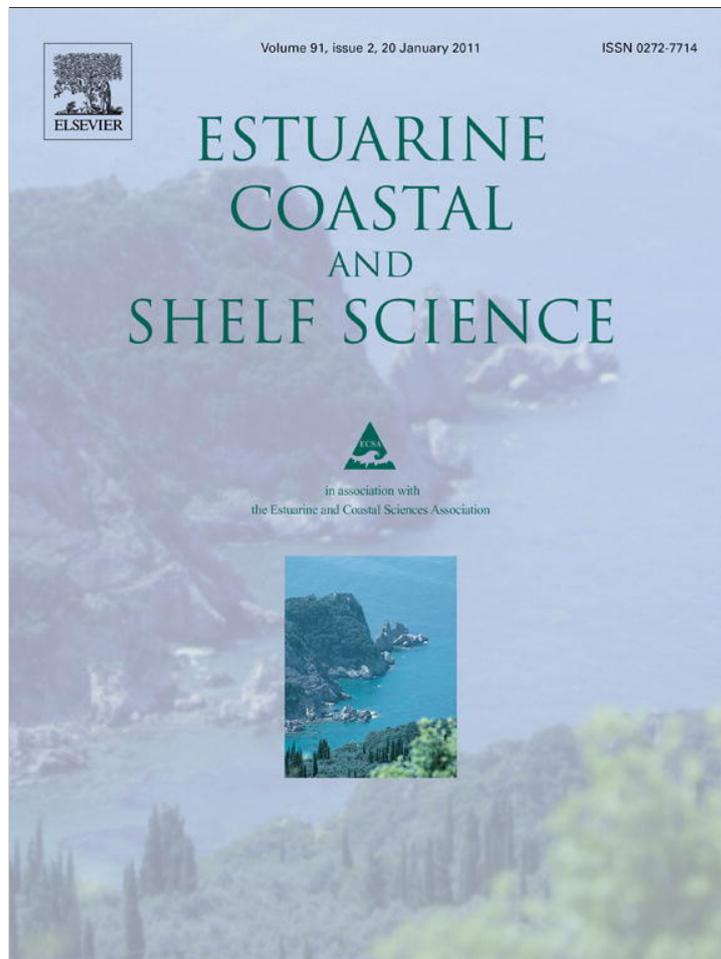


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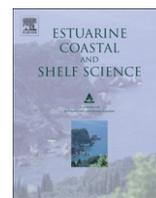
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## Subtidal macroalgal richness, diversity and turnover, at multiple spatial scales, along the southwestern Australian coastline

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### ABSTRACT

Patterns of species richness are governed by processes that act at vastly different spatial scales. In the marine system of southwest Australia, macroalgal assemblage structure and richness is thought to be strongly influenced by both the Leeuwin Current, which acts at large regional spatial scales, and small-scale processes such as competition, wave disturbance and habitat heterogeneity. We examined macroalgal species richness and diversity 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 almost 2000 km of temperate coastline. Macroalgal assemblages were highly speciose and the number, identity, and diversity of species varied considerably at all spatial scales. Small scale variability, at the scale of site or quadrat, contributed most to total variation in species richness and diversity, suggesting that small-scale processes are important drivers of ecological pattern in this system. Species richness, diversity and taxonomic distinctness increased sequentially along the coastline, from warmer to cooler waters. Small scale variability was most likely maintained by wave disturbance and habitat heterogeneity at these scales, while regional scale diversity and richness clines were attributed to the fact that most species had cool-water affinities and the southern coast of Australia is a hotspot of floral speciation and diversity. Macroalgal assemblages in southwest Australia are speciose and largely endemic, and biodiversity patterns are structured by multiple processes operating at multiple spatial scales.

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### 1. Introduction

Patterns of species richness are governed by processes that act at vastly different spatial scales. The consideration of multiple spatial scales – to enhance understanding of patterns and the processes that drive them at local to intermediate to regional extents – has been a central facet of modern ecology. Even so, our knowledge of spatial patterns of biodiversity on land far outweighs that of the sea, despite the fact that marine assemblages are well connected across multiple spatial scales, due to potentially long dispersal distances and generally weak geographical barriers (Cowen and Sponaugle, 2009). At large spatial scales, regional species pools are shaped by a combination of evolutionary, oceanographic and geological processes, which influence factors such as speciation, extinction, habitat availability and connectivity (Ricklefs and Schluter, 1993; Kotta and Witman, 2009). At smaller

spatial scales, local assemblage structure and richness may be driven by processes including disturbance, predation, competition, facilitation and local oceanography (Kotta and Witman, 2009).

Perhaps surprisingly, empirical examinations of biodiversity patterns of subtidal macroalgae at multiple spatial scales are relatively rare, despite their ecological importance as dominant habitat formers, space occupiers and food providers in nearshore habitats the world over (Kerwell, 2006). Understanding the role of spatial scale on ecological pattern is a useful approach to elucidating which processes (and at what spatial scales), are important drivers of biodiversity and community structure. The use of nested hierarchical sampling designs to examine both univariate and multivariate response variables at multiple spatial scales, has led to a greater appreciation of the importance of scale in ecology (Underwood and Chapman, 1996; Franchetti et al., 2005). Such designs provide unbiased and independent assessments of variability at pre-determined spatial scale to test structured hypotheses (Underwood and Chapman, 1996; Underwood et al., 2000). Here, we used this approach to examine patterns of biodiversity of subtidal macroalgae at spatial scales ranging from quadrats to regions.

