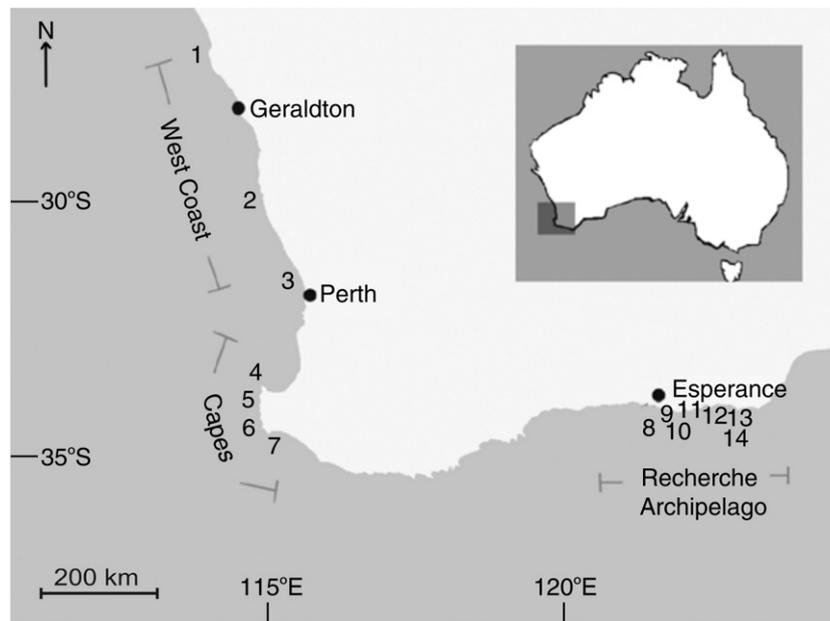
### 2.1. Study area

Samples were collected from three broad geographic regions: The West Coast, The Cape Naturaliste to Cape Leeuwin National Park (hereafter, 'Capes'), and The Recherche Archipelago (hereafter 'Recherche'). The study ranged from 27.5 to 35.5°S, encompassed about 2000 km of temperate coastline, and regions were separated by at least 300 km of coastline (Fig. 1). The three regions were delimited by geographical features: 'West Coast' sites were west facing limestone reef dominated locations within the 'West Coast Bioregion' (as defined by the Department of Fisheries, Western Australia); 'Capes' sites were located on the Cape Naturaliste to Cape Leeuwin Peninsula and were characterised by both granite and limestone reefs; and 'Recherche' sites were positioned on the Recherche Archipelago on the south coast of Australia. Patchily distributed subtidal reefs interspersed with areas of sand characterise the nearshore environment of all three regions. Reefs range in depth from the intertidal to >30 m depth in all regions. Subtidal reefs in all regions are exposed to oceanic swells and wind-driven waves, although inshore reefs are protected by offshore reefs and islands to some extent. Reef surfaces are dominated by macroalgae in all regions, with extensive patches of the kelp, *E. radiata*, a conspicuous feature of the subtidal community.

### 2.2. Sampling protocol

A fully nested hierarchal sampling design was designed to investigate ecological pattern at four spatial scales: region (3 levels in total), site (14 levels), patch (84 levels) and quadrat (504 replicates in total). Within each region, sampling was conducted at 3 (West Coast), 4 (Capes) or 7 (Recherche Archipelago) sites. Sites were at least 10 km apart and known to contain suitable habitat (i.e. low to moderate relief reef structures with an abundance of horizontal surfaces at 8 to 12 m depth). Within each site, 6 patches of reef were selected at random from a larger possible pool for sampling. Patches were at least 100 m apart at all sites. Sampling was targeted at 10 m depth, although actual depths ranged from 9 to 15 m in depth. Within each patch, 6 replicate 0.25 m<sup>2</sup> quadrats were haphazardly placed, between 5 and 10 m apart, and all macroalgae within the quadrat was harvested by Scuba divers. Material was returned to the laboratory for sorting, identifying and weighing (wet weight). In total, 504 quadrat samples were analysed, covering 126 m<sup>2</sup> of subtidal reef.

The imbalance in the number of sites within each region stemmed from the fact that data were compiled from 3 different projects for the current study. However, as the principal taxonomist, sampling protocol, and sampling area within each site were consistent between projects, the pooling of data from different studies did not confound the analyses presented here. Sampling was conducted in the austral summer between 2005 and 2007. Previous (Wernberg et al., 2003) and current research (Wernberg and Kendrick, unpublished dataset of macroalgal assemblage structure over 8 years) in this region have shown that temporal variability in assemblage structure, across both seasons and consecutive years, is minimal. As such, the inconsistency in sampling years did not confound the comparisons of spatial patterns presented here.



**Fig. 1.** Map of the southwest Australian coastline indicating location of 14 sampling sites nested within 3 regions. Inset shows study area relative to the Australian continent. Study sites were: 1) Kalbarri, 2) Jurien Bay, 3) Marmion Lagoon, 4) Cape Naturaliste, 5) Cape Freycinet, 6) Hamelin Bay, 7) Flinders Bay, 8) Figure 8 Island, 9) Frederick Island, 10) Modrain, 11) Thomas Island, 12) Mart, 13) Twin Peaks, 14) Middle Island.

### 2.3. Statistical analysis

Species level biomass data were analysed with a three-factor (region, site, and patch, with all factors random) hierarchical design using permutational multivariate analysis of variance (PERMANOVA, see Anderson, 2001). Permutations were based on a Bray–Curtis similarity matrix generated from fourth-root transformed data. This relatively severe transformation was chosen to down weight the influence of kelps and fucoids, which had biomass values of up to 3 orders of magnitude greater than understorey species in some samples. Measures of multivariate variability at different spatial scales were estimated from the mean squares of the PERMANOVA. The statistical significance of multivariate variance components were tested using a maximum of 9999 permutations under a reduced model with significance set, a priori, at  $P < 0.05$ . Regions were of no specific interest, chosen arbitrarily and treated as a random factor. However, it was of interest to conduct a posteriori pairwise comparisons between regions where differences were significant, to examine sequential shifts in assemblage structure along the coastline. As PERMANOVA is sensitive to within-factor differences in multivariate dispersions, a PERMDISP test was also performed for each factor in the model to examine heterogeneity in multivariate dispersion between groups (again using 9999 permutations). MDS plots based on the Bray–Curtis similarity matrix were generated to visualize multivariate patterns between regions, sites and patches. Ordinations with centroids averaged by patches were produced to visualize variability within and between sites, and ordinations averaged by site were produced to depict variability between regions. Finally, a model similarity matrix was generated from sequential site numbers along the coastline (i.e. site numbers in Fig. 1), and correlated with the biological matrix using the RELATE test with Spearman's rank correlation. In this way, it was possible to determine how closely similarities in macroalgal assemblage structure were linked to similarities in geographical separation. All multivariate procedures reported here were performed in the Primer 6 software (Clarke and Warwick, 2001) with the PERMANOVA add-on (Anderson et al., 2007).

