

Meegan J. Fowler-Walker · Sean D. Connell
Bronwyn M. Gillanders

Variation at local scales need not impede tests for broader scale patterns

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Abstract Ecologists are not always mindful of the constraints imposed by their scale of observation and sometimes prematurely attempt broad generalisations or become mesmerised by local details depending on their predilections. We specifically chose a character that is known for its local and unpredictable variation (morphology of kelp) to test the effect of scale on our ability to determine spatial patterns. We compared the morphology of *Ecklonia radiata* between monospecific and mixed stands of canopy-forming algae across temperate Australia (> 5,100 km coastal distance) within a hierarchy of several spatial scales. While *E. radiata* specimens were generally larger in monospecific than in mixed stands, we failed to observe differences in morphology between stands at many sites and locations. Despite substantial local variation, differences between stands became increasingly clear at broader scales. The frequency of inconsistent differences between stands was greatest at local scales (sites separated by kms), intermediate at intermediate scales (locations separated by 100s of kms) and least at regional scales (regions separated by 1,000s of kms). These observations support the idea that large scale patterns can emerge from apparent stochasticity at small scales, and that unaccountable variation at local scales need not impede tests for similar patterns at broader scales. Most ecologists work at scales where complexity tends to be greatest (i.e. local) and is likely to be explained by special and unique events. It is encouraging, therefore, to observe that patterns can emerge from complexity at local scales to provide new opportunities to answer some of the more

interesting questions about the relative importance of processes across the vast parts of the world's coast.

Introduction

Natural variation of pattern is an ecological phenomenon that ecologists first ignored, then recognised (McIntosh 1980) and now embrace (Underwood 1997; Benedetti-Cecchi 2003). Indeed, the word 'variation' is common to the titles of many papers and the most widely used test-statistic by ecologists (analysis of variance). Despite our apparent willingness to engage with and understand natural variation, we still grapple with understanding ecological patterns and dynamics across broad scales.

Most ecologists work at scales where complexity is greatest (i.e. local). It is not surprising, therefore, that we tend to be captivated by the description and explanation of local variation whilst being pessimistic about the existence of broader patterns that may be organised around a relatively simple set of rules (Lawton 1999). It is clear that continuing disinvestment in broad scale patterns will do little to allay the criticism that ecologists are primarily focused on the discovery of new details (dissimilarity in patterns) and publication of idiosyncratic patterns and processes (Peters 1991). A key step towards progress is the publication of well-conceived observational studies across broad spatial scales (Underwood et al. 2000), but a lack of such studies can only result in a potential bias against the development of ecological generality (Foster 1990), potentially hampering the development of broad scale ecology (Underwood and Petraitis 1993). This study demonstrates that large variation at local scales is not a major impediment to tests of patterns at broader scales.

Using a character (kelp morphology) known for its local and unaccounted variation (e.g. Rice et al. 1985; Cheshire and Hallam 1989; Rice and Kenchington 1990)

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M. J. Fowler-Walker · S. D. Connell (✉) · B. M. Gillanders
Southern Seas Ecology Laboratories,
School of Earth and Environmental Sciences,
University of Adelaide, DP 418, 5005 Adelaide,
South Australia, Australia
E-mail: sean.connell@adelaide.edu.au
Tel.: +61-8-83036224
Fax: +61-8-83034364

we tested for scale-dependent patterns on morphology (similarities versus dissimilarities) across several regions of temperate Australia. The morphology of the canopy-forming kelp, *Ecklonia radiata*, provides an appealing opportunity to assess the variation occurring at local through to regional scales because it spans the world's longest west-east continuous coastline (Fowler-Walker and Connell 2002; Irving et al. 2004). Moreover, a recent study of the morphology of this species across the same coast at similar sites emphasised local variation and morphologically discrete populations (Wernberg et al. 2003). Such local variation is common in algae (Rice et al. 1985; Blanchette et al. 2002; Wernberg et al. 2003) given their plastic growth which can vary as a function of their sensitivity to a wide range of environmental variables (Molloy and Bolton 1996; Andrew and Viejo 1998; Hurd 2000). Importantly, while we know the identity of the kinds of environmental variables that may affect morphology (e.g. depth: Molloy and Bolton 1996 and exposure; Blanchette 1997), there remains no predictive understanding of their relative contribution to observed variation. We assessed the model, therefore, that whilst the morphology of any one plant is likely to represent the outcome of many special and unique events, it may not preclude the existence of broad patterns.