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The marine flora of southern Australia is rich; about 1000 species of benthic macroalgae have been recorded, with over 50% of all genera endemic to the bioregion (Phillips, 2001; Kerswell, 2006). Such high richness and endemism have 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). At large spatial scales, the Leeuwin Current (LC), which originated over 40 Mya following the separation of Australia and Antarctica, influences the distribution of species along the southwest Australian coastline (McGowran et al., 1997; Kendrick et al., 2009; Smale et al., 2010a). The LC originates in the Indo-Pacific and flows polewards along the west coast of Australia, before deviating eastwards into the Great Australian Bight (Pearce, 1991; Smith et al., 1991). Its flow is strongest in winter, when it transports tropical (and subtropical) dispersal stages and nutrient-poor water polewards, which in turn 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 can be detected from northwest Australia to Tasmania, and it is thought to be an important driver of ecological pattern at regional scales.

At small spatial scales, biodiversity patterns are influenced by canopy–understorey interactions, habitat heterogeneity and provision of space by wave disturbance. Kelp beds are dominated by *Ecklonia radiata* in southwest Australia, which forms large monospecific stands and may regulate surrounding diversity through competitive exclusion (Kendrick et al., 1999; Wernberg et al., 2005). However, spatiotemporal variability in removal of the kelp canopy by wave disturbance creates a mosaic of patches at different successional stages, which promotes and maintains overall assemblage richness (Toohey et al., 2007; Toohey and Kendrick, 2008; Wernberg and Goldberg, 2008). Furthermore, substantial small-scale heterogeneity in the physical structure of limestone and granite reefs (i.e. topography, relief, aspect and rugosity, etc.) enhances niche availability and in turn promotes local biodiversity (Toohey et al., 2007).

In short, the marine flora of southwest Australia is unique in that it has evolved largely in isolation (with the exception of Antarctica, now largely covered by an ice sheet, Australia has been separated from all other land masses for the last 80 million years) and in nutrient-poor waters since the Eocene (Veevers, 1991; Phillips, 2001). Spatially, macroalgal assemblages are characterised by high species richness and turnover at local scales (Kendrick et al., 1999; Wernberg et al., 2003). However, while the flora inhabiting the cool waters of southern Australia are widely recognised as a biodiversity and endemism hotspot, most research has been either purely descriptive or quantitative but conducted across small or single spatial scales (but see Wernberg et al., 2003). Furthermore, most marine macroalgae have cool-water affinities and the southern coast of Australia is a well-known biodiversity hotspot for marine flora (Phillips, 2001; Kerswell, 2006), so that biodiversity of macroalgae is thought to increase with latitude (i.e. from warm to cool waters), as it does in other temperate systems (Kerswell, 2006). However, empirical descriptions of these diversity and richness clines are currently lacking from the temperate eastern boundary of the Indian Ocean.

Recent work has shown that assemblage structure and the biomass of key taxon vary across multiple spatial scales along this coastline, and that pronounced variability at small spatial scales is a common feature of the flora (Wernberg et al., 2003; Smale et al., 2010b). Here, we expand this information by quantitatively testing patterns of biodiversity at multiple spatial scales along almost 2000 km of temperate rocky coastline. This multi-scale approach provided an indication of the importance of the scale-dependent

processes that drive and maintain high regional biodiversity, while the surveys represented the most comprehensive and extensive quantification of the marine flora of southwest Australia to date. Specific hypotheses of interest were:

1. Species richness, diversity and turnover will vary at multiple spatial scales, but variability at small spatial scales will be the greatest contributor to overall variance;
2. Macroalgal biodiversity, in terms of richness, diversity and taxonomic distinctness, will increase along the coastline (from north to south to east) from warmer to cooler waters.

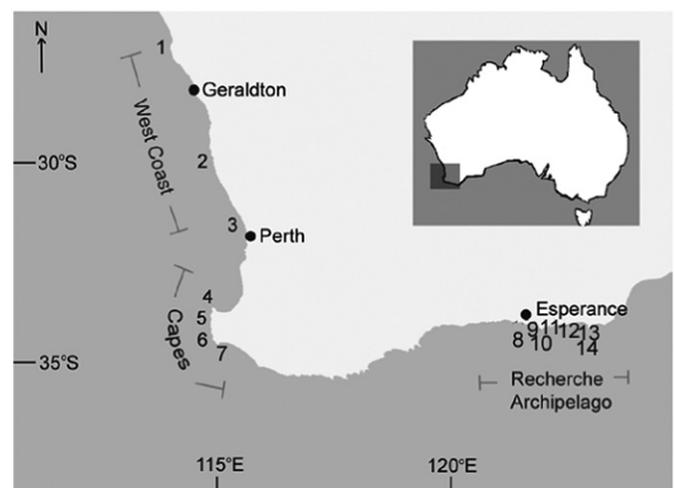
## 2. Methods

### 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 almost 2000 km of temperate coastline, and regions were separated by at least 300 km of coastline (Fig. 1). All three regions are characterised by a series of subtidal (predominantly) reefs that range from 3 m to >30 m depth. 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. Horizontal and gently sloping 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 employed to investigate ecological pattern at four spatial scales: region (3 levels in total), location (14 levels), site (84 levels) and quadrat (504 samples in total). Within each region, sampling was conducted at 3 (West Coast), 4 (Capes) or 7 (Recherche) locations. Locations 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