The methods described above were applied to the full dataset aggregated to various taxonomic levels, from genus to class, to examine multivariate patterns at different taxonomic resolutions. Subsequently, variance components from the PERMANOVA tests were compared

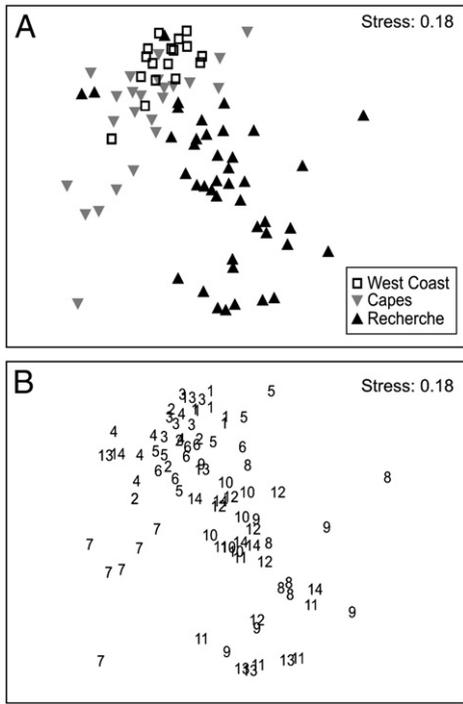
between taxonomic resolutions. Individual MDS plots were generated for each taxonomic level and were also related to one another using a second stage MDS plot. A second stage MDS plot effectively compiles a number of MDS ordinations into one, easily interpretable plot by using rank correlations between similarity matrices (in this case from different taxonomic resolutions). In addition to PERMANOVA, a two-way nested ANOSIM test was also performed for each taxonomic resolution, as the resultant ANOSIM  $R$  value provides an indication of the magnitude of dissimilarity between regions and is broadly comparable with values obtained in other studies. Samples were initially averaged by 'patch' and centroids were then permuted with 'site' factor nested within the 'region' factor. The tests again used 9999 random permutations.

To determine which taxa were major contributors to dissimilarity between regions, and therefore of particular importance, a SIMPER analysis (one-way, with 'region' factor) was conducted at each taxonomic resolution. Taxa that contributed most to dissimilarity between regions were examined using univariate statistical methods. Initially, plots of mean ( $\pm$ S.E.) biomass at the scale of site and region were constructed for these discriminatory taxa to visualize patterns along the coastline. ANOVA tests, using the hierarchical experimental design described above, were then used to determine which spatial scales were significant sources of variation in the univariate response variables. Prior to analysis, all biomass data required  $\ln(x+1)$  transformations to increase normality and achieve homogeneity of variance. For the reasons described above, it was also of interest to examine significant differences between regions (despite being a random factor). Where variables differed significantly between regions ( $P < 0.05$ ), pairwise comparisons were conducted a posteriori with Tukey's tests.

## 3. Results

### 3.1. Species level patterns of assemblage structure

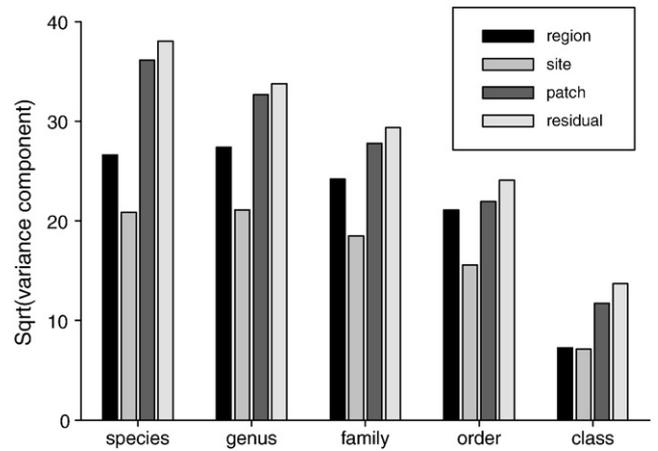
In total, 289 'species' were identified from 504 quadrat samples, of which only four were not unambiguously attributed to an exact species (i.e. distinct morphotypes that were identified to genus and included as 'species' in the analysis). By biomass, Laminariales (comprising entirely *Ecklonia* spp.) and Fucales (40 species) dominated the samples, but by



**Fig. 2.** MDS ordinations of macroalgal assemblages based on a Bray–Curtis similarity matrix of fourth-root transformed biomass data, with centroids as averages for ‘patch’ ( $n=6$  quadrat samples). Plot A indicates partitioning between regions, shown by symbols. Plot B indicates variability between replicate patches within each site, shown by site number labels: see Fig. 1 for key to site numbers.

frequency of occurrence Gigartinales (48 species) were dominant. Spatial patterns of species richness and diversity will be reported elsewhere (Smale, unpublished data), and a full list of taxa is available from the first author.

An MDS plot, with centroids as averages per patch, indicated distinct overall partitioning in multivariate structure between regions, with a general shift in structure along the coastline (Fig. 2A). A duplicate MDS plot indicating replicate patches within each location suggested that variability between reefs within certain sites was pronounced (Fig. 2B). These observations were supported by the PERMANOVA model, which detected highly significant variability at all spatial scales (Table 1). A breakdown of the variance components (square rooted) indicated that variability at the smallest scales of residual and patch were the major contributors to overall variability, and average Bray–Curtis dissimilarity between quadrats and between patches was ~35% (Fig. 3). As the PERMANOVA test is sensitive to heterogeneity in multivariate dispersion, a PERMDISP analysis was



**Fig. 3.** Size of multivariate variance components at each spatial scale for each taxonomic resolution. Results of PERMANOVA tests are given in Table 1.

conducted at each nested level within the hierarchy, to examine within-factor variability. As suggested by MDS ordination (Fig. 2) significant differences in multivariate dispersion were observed at the scale of patch ( $F_{83,420} = 7.33, P = 0.001$ ), site ( $F_{13,490} = 45.30, P = 0.001$ ) and region ( $F_{2,501} = 221.37, P = 0.001$ ). Pairwise comparisons within the region factor showed that dispersion at Recherche was significantly greater than at the Capes, which in turn was greater than the West Coast. In fact, multivariate dispersion was 50% greater at Recherche compared with West Coast.

This considerable variability in multivariate dispersion at various spatial scales would have influenced the PERMANOVA tests, and therefore the results of which should be treated conservatively. Even so, differences between macroalgal assemblages were highly significant at all spatial scales, which was almost certainly due to a combination of variability in both multivariate position and dispersion. Visual examination of a 3D plot of patch-averaged centroids (stress 0.10, plot not shown) supported this conclusion. Moreover, an MDS ordination with centroids as site averages demonstrated clear partitioning between sites and regions (Fig. 4). The similarity matrix based on assemblage structure was well correlated with the model matrix generated from distance between sites ( $\rho = 0.64, P = 0.01$ ), as determined by the RELATE procedure.

3.2. Taxonomic sufficiency

A comparison of MDS ordinations derived from data aggregated to different taxonomic resolutions indicated that spatial patterns in assemblage structure were fairly consistent, at least up to family level

**Table 1**

Permutational multivariate analyses of variance, based on Bray–Curtis similarity matrices of fourth-root transformed biomass data, at each of the taxonomic levels examined. The number of variables examined at each taxonomic level is shown in parentheses. All tests used 9999 permutations under the reduced model.

Source	df	Species level (289)			Genus level (151)			Family level (56)		
		MS	F	P	MS	F	P	MS	F	P
Region	2	136,000	5.46	0.001	141,160	5.99	0.001	109,400	6.14	0.001
Site (Re)	11	24,893	2.68	0.001	23,550	3.12	0.001	17,802	3.24	0.001
Patch (Si(Re))	70	9272	6.41	0.001	7543	6.61	0.001	5491	6.37	0.001
Residual	420	1444			1140			861		
Source	df	Order level (22)			Class level (4)					
			F	P	MS	F	P			
Region	2	81,833	6.70	0.001	11,072	3.91	0.022			
Site (Re)	11	12,200	3.52	0.001	2826	2.79	0.001			
Patch (Si(Re))	70	3465	5.97	0.001	1010	5.38	0.001			
Residual		580			187					