There are costs involved in the search for generality (Wiens 1989). These costs often sacrifice specific information for breadth and ignore some special feature of the environment which, when taken into account, could improve predictive power. The problem confronting ecology is not whether one should test for the existence of general or specific phenomena, but what balance should be sought between the two and what costs are involved in favouring one aspect over the other (Peters 1991). For example, while the morphology of *E. radiata* varies enormously at local scales across temperate Australasia (Wernberg et al. 2003), such variation may be attributed to both the type of stand (local and specific information) and region (regional and general information) from which the individual was sampled. If some local variable (e.g. morphology) is strongly associated with an unrecognised feature of the environment (e.g. type of stand), then tests of broad scale patterns may be compromised. Indeed, for every square meter of Western and South Australian rocky coast that contains *E. radiata* (0–18 m depth), it is estimated that more than half occur as mixed stands and the rest as monospecific stands (Goodsell et al. 2004). Differences in types of stand have consequences for understorey assemblages across Australia (Goodsell et al. 2004; Irving et al. 2004), but it remains to be tested as to whether the plants themselves differ, particularly their morphology.

We tested for the existence of broad scale patterns (generality) while incorporating such knowledge of local variation (specificity). We used a sampling protocol that partitioned our observations between types of stand (monospecific versus mixed stands) within a hierarchy of spatial scales. We focused on smaller scales of sampling

that were nested within successively larger scales that spanned the range of regions of interest. This use of hierarchical sampling is not novel, but is extraordinarily labour intensive and rarely used in tests of generality across regions. Instead, tests of generality often compare replicate sites (sometimes ordered into a hierarchy) between widely separated regions (e.g. New Zealand in South Pacific versus Oregon in North Pacific: Menge et al. 2002) with the expectation that similarity between distant regions provides powerful inferences for generality (i.e. between regions not studied). While these approaches create the opportunity for rapid progress, interpretation of spatial generalities are hampered because of lack of insight into the scales and places where similarity ends (e.g. spatial extent of generalities). We were interested in spatial generality across Australia (within a set latitude) and chose to distribute our hierarchy of observations across large proportions of the existing coast. While the use and advantages of the hierarchical approach are widely accepted, there remains much needed discussion on its use in extending ecological knowledge beyond high context-dependency and low predictability in local phenomena (Noda 2004).

We tested the hypotheses (1) that the morphology of *E. radiata* differs between monospecific and mixed stands of *E. radiata* across temperate Australia, and (2) that regional patterns of variation exist. We sampled sites within three specific regions [Western Australia (WA), South Australia (SA) and Eastern Australia (EA)]. Physical differences are likely to occur between stands and sites (e.g. hydrological differences such as the exposure to south-westerly swell that differs between WA and EA) and affect the biology of plants. Our sampling design did not intend to discriminate such differences (i.e. models about processes that account for spatial differences), but instead focused on testing the hypothesis that spatial differences in morphology occur between stands and regions (i.e. models about the existence of patterns). This study, therefore, not only seeks to contribute to fundamental knowledge of the broad scale ecology of the world's most widespread subtidal habitat, it also demonstrates that broad scale patterns are still possible to detect even if patterns are typically chaotic at small scales.

Materials and methods

The morphology of *E. radiata* was quantified between November 2001 and January 2002 across WA, SA and EA (Fig. 1; 3,800 km linear distance, > 5,100 km coastal distance). Sampling followed a fully-nested hierarchical design at three spatial scales: regions, locations (within regions) and sites (within locations). Regions were separated by 1,000s of km and chosen so that they fell between the latitudes 33°37'S and 37°08'S. This latitudinal restriction reduces potential variation in morphology caused by latitudinal effects (Rice et al. 1985; Cheshire and Hallam 1989). Within each region,