**Fig. 1.** Map of the southwest Australian coastline indicating location of 14 sampling locations 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 of 8 Island, 9) Frederick Island, 10) Modrain, 11) Thomas Island, 12) Mart, 13) Twin Peaks, 14) Middle Island.

surfaces at 8–12 m depth). Within each location, 6 sites were selected at random from a larger possible pool for sampling. Sites were at least 300 m apart at all locations. Sampling was targeted at 10 m depth, but in reality sites ranged from 9 to 13 m in depth. Within each site, 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 and identification. All specimens were identified to species or non-ambiguous genera (i.e. genera with only one unidentified species).

In total, 504 quadrat samples were included in the analysis, covering 126 m<sup>2</sup> of subtidal reef. The imbalance in the number of locations and the inconsistency of spatial separation between locations within each region stemmed from the fact that data from 3 different projects were compiled for the current study. However, as the principal taxonomist, sampling protocol, and sampling area within each location 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 has shown that temporal variability in assemblage structure, across both seasons and consecutive years, is minimal. As such, the inconsistency in sampling years is unlikely to confound the comparisons of spatial patterns presented here.

### 2.3. Statistical analysis

Biodiversity was represented by both species richness (SR) and Shannon-Wiener's index ( $H'$ ), and calculated for each quadrat, site (6 quadrats pooled), location (36 quadrats pooled) and region (between 108 and 252 quadrats pooled). In addition, SR and  $H'$  at each spatial scale were plotted against distance along coastline (from north to south to east), to account for the inconsistency in spacing between locations and because the coastline is characterised by a well-defined nearshore temperature gradient (Smale and Wernberg, 2009). Variability in SR and  $H'$  was examined at the different spatial scales with univariate PERMANOVA, conducting with Primer 6 software and PERMANOVA add-on (Clarke and Warwick, 2001a; Anderson et al., 2007). The design was fully hierarchical and all factors were treated as random. A similarity matrix based on Euclidean distance of untransformed species richness and  $H'$  was generated for the analyses, which used 4999 permutations under a reduced model. The PERMANOVA approach was adopted (as opposed to traditional ANOVA) because these data were non-normally distributed and did not pass Levene's homogeneity of variance tests.

To examine the influence of the macroalgal canopy on overall patterns of SR and  $H'$ , quadrats and sites within each region were sorted into three classes (low, moderate, high) based on the total biomass of dominant canopy forming species (*E. radiata*, *Scytothalia dorycarpa* and *Platythalia* spp.). Each class consisted of one third of the quadrats/site within each region and differences in SR and  $H'$  between canopy biomass classes were examined at the spatial scales of quadrat and site. Differences between classes were tested formally with ANOVA; all raw datasets met the assumptions of normality and homogeneity of variance (Shapiro–Wilk and Levene's tests respectively, at  $p > 0.05$ ).

Species turnover was calculated by constructing a Bray–Curtis similarity matrix based on presence/absence data for all samples, which is algebraically equivalent to the Sørensen index used to describe beta diversity (Clarke and Warwick, 2001a). PERMANOVA was conducted (design as above) to partition the variability in assemblage composition across the spatial scales. Furthermore,

Bray–Curtis similarity coefficients based on presence/absence were calculated from pairwise comparisons of quadrat samples within the same site ( $n > 1400$ ), samples in different sites within the same location ( $n > 8000$ ), samples in different locations within the same region ( $n > 53\,000$ ), and samples from different regions ( $n > 101\,000$ ).

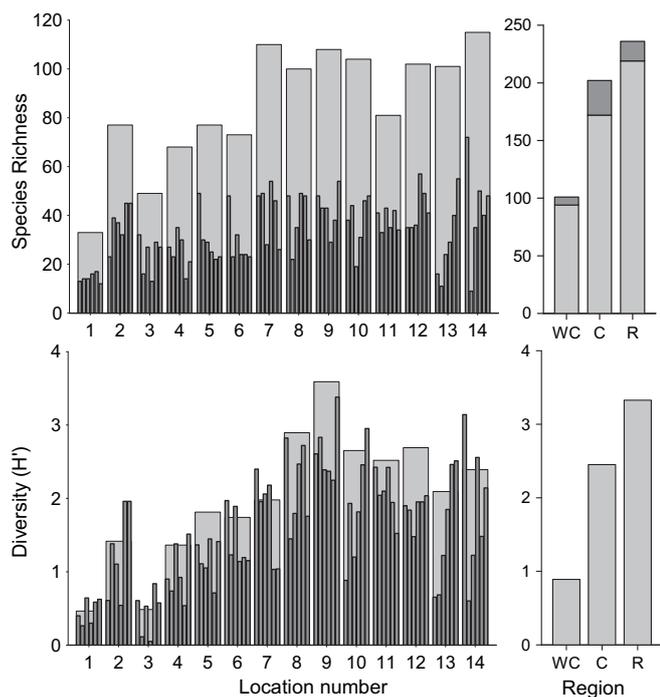
Regional richness and diversity were calculated by pooling all samples within each region. Species accumulation curves and plots from the Chao 2 species richness estimator were constructed for each region (using 999 permutations in the Primer software), to assess the likely completeness of the species sampling (i.e. whether species richness had reached asymptotic values). The Chao 2 estimator was used as it takes into account the effect of rare species on total richness, delivers a non-conservative estimate of richness, and performs well with few samples (Colwell and Coddington, 1994). As previous studies have suggested that macroalgal assemblages in WA are speciose and contain many rare species, and estimates of local richness were from relatively few samples (see below), this estimator was deemed the most appropriate.