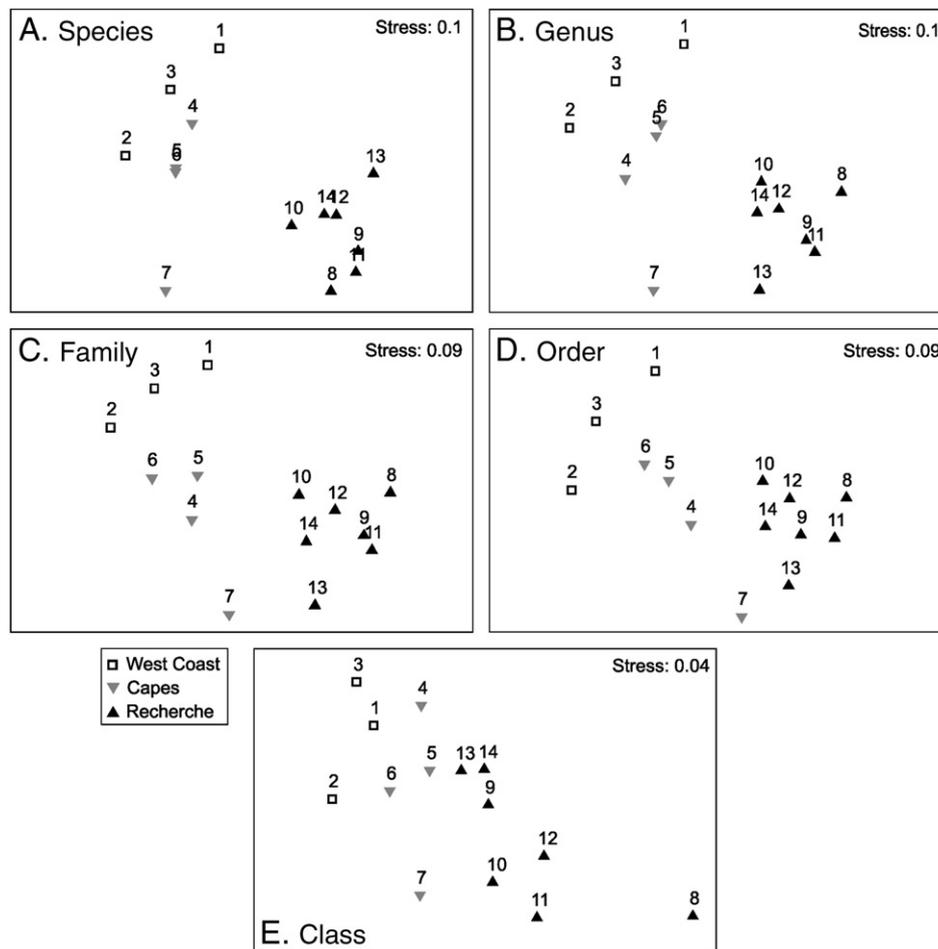


Fig. 4. MDS plots of macroalgal assemblage structure across sites (labels) and regions (symbols) for each taxonomic resolution. Plots are based on Bray–Curtis similarity matrices derived from fourth-root transformed biomass data, with centroids as site averages (36 replicate quadrats per site). See Fig. 1 for key to site numbers.

(Fig. 4). At taxonomic resolutions coarser than family partitioning between regions was less distinct, while certain sites became outliers from the main cluster (Fig. 4). A second stage MDS confirmed this observation, as centroids for species, genus and family were clustered fairly tightly, while order and (particularly) class level dissimilarity matrices were distinct outliers (Fig. 5). Quantitative correlations between species level patterns and patterns at coarser taxonomic resolutions, conducted with RELATE tests, supported this observation (genus:  $\rho=0.97$ ,  $P=0.001$ , family:  $\rho=0.95$ ,  $P=0.001$ , order:  $\rho=0.83$ ,  $P=0.01$ , and class:  $\rho=0.50$ ,  $P=0.01$ ). The magnitude of correlation between assemblage structure and geographical separa-

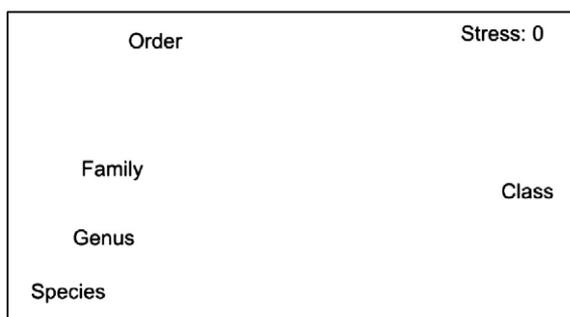


Fig. 5. Second stage MDS plot showing the relationship in similarity matrices of macroalgal biomass data derived from different taxonomic resolutions. The proximity of the labels indicates the extent to which different taxonomic resolutions captured the same multivariate pattern.

tion, also determined by RELATE tests, was consistent at all taxonomic resolutions except the coarsest level of class (species:  $\rho=0.64$ ,  $P=0.001$ , genus:  $\rho=0.63$ ,  $P=0.001$ , family:  $\rho=0.61$ ,  $P=0.001$ , order:  $\rho=0.58$ ,  $P=0.01$ , and class:  $\rho=0.29$ ,  $P=0.01$ ).

PERMANOVA tests conducted at each taxonomic resolution detected significant differences between patches, sites and regions (Table 1). In fact, spatial variability was still pronounced at the class level, which included only four variables. As could be predicted, the magnitude of the variance components associated with the tests decreased with diminishing taxonomic resolution, but patterns of relative contributions of each component to overall variability were consistent (Fig. 3). To expand, up to and including order level, tests conducted at all taxonomic resolutions indicated that residual variance was the greatest contributor to overall variability, followed by patch variance, then region, then site. Therefore, multivariate patterns at multiple spatial scales were relatively consistent across the taxonomic resolutions. Interestingly, the contribution of large scale variability to total variance increased with decreasing taxonomic resolution from species to order, but was diminished at the class level. The proportion of total multivariate variance arising from variability at the regional scale was  $\sim 0.22$  for species, 0.23 for genus, 0.24 for family, 0.26 for order and 0.19 for class level biomass data.

ANOSIM tests were also conducted, as ANOSIM  $R$  is comparable across studies, easily interpretable, and widely used in ecological monitoring in marine systems. Again, the magnitude and significance of ANOSIM  $R$  values were remarkably similar for species, genus, family and order level data (Table 2). The only discrepancy between these taxonomic resolutions is that a moderate but significant difference

**Table 2**

Results of two-way nested ANOSIM tests performed on Bray–Curtis similarity matrices generated from fourth-root transformed data, at each of the taxonomic levels examined. Pairwise comparisons within the region factor are also shown, where differences between regions and pairwise tests are significant at  $P < 0.05$  (WC = West Coast, C = Capes, and R = Recherche). Tests used 9999 permutations.

Taxonomic level	Region		Site (Re)		Pairwise <i>R</i> values (region factor)		
	<i>R</i>	<i>P</i>	<i>R</i>	<i>P</i>	WC/C	WC/R	C/R
	Species	0.60	0.002	0.36	0.001	0.41	0.81
Genus	0.67	0.002	0.35	0.001	ns	0.96	0.75
Family	0.71	0.001	0.35	0.001	ns	0.92	0.75
Order	0.64	0.001	0.32	0.001	ns	0.98	0.53
Class	0.10	0.205	0.11	0.003	–	–	–

was detected between West Coast and Capes at the species level, but not at coarser levels. Multivariate partitioning between factors was not evident when biomass data were aggregated to class (Table 2).

### 3.3. Spatial patterns of key taxa

Key taxa that were major contributors to the observed differences between regions were selected from each taxonomic resolution (except class) for further examination. Plots of mean biomass for each location and region are presented for 12 species, 6 genera, 4 families and 4 orders in Figs. 6–8, and the accompanying ANOVA results are given in Tables 3 and 4. In general terms, the plots depicted high variability among sites for most taxa regardless of taxonomic resolution, and also suggested that some taxa demonstrate clear regional patterns coherent with their location along the coastline. For example, *E. radiata*, *Osmundaria prolifera* and *Sargassum* spp. displayed strong geographical patterns when observed at large spatial scales. Furthermore, it was evident from the plots that some taxa, such as *Pterocladia lucida* and *O. prolifera*, had very patchy, almost disjunct distributions, as they were absent from large stretches of coastline in between presence at sites.