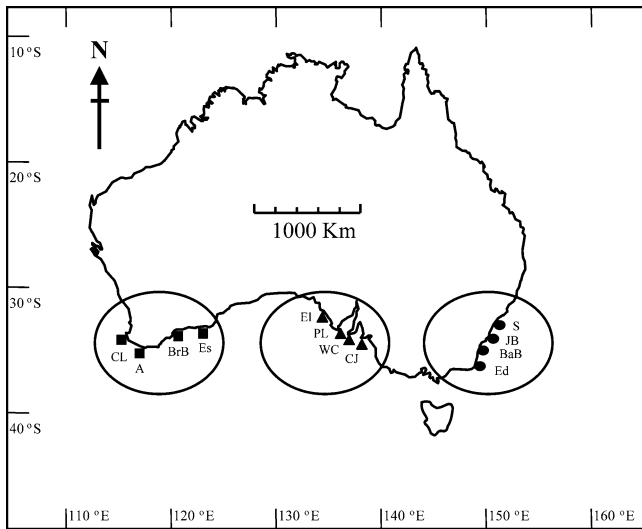


Fig. 1 The regions and locations of sampling which were chosen to minimise latitudinal variation (33°37'S to 37°08'S). From *left to right* locations were: Cape Leeuwin, Albany, Bremer Bay and Esperance (Western Australia ■); Elliston, Port Lincoln, West Cape and Cape Jervis (South Australia ▲); and Eden, Batemans Bay, Jervis Bay and Sydney (Eastern Australia ●)

four locations were selected (separated by 100s of km), with four sites (separated by km) within each location. Scales of separation were based on linear distance, and all sites were chosen so that they were comparable (e.g. high wave-exposure and connected to the mainland). The depth from which samples of kelp were taken averaged $7.9 \text{ m} \pm 0.4\text{SE}$ and did not differ among regions (ANOVA $F_{(2,9)} = 0.70$, $P > 0.50$), but was almost twice as deep at a single location (Eden: $13.4 \text{ m} \pm 1.9\text{SE}$ depth) where kelp could not be found shallower (ANOVA $F_{(9,36)} = 4.50$, $P < 0.001$; SNK tests). This location did not have any effect on regional patterns observed (see Results).

Within each site, five quadrats (1 m^2) were haphazardly placed within two types of algal stand (monospecific and mixed: see definitions below), where each replicate quadrat was separated by $\sim 10 \text{ m}$, and positioned $> 1 \text{ m}$ from the edge of a stand ($n = 5$ quadrats per stand). Within each 1 m^2 quadrat the density of *E. radiata* plants was recorded and a single, mature *E. radiata* plant brought to the surface, where morphological measurements were made (Table 1). Only mature, stage 3 plants (sensu Kirkman 1981) were used to reduce any effects of age on morphological characters, and only solitary individuals (no overlapping holdfasts) were collected. For consistency, plants fulfilling these requirements that were closest to the centre of the quadrat were chosen. Stands were defined at the scale of 1 m^2 as: 'monospecific' when $\geq 80\%$ of the canopy comprised *E. radiata* species, and 'mixed' when *E. radiata* comprised 40–60% of the canopy cover and the remainder of the canopy consisted of fucoid algae (e.g. *Cystophora* spp. and *Sargassum* spp.). These types of stands harbour quite different assemblages of

Table 1 Morphological characters measured on *Ecklonia radiata* plants

Morphological character	Procedure for measurement
Wet weight (g)	Wet weight of whole plant (without holdfast) measured on a spring balance, after excess water was shaken off.
Total plant length (cm)	Total length of plant from bottom of stipe to tip of central lamina.
Stipe length (cm)	From immediately above the holdfast to where the stipe widens into the meristematic region.
Lamina length (cm)	From where the stipe widens to the tip of the central lamina.
Stipe width (cm)	Measured above the holdfast, across the widest axis of the stipe.
Lamina width (cm)	Width measured half way up the central lamina.
Surface area (cm ²)	The stipe, central lamina and laterals were separated and placed on a white perspex sheet to avoid overlapping. A clear perspex sheet was laid on top to flatten pieces, and a digital photograph taken. Surface area measures (one-sided) were calculated using a colour image analysis program (Video Pro 32, Adelaide, South Australia), which was calibrated with paper strips of a known surface area.
Number of laterals	Count of secondary laterals ($> \text{ca. } 5 \text{ cm}$) branching off the central lamina.
Holdfast volume (ml)	Volume of holdfast measured by displacement.
Stipe ring count	Count of cortical growth rings in the stipe determined as described by Novacek (1981).
Medulla/cortex ratio	Transverse section of stipe taken 2 cm above the top-most haptera. Diameter measurements of the medulla and cortex taken across the shortest axis.