In addition to richness and diversity, the taxonomic breadth of assemblages at each location was assessed using average taxonomic distinctness (Av. TD) and variation in taxonomic distinctness (Var. TD) measures (again using Primer 6). This is a useful approach, as the diversity of any given assemblage is not simply the number of species represented, but also how closely related the species are in their phylogeny. Av. TD is calculated by summing the path lengths through a taxonomic tree connecting every pair of species in an assemblage, and then dividing by the total number of paths (Clarke and Warwick, 1998). Var. TD is simply the variance of the pairwise path lengths and reflects the unevenness of the taxonomic tree (Clarke and Warwick, 2001b). Whilst these metrics have been most frequently used to detect anthropogenic impacts, they are equally suitable for describing diversity patterns along large scale environmental gradients. Moreover, they are advantageous in that they are independent of sampling effort, and generally do not co-vary with species richness or diversity, thereby depicting a distinct facet of biodiversity.

### 3. Results

In total, 289 species of macroalgae were identified from the 504 quadrat samples. Rhodophytes contributed most to this diversity, with the orders Ceramiales (89 species) and Gigartinales (49 species) being particularly speciose. Phaeophytes were primarily represented by the Fucales (39 species) and Dictyotales (24 species), while the order Bryopsidales was the dominant contributor to Chlorophyte richness.

Species richness (SR) and diversity ( $H'$ ) at the scale of location peaked at 118 and 3.6 respectively, and was generally greater at the south facing locations of Capes and the Recherche compared with the west facing locations of Capes and the West Coast (Fig. 2). SR and  $H'$  at the scale of site peaked at 74 and 3.4 respectively, and were markedly variable between sites within the same location. For example, at Middle Island in the Recherche Archipelago SR ranged from 9 to 74 per site and  $H'$  ranged from 0.6 to 3.4 (Fig. 2). Univariate PERMANOVA indicated that SR was considerably variable at all spatial scales (Table 1). However, variability between regions was not significant, whereas variability between the smaller spatial scales of site and location was highly significant (Table 1). With respect to variance components, the relative importance of small-scale variability (i.e. residual and site) far outweighed that of large scale variability (i.e. location and region).  $H'$  varied significantly at all spatial scales (Table 1). Examination of variance components suggested that variability at the smallest scale (quadrat) and the largest scale (region) was greater in



**Fig. 2.** Species richness and diversity ( $H'$ ) of southwest Australian macroalgal assemblages at multiple spatial scales. Local richness and diversity is shown for each of the 14 locations ( $n = 36$ , light grey bars) and for each of the six sites within each location ( $n = 6$ , black bars). Location numbers run sequentially along the coastline from north to south to east, and correspond to those in Fig. 1. Right-hand plots show total regional richness and diversity (light grey bars), and estimated total species richness using the Chao 2 estimator (dark grey bars), for West Coast (WC), Capes (C) and Recherche (R).

magnitude than variability at the intermediate spatial scales. The multivariate data on assemblage composition showed that species turnover was significant at all spatial scales, and that variability at small spatial scales contributed most to the overall variability (Table 1).

Regional (gamma) SR was twice as high in the Recherche region compared with the West Coast, in terms of both observed and predicted values (Fig. 2). Logically, this comparison was confounded to some extent by the inconsistency in sampling area, as 7 locations were sampled in the Recherche compared with 3 in the West Coast.

**Table 1**

PERMANOVA results based on Euclidian distance measures for untransformed species richness and diversity ( $H'$ ) data and Bray–Curtis similarity coefficients derived from presence/absence data for species turnover. All tests used 4999 permutations under a reduced model. Estimates of (pseudo) variance components, and their relative contribution to total variance, are also shown.