Overall, ANOVA showed that high variability at the small spatial scale of patch was a ubiquitous pattern, while individual taxa were often more evenly distributed between sites within the same region. Examination of estimates of variance components showed that, in general, small scale variability between quadrats and patches was the principal contributor to total variability, while the intermediate spatial scale of site was of least importance. Notable exceptions to this trend were the genus *Sargassum*/family Sargassaceae, which had greatest variability at the large spatial scale of region, and the species *Amphiroa anceps*/genus *Amphiroa*, which had least variability across regions.

Canopy forming species are known to be important drivers of ecological pattern in these systems, and therefore warrant particular attention. *E. radiata* was recorded at all sites and was the dominant (by weight) species at all west facing sites, from Kalbarri through Hamelin Bay. *E. radiata* formed largely monospecific stands at all west facing sites, with the exception of Cape Naturaliste, where it was equalled by *Scytothalia dorycarpa* as the major canopy forming species. Along the south coast, from Flinders Bay through the easternmost sites of Recherche the canopy was more diverse, as *E. radiata*, *S. dorycarpa*, and the diverse genera of *Sargassum* and *Cystophora* were all fairly equal contributors to canopy biomass. Interestingly, the study encompassed a number of canopy forming taxa at the northern limit of their distributions. To expand, *Platythalia quercifolia*, *S. dorycarpa* and *Cystophora* spp. were not sampled from the northernmost sites (in fact *P. quercifolia* and *Cystophora* spp. were not sampled from the entire West Coast region), which corresponds well with published distributions for these species and for species within the *Cystophora* genus (Huisman, 2000).

Even at the coarse taxonomic levels of family and order, most discriminatory taxa were unevenly distributed at all spatial scales, and differed significantly between regions, sites and patches. Some taxa, such as the Cystoseiraceae and the Sargassaceae, demonstrated clear geographical patterns, and generally increased in biomass from the West Coast to Recherche. The family Lessoniaceae and the order Laminariales were represented solely by the genus *Ecklonia*, and therefore the pattern of decreasing biomass from West Coast to Recherche was consistent throughout the taxonomic hierarchy.

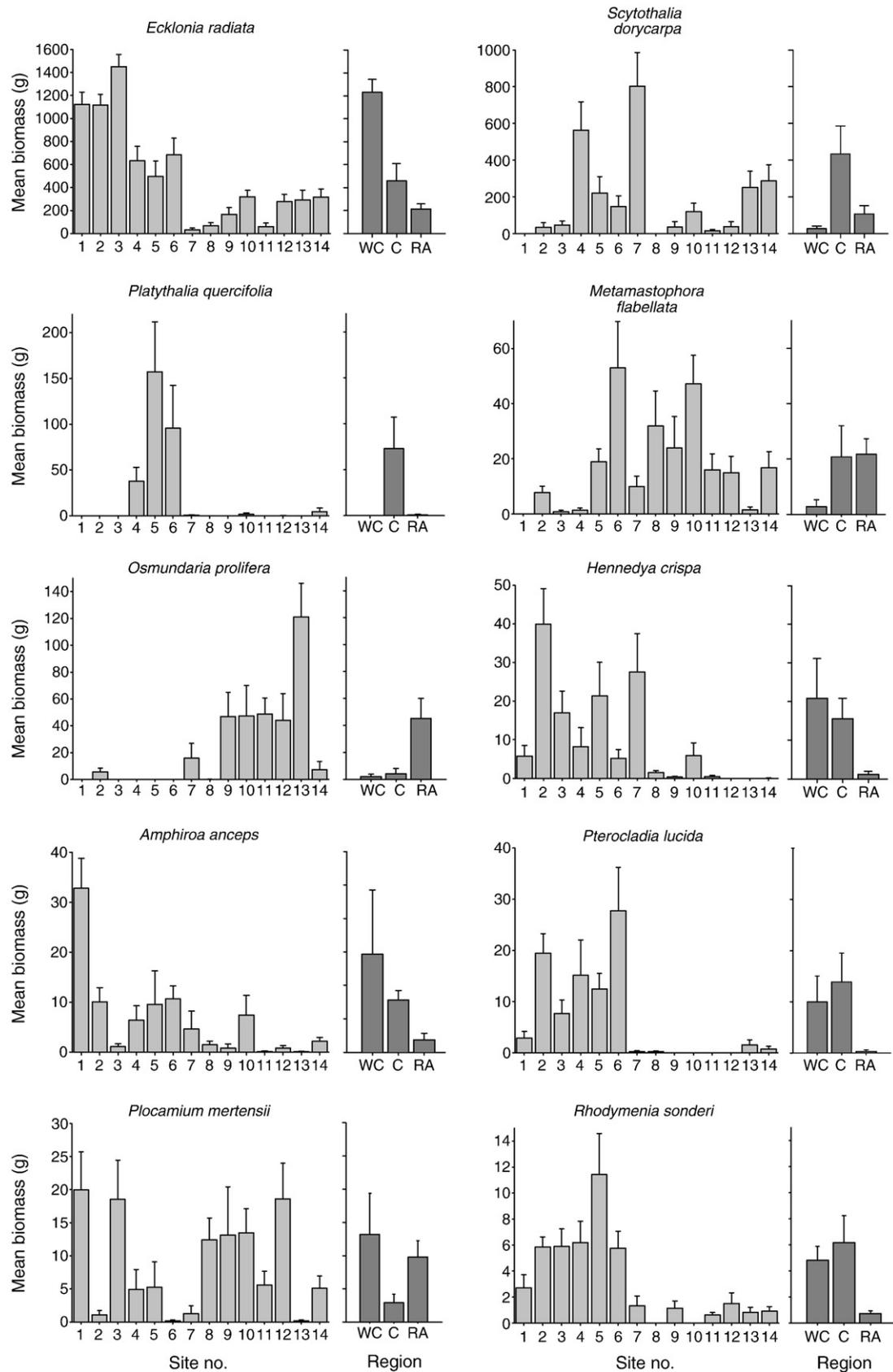
## 4. Discussion

The marine flora of southwest Australia exhibits very high species turnover at small spatial scales in comparison to turnover between sites and regions. Similar patterns of species turnover are also a characteristic of the terrestrial flora of southwest Australia (Hopper and Gioia, 2004). Underlying causes for such patterns include the lack of orogeny and glaciation in southwest Australia for >40 million years, and the activity of the Leeuwin Current (LC) that has been a feature of the oceanography for just as long. The Leeuwin Current has greatest influence during the austral winter and effectively elevates winter water temperatures and minimises seasonal temperature differences, even in inshore waters (Pearce, 1991; Smale and Wernberg, 2009). Perhaps as a result, the study region is effectively an expansive transition zone between the tropical flora of northwest Australia and the cool temperate flora of southern Australia, which is characterised by a diversity of Fucales and Ceramiales.

Our results supported the first hypothesis, which predicted that macroalgal assemblage structure would vary significantly at all spatial scales examined, and be most pronounced at small spatial scales. Relatively, small scale variability – between replicate quadrats within a patch and between patches within a site – was of most importance and consistently the principal contributor to total variance. High turnover of species and assemblages across small spatial extents is a characteristic trait of these kelp-dominated systems, and has been reported previously (Wernberg et al., 2003). The current study examined the most spatially extensive dataset compiled thus far for WA, and showed that variability at the scales of metres (i.e. between quadrats) is almost twice as important as variability at the scale of 10s of km (i.e. between sites) as a contributor to total variance.