understorey algae and invertebrates (Goodsell et al. 2004; Irving et al. 2004). Both types of stand (typically ranging in size from 1 to 10 m²; Irving and Connell, unpublished data) were interspersed with each other, forming mosaic patches.

The subtidal ecology of temperate Australasia may be comprised of marked differences among key biogeographic regions (Irving et al. 2004) and be useful to understand in their own right. Hence, we nominated 'region' as a fixed factor because each level of region incorporated these biogeographic differences (WA versus SA versus EA: Fowler-Walker and Connell 2002); i.e. a priori, these three levels of sampling were the only three of interest. The other spatial scales (location and sites) were treated as random factors because there was no a priori reason to choose them from the large number of possible locations and sites across temperate Australia. Morphological characters were analysed simultaneously (multivariate analysis: Anderson 2001) and separately (Underwood 1997) to test whether they differed between stands at each spatial scale. Variance components were calculated for individual characters at each spatial scale (region, location, site and quadrat) using methods for mixed models outlined by Quinn and Keough (2002). Where negative variance components were found, they were set to zero for the calculation of percentage variance explained by each level. These calculations were done separately on monospecific and mixed stands as there were a number of significant interactions between the factor 'stand' and the different spatial scales (see Table 3). Such interactions made it impossible to specify the magnitude of effect of either stand or the various spatial scales since these factors are dependent on one another (Underwood 1997).

Results

Patterns of multivariate variation in morphology

The morphology of *E. radiata* differed between stands (monospecific \neq mixed) across all regions of temperate Australia (Fig. 2, Table 2a). Significant interactions at the smaller spatial scales (Table 2a; stand \times site and stand \times location interaction terms) revealed large inconsistencies in differences between stands at these scales. That is, pairwise tests showed no differences between stands (monospecific = mixed) at some sites (within each location), and some locations (within each region). However, the lack of a significant stand \times region interaction and the significant stand and region effects indicated distinctive morphologies between stands and across regions. Comparisons of morphology among regions, within each type of stand, revealed that for both monospecific and mixed stands, WA and SA did not differ, whilst WA and EA had the largest difference, and SA and EA the smallest difference (Table 2b; pairwise comparisons: WA = SA \neq EA). Taken together, these multivariate tests and pairwise comparisons provide

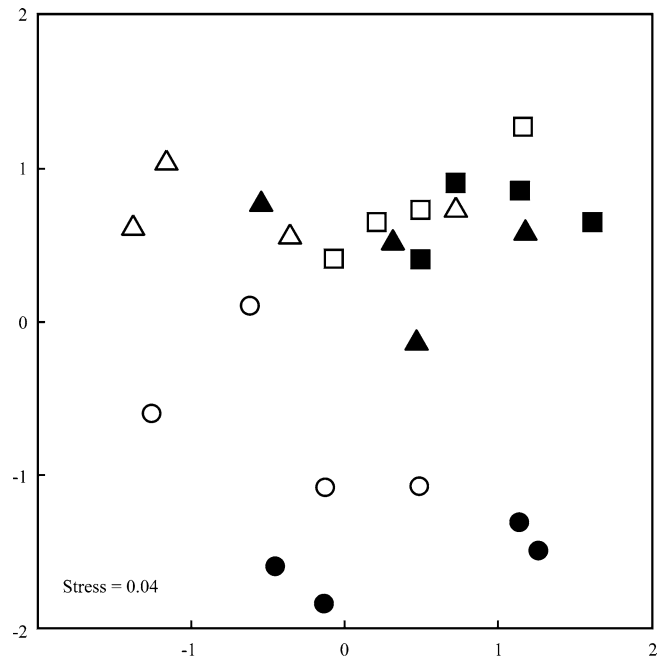


Fig. 2 Constrained ordination (canonical discriminant analysis) of centroids (averages) of replicate sites representing variation in *Ecklonia radiata* morphology between monospecific stands (filled symbols) and mixed stands (unfilled symbols) for each location ($n=4$) within each region, Western (■), South (▲) Australia

direct tests of, and support for the hypotheses that morphology (1) is different between monospecific and mixed stands of *E. radiata* across Australia and (2) that