Source	df	MS	F	P	Var. comp (%)
<i>a. Species richness</i>					
Region	2	1030.1	2.91	0.098	4.3 (8.7)
Location (Re)	11	354.6	2.38	0.007	5.7 (11.6)
Site (Lo(Re))	70	148.7	8.49	0.001	21.8 (44.3)
Res.	420	17.5			17.5 (35.4)
<i>b. H'</i>					
Region	2	27.4	9.90	0.003	0.16 (28.9)
Location (Re)	11	2.76	2.79	0.006	0.05 (9.1)
Site (Lo(Re))	70	0.99	4.82	0.001	0.13 (24.1)
Res.	420	0.21			0.21 (37.9)
<i>c. Species turnover</i>					
Region	2	141 830	5.43	0.001	737 (19.2)
Location (Re)	11	26 100	2.97	0.001	480 (12.5)
Site (Lo(Re))	70	8787	6.33	0.001	1233 (32.1)
Res.	420	1386			1386 (36.1)

However, this observation was validated with species accumulations curves (generated from 999 randomisations, curves not shown here) which indicated that the Recherche was by far the most speciose region even when sampling effort was standardised to 108 samples. Of the 289 species recorded, 51% were observed in only one region; 34% were unique to Recherche, and 13% and 4% were unique to Capes and West Coast, respectively. Around 20% of all species were cosmopolitan (i.e. recorded in all 3 regions), and the remaining 29% were recorded in two regions. Furthermore, regional  $H'$  increased considerably from West Coast, to Capes to Recherche (Fig. 2).

SR and  $H'$  increased along the coastline from the warmer waters of the West Coast to the cooler waters of the Recherche. Crucially, this pattern was markedly scale-dependent (Fig. 3), so that the diversity cline was strongest at the largest spatial scale (region) and weakest at the smallest spatial scale (quadrat). Pronounced variability at small spatial scales resulted in 'noisy' signals for quadrat and site level plots, whereas patterns were more predictable and prominent at the large spatial scales of location and region (Fig. 3).

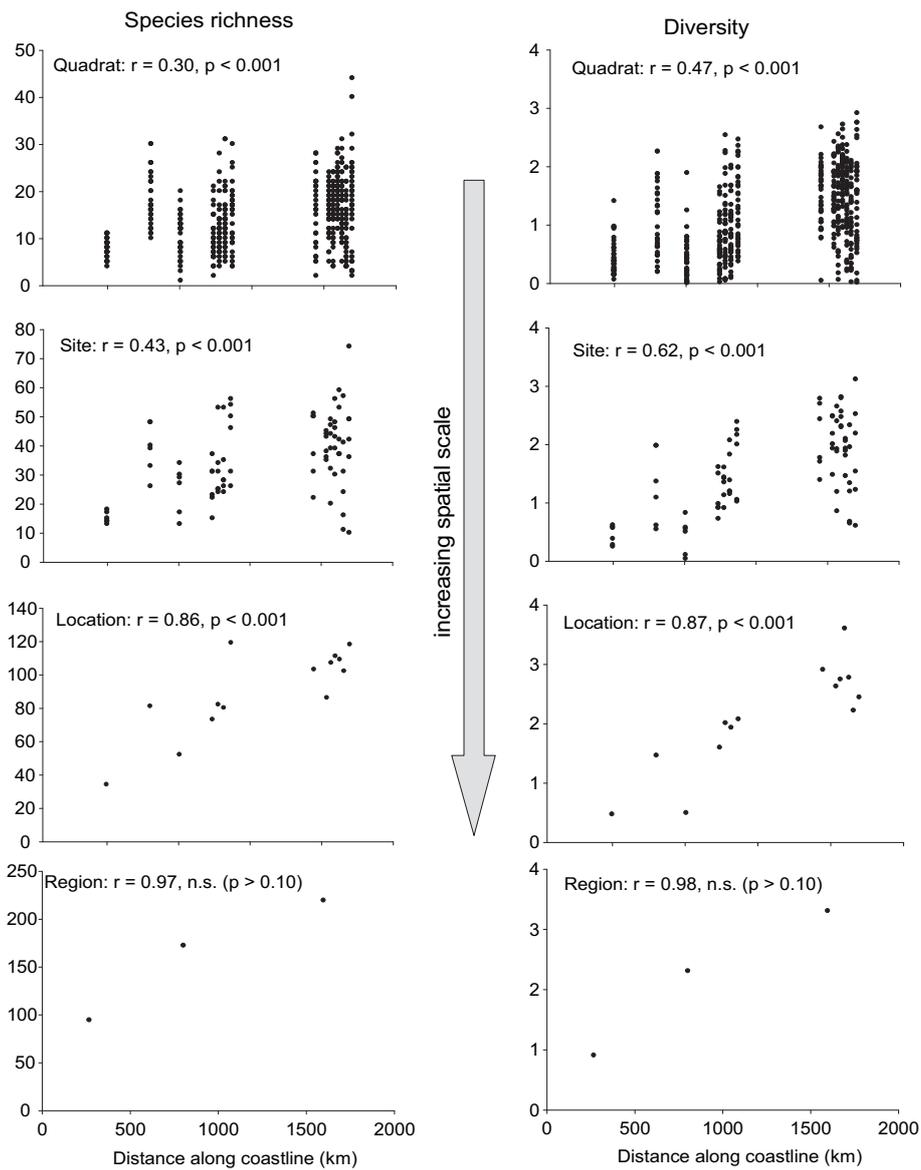
At both West Coast and Recherche, SR was significantly lower in quadrats with high biomass of canopy forming species, while  $H'$  decreased with increasing canopy biomass, to some extent, in all three regions (Fig. 4). For example, within the West Coast region  $H'$  was, on average, a third lower in quadrats with high canopy biomass compared with quadrats with a low biomass of large canopy forming species. At the larger scale of site, differences between canopy biomass groups were less pronounced (Fig. 4). Even so, SR was significantly lower at sites with high canopy biomass at Recherche, and  $H'$  was lower at high canopy biomass sites at both Capes and Recherche.