Local patchiness is likely to be largely driven by habitat heterogeneity and the density of canopy formers (specifically *E. radiata*), both of which vary at small spatial scales. Wave action is intense along the coastline of WA, and removal of kelps generates high variability in canopy density and cover on subtidal reefs (Wernberg and Connell, 2008). Canopy formers alter the immediate physical environment and influence macroalgal assemblage structure through canopy–understorey interactions (Wernberg et al., 2005), and can therefore be considered ‘ecosystem engineers’ in these habitats (sensu Jones et al., 1994). Furthermore, subtidal reefs in coastal southwest Australia are both extensive and heterogeneous, and vary in terms of relief, topography, aspect, and structural integrity across small spatial extents. Therefore the physical habitat, in terms of the substratum, light availability and hydrodynamic force is notably heterogeneous at the scale of metres, which promotes variability in canopy removal and niche availability through the diversification of microhabitat structure (Kendrick et al., 1999; Toohey et al., 2007).

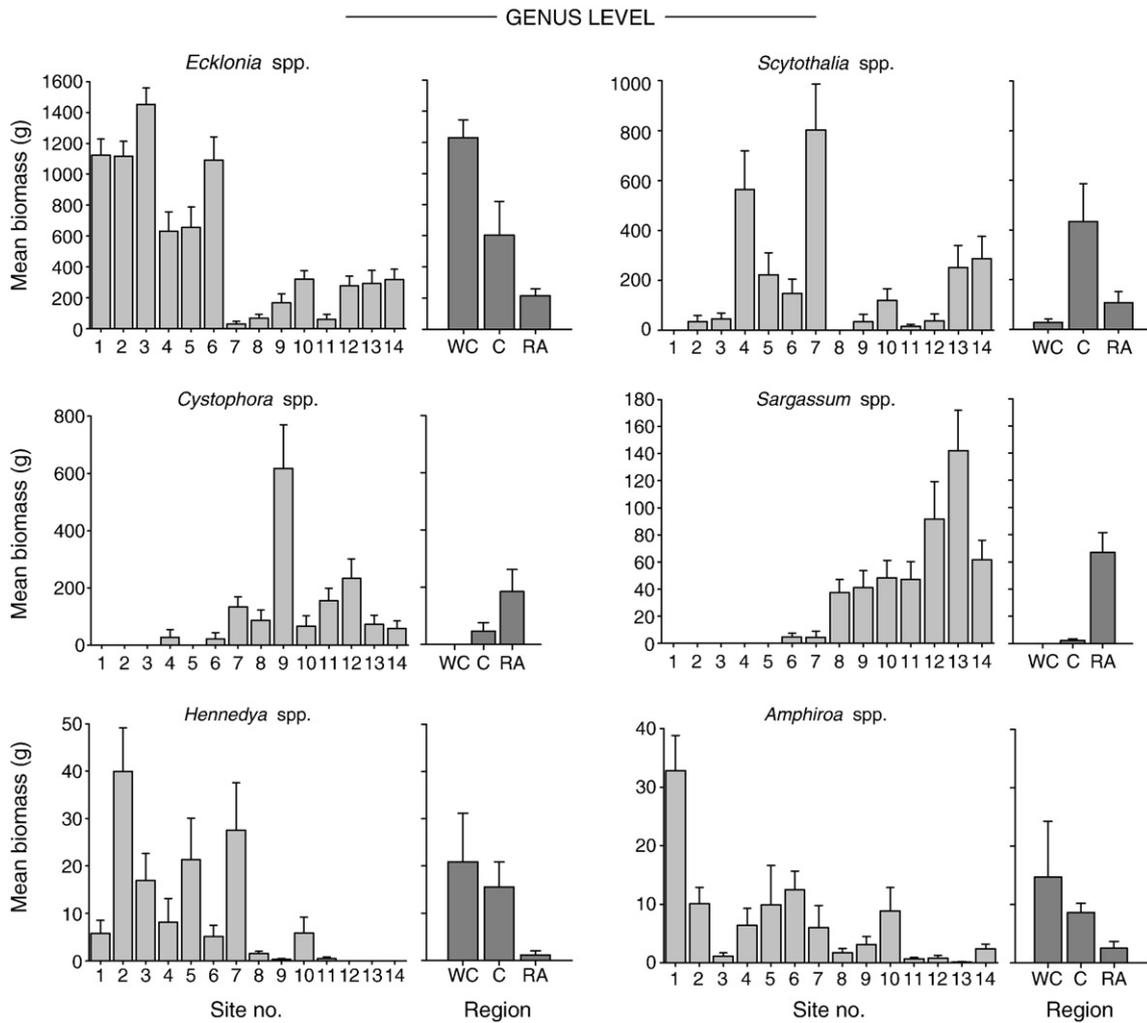
Multivariate assemblage structure and the distribution of key taxa also varied considerably at regional spatial scales. Processes driving ecological pattern at large spatial scales are, of course, distinct from those described above that act at small spatial scales. The temperate coastline of southwest Australia is characterised by a nearshore temperature gradient of ~4 °C (Smale and Wernberg, 2009; Van Hazel, 2001), which broadly correlates with latitude but varies in time and space because of the influence of the Leeuwin Current (LC). Therefore, temperature-dependent physiological and biogeographical processes that determine the distribution of species along the coastline



**Fig. 6.** Mean ( $\pm$ S.E.) biomass values for key discriminatory species at each site and each region. See Fig. 1 for key to site numbers. Regions sampled were: WC = West Coast, C = Capes and RA = Recherche Archipelago.

also, to some extent, drive changes in assemblage structure between regions. For example, cold water taxa such as *Cystophora* spp. and *S. dorycarpa* were dominant in the Recherche and Capes regions but

largely absent from the warmer West Coast region. Regional differences may also be influenced by the geomorphology of the coastline and oceanic currents, which affect the available niches for colonisation and



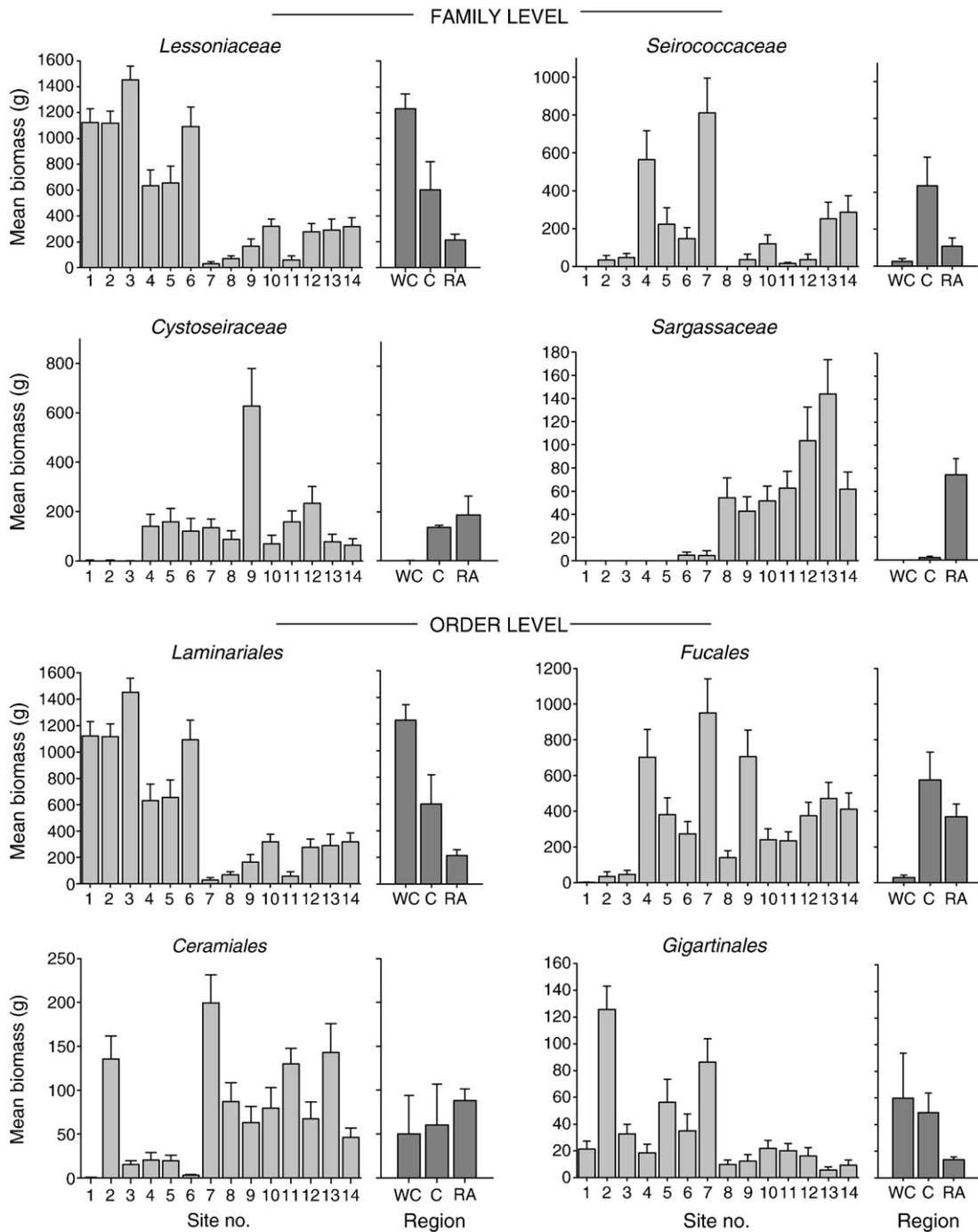
**Fig. 7.** Mean ( $\pm$ S.E.) biomass values for key discriminatory genera at each site and each region. See Fig. 1 for key to site numbers. Regions sampled were: WC = West Coast, C = Capes and RA = Recherche Archipelago.