Table 2 Results of (a) a four-factor NP-MANOVA testing the relative and interactive effects of stand (monospecific vs mixed), region (WA Western Australia, SA South Australia, EA Eastern Australia), location ($n=4$) and site ($n=4$) on the morphology of *E. radiata*, and (b) pairwise comparisons of morphology within each type of stand, across regions. Multivariate analyses were done on untransformed Gower dissimilarities (Gower 1967), recommended for dealing with simultaneous analysis of variables measured at different scales of magnitude (Podani 1999). Permutation of residuals (full model, $n=5,000$) was used (Anderson 2001). Analysis treated 'stand' and 'region' as fixed and orthogonal to one another, and 'location' and 'site' as random factors nested within the hierarchy of spatial scales

(a) Treatment	df	MS	F	P
Stand	1	31.06	13.95	***
Region	2	60.03	3.77	***
Location (region)	9	15.93	5.39	***
Site [location (region)]	36	2.95	4.20	***
Stand \times region	2	2.96	1.33	ns
Stand \times location (region)	9	2.23	2.20	**
Stand \times site [Location(region)]	36	1.06	1.51	**
Residual	384	0.70		
(b) Pairwise comparisons		<i>t</i>	<i>P</i>	
Region (monospecific)				
	WA vs SA	1.13	ns	
	WA vs EA	2.60	**	
	SA vs EA	1.94	*	
Region (mixed)				
	WA vs SA	1.66	ns	
	WA vs EA	1.91	*	
	SA vs EA	1.90	*	

ns Non significant, $P > 0.05$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

regional patterns of variation exist (within each type of stand). They also demonstrate that the considerable inconsistency in morphology between stands at smaller spatial scales (sites and locations) did not obscure the regional patterns within both monospecific and mixed stands.

Fig. 3 Mean measures (\pm SE; $n=80$) of morphological characters of *E. radiata*, between monospecific and mixed stands within each region (*WA* Western Australia, *SA* South Australia, *EA* Eastern Australia)

Patterns of univariate variation in morphology

All morphological characters were of greater magnitude in monospecific stands than in mixed stands, except for the medulla/cortex ratio that did not differ between stands (Fig. 3, Table 3; SNK tests). Indeed, plants in monospecific stands tended to be larger, heavier, taller and thicker than those in mixed stands. This pattern was consistent across all three regions, for all morphological characters that detected differences between stands,