Species turnover (beta diversity) increased with increasing spatial scale, so that average similarity between sample pairs was greatest at the scale of quadrat and least at the scale of region (Fig. 5). Even so, similarity between sample pairs was low at small scales, suggesting that species turnover is very high along the southwest coast of Australia. For example, average similarity between quadrats from the same site, just a few metres apart, was less than 50%. Moreover, the difference in overall dissimilarity between the spatial scales of site and location was low (28% compared with 21%), indicating that species turnover was almost as pronounced across 100 s of metres as it was across scales of ~10 km.

Taxonomic distinctness values, both Av. TD and Var. TD, are superimposed on funnel plots in Fig. 6. In this case, funnels represent 95% probability estimates for Av. TD and Var. TD from 1000 independent simulations, drawn randomly from the master taxonomy list of 289 species. The plots showed that both Av. TD and Var. TD tended to increase sequentially between regions, from West Coast to Capes to Recherche (Fig. 6), although there was notable variability between locations within regions. For Av. TD, only one location from the Recherche (Mart) fell above the 95% confidence limit, while two locations from the West Coast (Jurien and Marmion), were well below the limit. With regards to Var. TD, four locations from the Recherche region were outside and above the 95% confidence limit.

#### 4. Discussion

Subtidal macroalgae assemblages of southwest Australia are highly speciose, and exhibit high species turnover at multiple spatial scales. In total, we recorded almost one-third of the 1000 species of macroalgae described from the southern coastline of Australia, but the number of species we recorded at each spatial scale varied considerably. At the smallest scale of quadrat, we observed 1 to 44 species, while at the intermediate scales of site

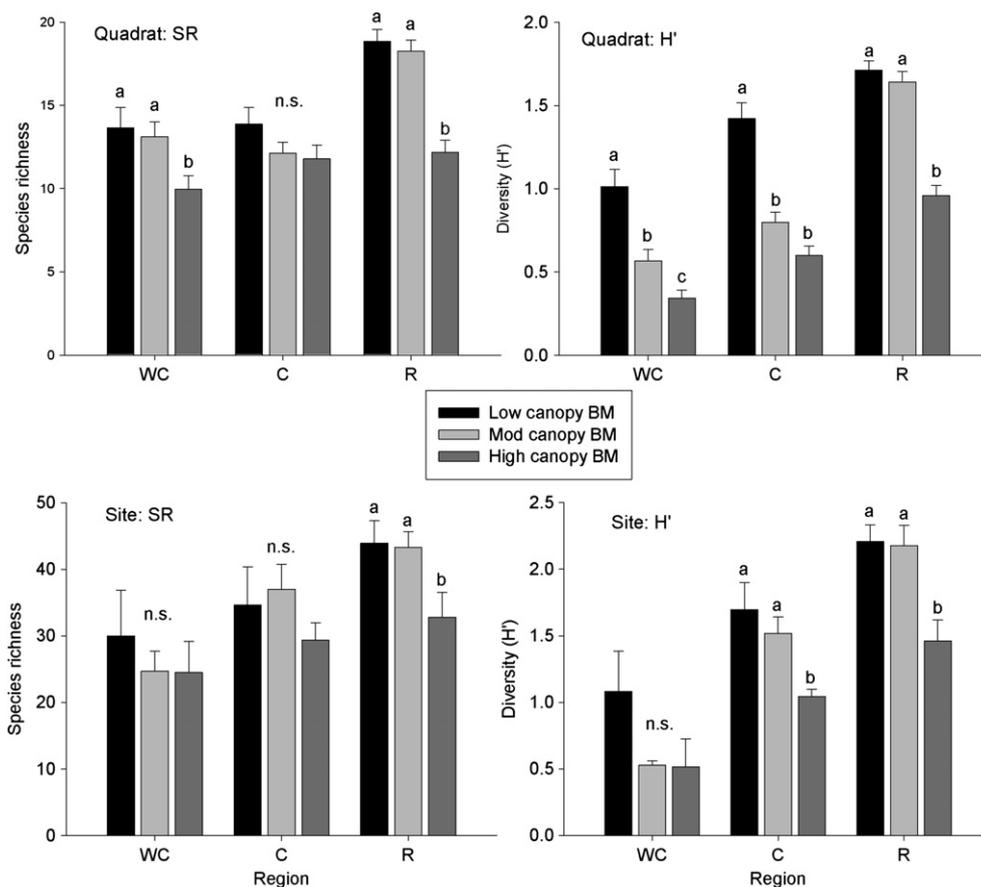


**Fig. 3.** Species richness (left) and diversity (right) of macroalgal assemblages at multiple spatial scales, plotted against geographic position on southwest Australian coastline. Samples are pooled for each relevant scale and richness/diversity values are plotted against distance (km) from the northernmost sampling location (Kalbarri in West Coast region). Species richness is shown as the total number of species recorded at each spatial scale at each location and diversity is represented by  $H'$ . Pearson's correlation coefficient ( $r$ ) is shown for each plot.