dispersal and retention of macroalgal propagules. The relative importance of temperature-dependent physiological processes versus oceanographic barriers to dispersal on contemporary distributions remains uncertain. Even so, the West Coast and Capes regions are strongly, but seasonally, influenced by the LC, which transports warm water species from the north. The LC, however, is far less influential at the Recherche, which supports a flora with greater affinity to the cool-water assemblages of South Australia (Kendrick et al., 2009).

Concerning the second hypothesis, our results showed that taxonomic aggregation from species to genus, family and order biomass data did not considerably alter spatial patterns in assemblage structure. Patterns were remarkably consistent at these taxonomic resolutions, as shown by very similar MDS plots and PERMANOVA, ANOSIM and RELATE results. However, the second stage MDS plot indicated that aggregation to order did result in moderate dissimilarity between resemblance matrices, so aggregation to family would seem the most appropriate resolution for cost effective ecological research and monitoring. Data collection at the family level would require identification of 56 taxa compared with 289 taxa for species level biomass; representing an 80% reduction in taxonomic expertise needed to process samples. Family level biomass data as surrogates for species level patterns have been recommended for the Recherche previously (Goldberg et al., 2006), and the present study extends this recommendation to southwest Australian macroalgae as a whole. Our examination of taxonomic resolution perhaps indicates the significant age of the

southwest Australian marine flora, where patterns of species turnover are reflected in genera, families and orders. These observations, combined with high levels of endemism in the region (Phillips, 2001) and evidence of explosive *in situ* speciation from the terrestrial flora (Hopper and Gioia, 2004), provide further evidence for the widespread *in situ* speciation of many components of the southwest Australian marine flora.

Anderson et al. (2005a,b) used invertebrate holdfast assemblages in New Zealand as model systems to assess the effect of taxonomic aggregation on multivariate variance components at different spatial scales. For compositional data (presence, absence and fourth-root transformed abundance data), they reported a slight decrease in the relative importance of large scale variability from species to order aggregations, followed by a marked increase at the coarse resolutions of class and phylum. Interestingly, the patterns we observed for macroalgal assemblages differed in two ways. First, variability at the scale of tens of metres was consistently the second most important source of variability in the current study, behind residual variance, whereas this spatial scale was of less importance for invertebrate holdfast assemblages. Second, the relative importance of large scale variability (i.e. regions and sites in the current study) increased with decreasing taxonomic resolution for macroalgal assemblages from species to order, before decreasing in relative importance at the resolution of class (i.e. the inverse pattern observed for holdfast assemblages). This comparison suggests, therefore, that patterns of



**Fig. 8.** Mean ( $\pm$ S.E.) biomass values for key discriminatory families and orders at each site and each region. See Fig. 1 for key to site numbers. Regions sampled were: WC = West Coast, C = Capes and RA = Recherche Archipelago.

spatial variability through taxonomic aggregations may vary between ecosystems and between taxa: clearly this is an area of research that merits further work.

As to the third and final hypothesis, we observed both consistency and variability in spatial patterns of individual taxa across multiple scales. In general, small scale variability (i.e. patches and quadrats) was the greatest contributor to total variance, and variability between sites was the least important source of difference, for most taxa. The processes described above, acting on entire assemblages, are likely to drive small scale patchiness for specific taxa. Almost half of the taxa analysed did not vary significantly between sites and relatively low variability at the scale of 10s of km was a ubiquitous pattern. This perhaps suggested that process acting at very large spatial scales, such as

the Leeuwin Current, and very small spatial scales, such as canopy removal and reef heterogeneity, are of relatively more importance than those acting at intermediate scales, such as local recruitment patterns, exposure and substrate availability. There were no clear patterns of difference in the relative importance of variance components throughout the taxonomic hierarchy.

However, there were detectable differences in patterns of spatial variability between taxa, providing some support for the third hypothesis. Interestingly, only half of the taxa examined at each taxonomic resolution varied significantly at every spatial scale, while regional variability was notably high for *Sargassum* spp. (and *Sargassaceae*) and comparatively low for *A. anceps* (and *Amphiroa* spp.), *Metamastophora flabellata* and *Ceramiales* as a whole. High variability between regions for *Sargassum*

**Table 3**

Results of fully nested ANOVA tests on macroalgal biomass data for key taxa at various taxonomic resolutions. All data were  $\ln(x+1)$  transformed, significance is indicated by: \* =  $P < 0.05$ , \*\* =  $P < 0.01$ , and \*\*\* =  $P < 0.001$ . DF for all tests were: region = 2, site (region) = 11, patch (site, region) = 70, and residual = 420. The outcomes of pairwise comparisons among regions are given, where appropriate: 'ns' indicates that no significant differences were detected while inequalities indicate the direction of significant differences between regions. WC = West Coast, C = Capes and R = Recherche.

Response variable	Region		Site		Patch		Pairwise tests ('region' term)
	MS	F	MS	F	MS	F	
<i>Ecklonia radiata</i>	755.4	11.76**	64.3	4.10***	15.7	3.31***	WC>C>R
<i>Scytothalia dorycarpa</i>	159.2	4.81*	33.1	1.96*	16.9	4.90***	C>WC=R
<i>Platythalia quercifolia</i>	53.2	9.16**	5.8	1.27	4.6	5.90***	C>WC=R
<i>Metamastophora flabellata</i>	34.4	1.62	21.3	2.81**	7.57	5.53***	ns
<i>Osmundaria prolifera</i>	79.6	4.83*	16.5	1.35	12.2	21.8***	R>WC=C
<i>Henedya crisa</i>	83.8	8.65**	9.7	1.60	6.1	9.10***	WC>C>R
<i>Amphiroa anceps</i>	67.2	4.40*	15.3	5.17***	2.9	4.57***	WC>C>R
<i>Pterocladia lucida</i>	87.6	7.16*	12.2	4.01***	3.1	5.02***	WC=C>R
<i>Plocamium mertensii</i>	33.6	3.44	9.8	1.92	5.07	4.45***	ns
<i>Rhodymenia sonderi</i>	60.7	12.50**	4.9	3.22**	1.5	2.82***	WC=C>R
<i>Ecklonia</i> spp.	737.4	9.19**	80.2	4.76***	16.9	4.01***	WC>C>R
<i>Scytothalia</i> spp.	159.2	4.81*	33.1	1.96*	16.9	4.90***	C>WC=R
<i>Cystophora</i> spp.	239.5	6.39*	37.5	2.97**	12.6	5.17***	R>C>WC
<i>Sargassum</i> spp.	414.2	50.3***	8.2	1.21	6.8	4.58***	R>C>WC
<i>Henedya</i> spp.	83.8	8.65**	9.7	1.60	6.1	9.10***	WC=C>R
<i>Amphiroa</i> spp.	52.1	3.36	15.5	4.50***	3.4	4.86***	ns
Lessoniaceae	737.4	9.19**	80.2	4.76***	16.9	4.01***	WC>C>R
Seirococcaceae	166.2	4.90*	33.9	2.07*	16.4	4.67***	C>WC=R
Cystoseiraceae	182.9	7.04*	25.9	1.55	16.7	5.09***	R=C>WC
Sargassaceae	456.7	64.0***	7.1	0.96	7.4	5.05***	R>WC=C
Laminariales	737.4	9.19**	80.2	4.76***	16.9	4.01***	WC>C>R
Fucales	507.3	22.1***	22.9	1.73	13.2	3.33***	R=C>WC
Ceramiales	85.8	1.46	58.8	4.81***	12.2	8.62***	ns
Gigartinales	125.3	5.69*	22.0	3.28***	6.7	4.44***	WC=C>R