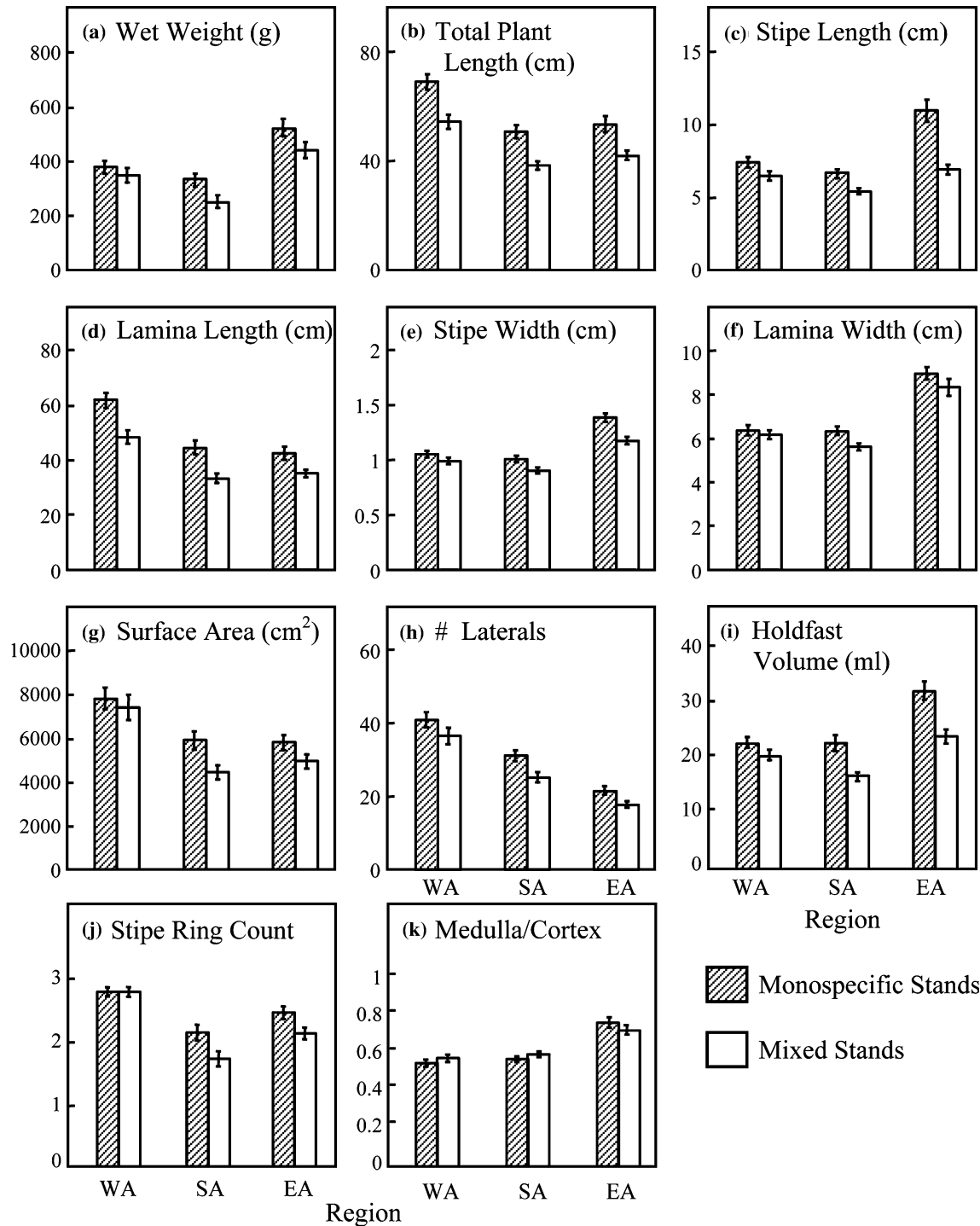


Table 3 ANOVA testing differences of eleven individual morphological characters of *E. radiata* among stands (monospecific vs mixed), regions (WA, SA and EA), locations ($n=4$) and sites ($n=4$). Analysis treated 'stand' and 'region' as fixed and orthogonal to one another, and 'location' and 'site' as random factors nested within the hierarchy of spatial scales