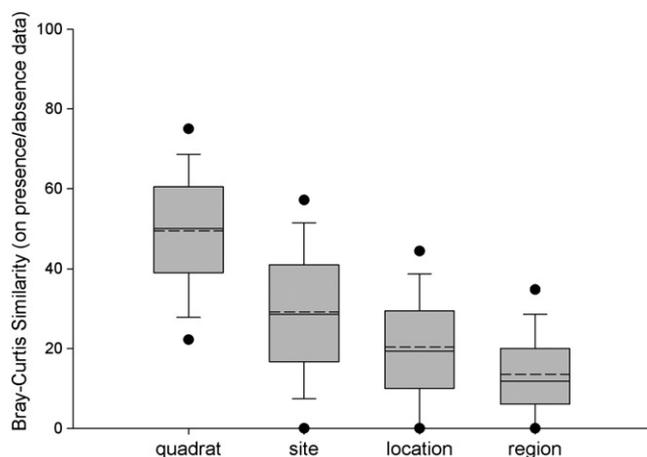
and location we recorded 10 to 74 species and 34 to 118 species, respectively. At regional spatial scales, species richness (SR) ranged from 94 to 219. Diversity ( $H'$ ) was similarly variable across spatial scales. Our first hypothesis, that species richness, diversity and turnover would vary at multiple spatial scales, and that variability at small spatial scales will be the greatest contributor to overall variance, was supported by species diversity and turnover but not richness. SR did not vary significantly between regions, and variability between quadrats was less pronounced than variability between sites. Even so, combined variability at these smallest scales accounted for 80% of the total variance (Table 1).

Small scale variability in the number, diversity and turnover of macroalgal species is likely to be largely driven by variation in the density, identity and morphology of canopy formers (such as *E. radiata*), and habitat heterogeneity inherent in rocky subtidal reefs, both of which vary at small spatial scales. Wave action is intense along the coastline of southwest Australia, and removal of kelps

generates patchiness in canopy density and cover on subtidal reefs (Wernberg and Connell, 2008). Canopy formers alter the immediate physical environment and influence the richness and structure of the macroalgal assemblage through canopy–understorey interactions (Wernberg et al., 2005). Specifically, large dominant canopy formers may competitively exclude other understorey or turfing species by reducing light levels and scouring recruits or juveniles during turbulent conditions. In all 3 regions, we recorded lower SR and/or  $H'$  in quadrats or sites characterised by high canopy biomass, which suggested that competitive exclusion by dense patches of canopy formers may be a common ecological feature of the flora. It is likely, however, that the presence of canopy formers, perhaps in moderate densities, facilitates the existence of other species by moderating the physical environment (e.g. by dampening hydrodynamic forces) but this was not represented in the data. Furthermore, subtidal reefs in coastal southwest Australia are both extensive and heterogeneous, and vary in terms of relief,



**Fig. 4.** Species richness and diversity versus the total biomass of dominant canopy formers (*E. radiata*, *S. dorycarpa* and *Platythalia* spp.) within each region. Canopy biomass classes were determined a-posteriori by sorting quadrats or sites (6 quadrats pooled) into three equal classes based on total canopy biomass. Mean ( $\pm$ SEM) values are plotted for each region and for each spatial scale; for each canopy biomass class,  $n = 36$  (quadrat) and 6 (site) for West coast, 48 (quadrat) and 8 (site) for Capes and 84 (quadrat) and 14 (site) for Recherche. Differences in SR and H between canopy biomass classes within each region were tested with one-way ANOVA; significance was set at  $P < 0.05$  and post-hoc pairwise comparisons were conducted with SNK tests (differences between groups indicated on plots with lower case letters).

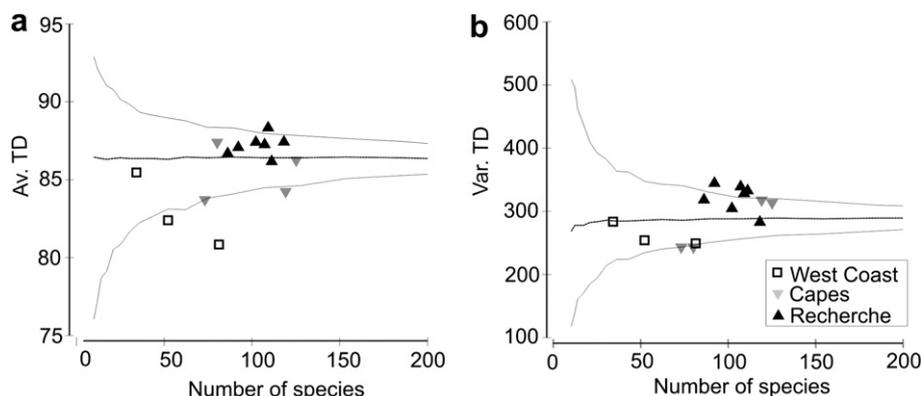


**Fig. 5.** Box and whisker plots of beta diversity (Bray–Curtis similarity coefficients on presence/absence data) at different spatial scales. Solid line represents median value, dotted line represents mean value and grey box indicates 25th and 75th percentile. Error bars indicate 10th and 90th percentile and dots show range of data. Values were calculated from pairwise comparisons of samples across the four spatial scales ( $n$  ranged from  $>1000$  to  $>100,000$  comparisons).

topography, aspect, and structural integrity across small spatial extents. Therefore, the physical habitat is notably heterogeneous at the scale of metres, which promotes variability in canopy removal and increases niche availability through the diversification of microhabitat structure (Kendrick et al., 1999; Toohy et al., 2007).