spp. is somewhat counterintuitive, as it is a widespread genus in Australian waters, common in both tropical and cool waters. Individual species of this diverse genus, however, may have limited dispersal

**Table 4**

Estimates of variance components of different spatial scales for each taxon examined. Details and results of ANOVA used to generate variance components are shown in Table 3. Patterns of difference in various components between spatial scales are shown: R = region, S = site, P = Patch and Q = quadrat (residual).

Response variable	Region	Site	Patch	Quad.	Pattern
<i>Ecklonia radiata</i>	4.41	1.32	1.81	4.73	Q>R>P>S
<i>Scytothalia dorycarpa</i>	0.80	0.43	2.25	3.53	Q>P>R>S
<i>Platythalia quercifolia</i>	0.32	0.11	0.65	0.73	Q>P>R>S
<i>Metamastophora flabellata</i>	0.16	0.40	1.07	1.44	Q>P>S>R
<i>Osmundaria prolifera</i>	0.44	0.10	1.95	0.69	P>Q>R>S
<i>Henedya crisa</i>	0.41	0.12	0.97	0.65	P>Q>R>S
<i>Amphiroa anceps</i>	0.31	0.38,	0.43	0.62	Q>P>S>R
<i>Pterocladia lucida</i>	0.52	0.36	0.42	0.66	Q>R>P>S
<i>Plocamium mertensii</i>	0.23	0.10	0.77	1.25	Q>P>R>S
<i>Rhodymenia sonderi</i>	0.42	0.15	0.23	0.50	Q>R>P>S
<i>Ecklonia</i> spp.	4.14	1.83	2.13	4.26	Q>R>P>S
<i>Scytothalia</i> spp.	0.86	0.44	2.24	3.46	Q>P>R>S
<i>Cystophora</i> spp.	1.31	0.75	1.76	2.42	Q>P>R>S
<i>Sargassum</i> spp.	2.60	0.10	0.21	1.52	R>Q>P>S
<i>Henedya</i> spp.	0.55	0.17	0.95	0.77	P>Q>R>S
<i>Amphiroa</i> spp.	0.25	0.32	0.50	0.75	Q>P>S>R
Lessoniaceae	4.14	1.83	2.13	4.26	Q>R>P>S
Seirococcaceae	0.82	0.53	2.14	3.50	Q>P>R>S
Cystoseiraceae	1.04	0.36	2.29	3.38	Q>P>R>S
Sargassaceae	2.90	0.00	1.02	1.59	R>Q>P>S
Laminariales	4.14	1.83	2.13	4.26	Q>R>P>S
Fucales	3.17	0.37	1.50	4.05	Q>R>P>S
Ceramiales	0.20	1.35	1.80	1.44	P>Q>S>R
Gigartinales	0.74	0.45	0.98	1.50	Q>P>R>S

capabilities (Kendrick and Walker, 1995), which, in conjunction with extensive stands of the highly competitive *E. radiata* in the Capes and West Coast regions, may restrict *Sargassum* spp. to relative dominance at Recherche but not at the other study regions. The taxa that were most evenly distributed between regions were all common understorey red algae of the class Florideophyceae. This included species such as *A. anceps* and *M. flabellata*, which are distributed throughout Australia and beyond and are cosmopolitan occupiers of newly-created space in temperate kelp beds (Kendrick et al., 1999; Kennelly, 1987). Therefore, it was not surprising that such taxa were common components of macroalgal assemblages in all regions encompassed by this study.

In conclusion, ours is not the first study to report highly significant variability in subtidal assemblage structure at all scales within a spatial hierarchy. Considerable variability at scales of 100s of km to metres in the structure of subtidal reef assemblages has been recorded in Western Australia (Wernberg et al., 2003), the Western Mediterranean Sea (Fraschetti et al., 2005; Fraschetti et al., 2001), and New Zealand (Anderson et al., 2005a,b). So is significant variability at all spatial scales, from metres to 10s of km to 1000s of km, a ubiquitous pattern for subtidal reef assemblages? Of the 9 subtidal rocky reef studies included in the review by Fraschetti et al. (2005), all detected significant variability at all spatial scales examined. Moreover, 3 further studies and the present research have all documented significant variability in assemblage structure at multiple spatial scales (Anderson et al., 2005a,b; Tuya and Haroun, 2006; Wernberg et al., 2003). This consistency in variability provides further evidence that subtidal reef communities, even when biogeographically and taxonomically distinct, are influenced by complex physical and biological processes that act at varying spatial scales.

It is important to note, however, that macroalgal assemblages along the coastline of Western Australia may be particularly unique and idiosyncratic, and that pronounced variability at multiple spatial scales in algal systems is not universal. For example, pioneering work conducted across Australia has highlighted overarching similarities in ecological pattern and process, despite marked differences at small spatial scales (see review by Connell, 2007). Clearly, 'variability' is a relative concept that is dependent on both the spatial scale of the study (i.e. in a broader context that included the south and east coasts of Australia much of the variability observed within WA could be overshadowed by variability at the broader scale of 'Province') and the nature of the response variable (i.e. species level data are generally much noisier than functional/morphological group data for marine algae). Our study relates only to the speciose macroalgal assemblages of southwest Australia, but emphasises the importance of variability in assemblage structure at multiple spatial scales, which in turn points to the scale-dependent nature of key processes operating along this vast and unique coastline.

## Acknowledgements

DS is funded through the Western Australian Marine Science Institute (WAMSI). An ARC Discovery grant (DP0555929) awarded to TW and GAK supported fieldwork in the West Coast region. Fisheries Research Development Corporation (FRDC 2001/060) and Coastal CRC are acknowledged for funding algal collections in the Recherche Archipelago. South West Catchment Council (project CM-01A) funded algal collections in the Cape Naturaliste to Flinders Bay region. Finally, sincere thanks to Nisse Goldberg (Recherche) and Mark Westera (Capes) for their support in collection and identification of algae and access to these data. [ST]

## References

- Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26, 32–46.
- Anderson, M.J., Diebel, C.E., Blom, W.M., Landers, T.J., 2005a. Consistency and variation in kelp holdfast assemblages: spatial patterns of biodiversity for the major phyla at