Source	<i>df</i>	MS	<i>F</i>	<i>P</i>	MS	<i>F</i>	<i>P</i>	
		Wet weight				Total plant length		
Stand	1	6.58	8.41	*	1949857.60	22.55	**	
Region	2	12.14	2.48	ns	1348088.03	1.66	ns	
Location (region)	9	4.90	3.99	**	811060.32	9.34	***	
Site [location (region)]	36	1.23	6.14	***	86881.06	4.87	***	
Stand × region	2	0.30	0.38	ns	10711.81	0.12	ns	
Stand × location (region)	9	0.78	2.80	*	86481.49	2.23	*	
Stand × site [location (region)]	36	0.28	1.40	ns	38852.61	2.18	***	
Residual	384	0.20			17834.47			
		Stipe length ^a				Lamina length		
Stand	1	7.94	30.61	***	1352891.41	22.18	**	
Region	2	3.95	3.31	ns	1406372.99	2.00	ns	
Location (region)	9	1.19	3.41	**	704320.09	10.28	***	
Site [location (region)]	36	0.35	4.59	***	68504.94	4.24	***	
Stand × region	2	0.91	3.52	ns	40914.28	0.67	ns	
Stand × location (region)	9	0.26	2.05	ns	61004.25	1.80	ns	
Stand × site [location (region)]	36	0.13	1.66	*	33894.20	2.10	***	
Residual	384	0.08			16173.57			
		Stipe width				Lamina width		
Stand	1	195.33	27.93	**	2711.30	7.91	*	
Region	2	471.47	14.13	*	31202.43	7.24	*	
Location (region)	9	33.38	4.60	**	4312.26	2.90	*	
Site [location (region)]	36	7.26	2.43	***	1485.31	7.06	***	
Stand × region	2	24.92	3.56	ns	280.26	0.82	ns	
Stand × location (region)	9	6.99	0.96	ns	342.96	1.46	ns	
Stand × site [location (region)]	36	7.25	2.43	***	234.70	1.12	ns	
Residual	384	2.99			210.37			
		Surface area ^a				No. laterals ^a		
Stand	1	5.06	8.04	*	4.51	21.00	***	
Region	2	6.85	1.10	ns	15.75	5.26	*	
Location (region)	9	6.25	5.98	***	2.99	7.70	***	
Site [location (region)]	36	1.04	5.26	***	0.39	3.90	***	
Stand × region	2	0.35	0.56	ns	0.08	0.39	ns	
Stand × location (region)	9	0.63	2.52	*	0.21	1.50	ns	
Stand × site [location (region)]	36	0.25	1.26	ns	0.14	1.44	ns	
Residual	384	0.20			0.10			
		Holdfast volume ^a				Stipe ring counts		
Stand	1	5.76	24.67	***	7.25	18.42	**	
Region	2	5.25	2.83	ns	28.71	2.28	ns	
Location (region)	9	1.85	4.64	***	12.62	13.88	***	
Site [location (region)]	36	0.40	2.98	***	0.91	1.83	**	
Stand × region	2	0.42	1.81	ns	1.89	4.80	*	
Stand × location (region)	9	0.23	0.83	ns	0.39	0.64	ns	
Stand × site [location (region)]	36	0.28	2.11	***	0.61	1.23	ns	
Residual	384	0.13			050			
		Medulla/cortex ratio ^a						
Stand	1	0.002	0.01	ns				
Region	2	2.90	6.09	*				
Location (region)	9	0.48	2.70	*				
Site [location (region)]	36	0.18	2.25	***				
Stand × region	2	0.10	0.49	ns				
Stand × location (reg)	9	0.21	2.96	**				
Stand × site [location (region)]	36	0.07	0.91	ns				
Residual	384	0.08						

ns Non significant, $P > 0.05$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

^a Ln (x) transformation was necessary for these morphological characters to homogenise variances (Cochran's C -test: $P > 0.05$)

except for stipe ring counts where there was a significant interaction between stand and region, where more rings were counted in plants growing in monospecific stands compared with mixed stands in SA and EA (Fig. 3j, Table 3j). Local scale patterns (among sites and locations) between stands were not always consistent with

regional scale patterns. Of the 10 morphological characters that detected differences between stands only 2 (lamina width and number of laterals; Fig. 3f, h, Table 3f, h) showed differences among stands that were consistent across all spatial scales. Importantly, inconsistent differences between stands were greatest at the

scale of sites (stand \times site interaction, $n=5$ morphological characters: total plant length, stipe length, lamina length, stipe width and holdfast volume; Table 3b, c, d, e, i; SNK tests), intermediate at the scale of locations (stand \times location interaction, $n=3$ morphological characters: wet weight, total plant length, and surface area; Table 3a, b, g; SNK tests) and least at the scale of regions (stand \times region interaction, $n=1$ morphological character: stipe ring counts; Table 3j; SNK tests).

Regional differences in the morphology of *E. radiata* plants (for both monospecific and mixed stands) were detected (SNK: WA=SA \neq EA) for 4 of the 11 morphological variables (stipe width, lamina width, number of laterals and the medulla/cortex ratio; Fig. 3e, f, h, k, Table 3e, f, h, k). Plants in EA were generally smaller in thallus size (i.e. smaller number of laterals), but thicker in width (both stipe and lamina width) and had larger medulla/cortex ratios, compared with WA and SA plants.