Interestingly, grazing pressure, which is known to generate small-scale patchiness in other benthic systems, is unlikely to be a key explanatory process here, as the abundance and influence of herbivores in southwest Australia is relatively low (Fowler-Walker and Connell, 2002; Vanderklift and Kendrick, 2004; Wernberg et al., 2008). Our study suggests that the small-scale processes of wave-driven canopy dynamics and habitat heterogeneity are consistently important across geographically distinct regions of coastline, and that richness and diversity vary considerably at scales of metres to 10 s m in southwest Australia. Pronounced variability in richness and assemblage structure at small spatial scales is a common pattern for marine benthic communities (Fraschetti et al., 2005), and is a strong feature of the southwest Australian subtidal flora.

Our second hypothesis, that macroalgal richness, diversity and taxonomic distinctness, would increase along the coastline (from north to south to east) from warmer to cooler waters, was largely supported by the data, although these patterns were markedly scale dependent. Richness and diversity clines were more evident at larger spatial scales, as pooling of samples aggregated small-scale environmental heterogeneity. This ‘averaging out’ of local complexity at broader spatial scales to reveal strong biogeographic



**Fig. 6.** (a) Average taxonomic distinctness (Av. TD) and (b) variation in taxonomic distinctness (Var. TD) of subtidal macroalgal assemblages for each location. Funnels represent 95% probability for both indices, estimated from 1000 simulations drawn randomly from the 289 subtidal macroalgae species.

patterns has been previously discussed for both general ecological communities (Lawton, 1999) and more specifically for Australian macroalgal assemblages (Fowler-Walker and Connell, 2002). Clearly, macroalgal biodiversity in southwest Australia is highly variable over small spatial scales (driven by wave induced canopy removal and habitat heterogeneity) and, as a result, important clines in diversity (driven by processes acting at large spatial and temporal scales, such as connectivity and speciation) may only be discernible at broad spatial scales. This has important implications for detecting and predicting the effects of environmental change on biodiversity in the region, and for generalising the outcomes of locally-conducting experiments to other places or spatial scales.

When regional diversity and richness were considered (and sampling area was standardised), SR and H' were 2 and 3 times greater at Recherche compared with West Coast, respectively. This pattern of increasing richness and diversity from warm to cool waters is somewhat intuitive, as most marine macroalgae have cool-water affinities and the southern coast of Australia is a well-known biodiversity hotspot for marine flora (Phillips, 2001; Kerswell, 2006). Even so, the results suggest that this stretch of coastline represents an important transition zone between the coral dominated assemblages of the sub-tropics and the speciose macroalgal assemblages of the south coast.

We also assessed macroalgal diversity patterns with two recently developed metrics, av. TD and var. TD, which, to date, have been applied to very few benthic algae datasets (Price et al., 2006; Ceschia et al., 2007). Although av. TD and var. TD describe a distinct facet of biodiversity to, and are independent of, species richness and H', these metrics showed similar patterns along the coastline, with a general increase from West Coast to Capes to Recherche. Distinctness measures are most commonly applied to environmental impact studies, as ecological theory predicts that av. TD will decrease and var. TD will increase along a disturbance gradient. However, where anthropogenic impacts or pollution stress is relatively low, these metrics may be influenced by ecological artefacts and evolutionary history. For example, *relative* habitat diversification across the islands of the Recherche Archipelago, in terms of reef structure and wave exposure, would lead to greater biological diversity at coarser taxonomic levels, and therefore higher av. TD values compared with the other regions. Evolutionary causes are perhaps more likely, as the southern coast of Australia is considered an adaptive zone in which rapid speciation of marine flora has been driven by, amongst other factors, variability in the Leeuwin Current and sea level change (McGowran et al., 1997; Phillips, 2001). For example, the Leeuwin Current, 'switches' on and off in the Great Australian Bight in tandem with global climate

cycles, which strongly influences seawater temperature along the southern coast of Australia (McGowran et al., 1997). Therefore, fluctuating environmental conditions and habitat heterogeneity/availability may facilitate the co-existence of taxonomically distinct macroalgal species. Recent data suggest that demersal fish assemblages at Recherche are also more taxonomically distinct than those elsewhere in Western Australia (L. Beckley, pers. comm.), and this unique archipelago should be considered an important region for biodiversity research and conservation.

In conclusion, the marine flora of southwest Australia is known to be a global biodiversity hotspot, with high levels of endemism (Phillips, 2001; Kerswell, 2006). Our study suggests that processes acting over multiple spatial (and temporal) scales have shaped this biodiversity, and that high variability in the number, diversity and identity of species over small spatial scales is a prominent feature of this system. The flora has evolved in relatively undisturbed isolation, surrounded by oligotrophic waters, for at least 40 million years, so that regional and local species pools may be well established and connected. Superimposed onto this evolutionary stability, persistent wave-driven disturbance and habitat heterogeneity seem to operate over small spatial and temporal scales to promote and maintain high (but variable) local biodiversity.

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