- different taxonomic resolutions. *Journal of Experimental Marine Biology and Ecology* 320, 35–56.
- Anderson, M.J., Connell, S.D., Gillanders, B.M., Diebel, C.E., Blom, W.M., Saunders, J.E., Landers, T.J., 2005b. Relationships between taxonomic resolution and spatial scales of multivariate variation. *Journal of Animal Ecology* 74, 636–646.
- Anderson, M.J., Gorley, R.N., Clarke, K.R., 2007. PERMANOVA+ for primer: guide to software and statistical methods. PRIMER-E, Plymouth.
- Ayvazian, S.G., Hyndes, G.A., 1995. Surf-zone fish assemblages in south-western Australia: do adjacent nearshore habitats and the warm Leeuwin Current influence the characteristics of the fish fauna? *Marine Biology* 122, 527–536.
- Bates, C.R., Scott, G., Tobin, M., Thompson, R., 2007. Weighing the costs and benefits of reduced sampling resolution in biomonitoring studies: perspectives from the temperate rocky intertidal. *Biological Conservation* 137, 617–625.
- Caputi, N., Fletcher, W.J., Pearce, A., Chubb, C.F., 1996. Effect of the Leeuwin Current on the recruitment of fish and invertebrates along the Western Australian coast. *Marine and Freshwater Research* 47, 147–155.
- Clarke, K.R., Warwick, R.M., 2001. Change in marine communities: an approach to statistical analysis and interpretation. PRIMER-E Ltd., Plymouth.
- Colwell, R.K., Coddington, J.A., 1994. Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society B: Biological Sciences* 345, 101–118.
- Connell, S.D., 2007. Subtidal temperate rocky habitats: habitat heterogeneity at local to continental scales. In: Connell, S.D., Gillanders, B.M. (Eds.), *Marine Ecology*. Oxford University Press, Melbourne.
- Fraschetti, S., Bianchi, G., Terlizzi, A., Fanelli, G., Morri, C., Boero, F., 2001. Spatial variability and human disturbance in shallow subtidal hard substrate assemblages: a regional approach. *Marine Ecological Progress Series* 212, 1–12.
- Fraschetti, S., Terlizzi, A., Benedetti-Cecchi, L., 2005. Patterns of distribution of marine assemblages from rocky shores: evidence of relevant scales of variation. *Marine Ecological Progress Series* 296, 13–29.
- Goldberg, N.A., Kendrick, G.A., Walker, D.I., 2006. Do surrogates describe patterns in marine macroalgal diversity in the Recherche Archipelago, temperate Australia? *Aquatic Conservation: Marine and Freshwater Ecosystems* 16, 313–327.
- Hewitt, J.E., Thrush, S.F., Dayton, P.K., Bonsdorff, E., 2007. The effect of spatial and temporal heterogeneity on the design and analysis of empirical studies of scale dependent systems. *The American Naturalist* 169, 398–408.
- Hopper, S.D., Gioia, P., 2004. The southwest Australian floristic region: evolution and conservation of a global hot spot of biodiversity. *Annual Review of Ecology, Evolution, and Systematics* 35, 623–650.
- Huisman, J.M., 2000. *Marine Plants of Australia*. University of Western Australia, Nedlands.
- Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. *Oikos* 69, 373–386.
- Kendrick, G.A., Walker, D.I., 1995. Dispersal of propagules of *Sargassum* spp. (Sargassaceae, Phaeophyta) – observations of local patterns of dispersal and consequences for recruitment and population structure. *Journal of Experimental Marine Biology and Ecology* 192, 273–288.
- Kendrick, G.A., Lavery, P.S., Phillips, J.C., 1999. Influence of *Ecklonia radiata* kelp canopy on structure of macro-algal assemblages in Marmion Lagoon, Western Australia. *Hydrobiologia* 398 (399), 275–283.
- Kendrick, G.A., Goldberg, N.A., Harvey, E.S., McDonald, J., 2009. Historical and contemporary influence of the Leeuwin Current to the marine biota of the Southern Western Australian Continental Shelf and the Recherche Archipelago. *Journal of the Royal Society of Western Australia* 92, 209–217.
- Kennelly, S.J., 1987. Physical disturbances in an Australian kelp community. II. Effects on understorey taxa due to differences in kelp cover. *Marine Ecology Progress Series* 40, 155–165.
- Kerswell, A.P., 2006. Biodiversity patterns of benthic marine algae. *Ecology* 87, 2479–2488.
- Magierowski, R.H., Johnson, C.R., 2006. Robustness of surrogates of biodiversity in marine benthic communities. *Ecological Applications* 16, 2264–2275.
- McGowran, B., Li, Q., Cann, J., Padley, D., McKirdy, D.M., Shafik, S., 1997. Biogeographic impact of the Leeuwin Current in southern Australia since the late middle Eocene. *Palaeogeography, Palaeoclimatology, Palaeoecology* 136, 19–40.
- Olsford, F., Somerfield, P.J., 2000. Surrogates in marine benthic investigations – which taxonomic unit to target? *Journal of Aquatic Ecosystem Stress and Recovery* 7, 25–42.
- Olsford, F., Brattegard, T., Holthe, T., 2003. Polychaetes as surrogates for marine biodiversity: lower taxonomic resolution and indicator groups. *Biodiversity and Conservation* 12, 1033–1049.
- Pearce, A.F., 1991. Eastern boundary currents of the southern hemisphere. *Journal of the Royal Society of Western Australia* 74, 35–45.
- Phillips, J.A., 2001. Marine macroalgal biodiversity hotspots: why is there high species richness and endemism in southern Australian marine benthic flora? *Biodiversity and Conservation* 10, 1555–1577.
- Smale, D.A., Wernberg, T., 2009. Satellite-derived SST data as a proxy for water temperature in nearshore benthic ecology. *Marine Ecology Progress Series* 387, 27–37.
- Smith, R.L., Huyer, A., Godfrey, J.S., Church, J.A., 1991. The Leeuwin Current off Western Australia. *Journal of Physical Oceanography* 21, 323–345.
- Toohey, B., Kendrick, G., 2008. Canopy-understorey relationships are mediated by reef topography in *Ecklonia radiata* kelp beds. *European Journal of Phycology* 43, 133–142.
- Toohey, B.D., Kendrick, G.A., Harvey, E.S., 2007. Disturbance and reef topography maintain high local diversity in *Ecklonia radiata* kelp forests. *Oikos* 116, 1618–1630.
- Tuya, F., Haroun, R.J., 2006. Spatial patterns and response to wave exposure of shallow water algal assemblages across the Canarian Archipelago: a multiscaled approach. *Marine Ecological Progress Series* 311, 15–28.
- Underwood, A.J., Chapman, M.G., 1996. Scales of spatial pattern of distribution of intertidal invertebrates. *Oecologia* 107, 212–224.
- Underwood, A.J., Chapman, M.G., Connell, S.D., 2000. Observations in ecology: you can't make progress on processes without understanding the patterns. *Journal of Experimental Marine Biology and Ecology* 250, 97–115.
- Van Hazel, J., 2001. *The climate and physical oceanography of the Recherche Archipelago and adjacent waters*. University of Western Australia.
- Warwick, R.M., 1988. The level of taxonomic discrimination required to detect pollution effects on marine benthic assemblages. *Marine Pollution Bulletin* 19, 259–268.
- Wernberg, T., Connell, S.D., 2008. Physical disturbance and subtidal habitat structure on open rocky coasts: effects of wave exposure, extent and intensity. *Journal of Sea Research* 59, 237–248.
- Wernberg, T., Goldberg, N., 2008. Short-term temporal dynamics of algal species in a subtidal kelp bed in relation to changes in environmental conditions and canopy biomass. *Estuarine, Coastal and Shelf Science* 76, 265–272.
- Wernberg, T., Kendrick, G.A., Phillips, J.C., 2003. Regional differences in kelp-associated algal assemblages on temperate limestone reefs in south-western Australia. *Diversity and Distributions* 9, 427–441.
- Wernberg, T., Kendrick, G.A., Toohey, B.D., 2005. Modification of the physical environment by an *Ecklonia radiata* (Laminariales) canopy and its implications to associated foliose algae. *Aquatic Ecology* 39, 419–430.