The density of *E. radiata* plants did not vary among regions within monospecific stands (ANOVA: $F_{(2,192)}=0.23$, $P=0.802$), nor within mixed stands (ANOVA: $F_{(2,192)}=2.18$, $P=0.169$), indicating that the regional patterns in morphology are not explained by the density of *E. radiata*. Whilst depth did not vary among regions, the depth at Eden was almost twice that of other locations sampled (see Methods). The morphological characters that differed among regions (WA=SA \neq EA), did not differ between Eden and the three other locations representing EA (SNK tests), hence this one location (Eden) did not drive the regional differences detected.

The percentage of explained variance was overwhelmingly greatest at the smallest spatial scale in both types of stand (Table 4). In monospecific stands, 7 of the 11 morphological characters (weight, stipe length, surface area, number of laterals, holdfast volume, stipe ring count and medulla/cortex ratio) showed the greatest variation in morphology at the smallest spatial scale (i.e. among replicate quadrats within sites; Table 4). Of the remaining characters, the greatest variation occurred among locations for total plant height and lamina length and among regions for stipe and laminae width. In mixed stands, the greatest variation occurred at the smallest spatial scale for all 11 characters (Table 4).

Discussion

This study highlights the pivotal function of scale and understanding scale-dependent patterns in assessments of generality. While specimens of *E. radiata* were larger in monospecific than in mixed stands (Fig. 3; i.e. greater thallus size, weight and thickness), this difference was often not detected at local scales (i.e. sites separated by km), was more frequently detected at intermediate scales (i.e. locations separated by 100s of km), and was discernable at regional scales (i.e. samples separated by 1,000s of km). This potential for large scale patterns to

Table 4 Variance components at four levels for *E. radiata* growing in *monospecific* and *mixed stands*. Note: *Regions* = among regions, *locations* = among locations within regions, *sites* = among sites within locations, *quadrat* = among replicate quadrats within sites

Morphological character	% Regions	% Locations	% Sites	% Quadrats
Monospecific stands				
Weight	10	16	22	52
Total plant height	2	44 ^a	21	33
Stipe length	19	12	23	46 ^a
Lamina length	8	42 ^a	18	32
Stipe width	52 ^a	8	9	31
Lamina width	37 ^a	12	18	33
Surface area	1	0	0	99 ^a
No. laterals	29	29	10	32 ^a
Holdfast volume	12	12	12	64 ^a
Stipe ring count	0	43	1	56 ^a
Medulla/cortex ratio	21	9	10	60 ^a
Mixed stands				
Weight	9	22	20	49 ^a
Total plant height	13	32	14	41 ^a
Stipe length	6	11	20	63 ^a
Lamina length	14	31	13	42 ^a
Stipe width	27	10	18	45 ^a
Lamina width	23	14	27	37 ^a
Surface area	1	0	0	99 ^a
No. laterals	28	19	13	40 ^a
Holdfast volume	9	5	25	61 ^a
Stipe ring count	22	19	10	49 ^a
Medulla/cortex ratio	10	4	7	79 ^a

^a Indicates the level where the greatest variation occurred for each morphological character

emerge from stochasticity at small scales is recognised (Chesson 1996). Populations may be shaped over vast areas, with locally varied environments to which individuals respond, across which their ecology is regulated by powerful constraints (e.g. Chesson 2000). In this way, heterogeneity at small spatial scales may average out to produce patterns at large spatial scales.

Importantly, large variation across several spatial scales indicates that comparisons among local studies, even if done at several sites within a single location, provide a difficult basis to understand the generality of pattern. For example, comparisons of several locations (separated by 1,000s of kms) using several local samples (separated by kms) reveals no consistent patterns of spatial variation in morphology of *E. radiata* across Australia (e.g. Wernberg et al. 2003). This situation arises because the within-region variation has not been adequately estimated by the replicate samples, preventing interpretable comparison among regions. This difficulty can be resolved by hierarchical sampling (Green 1979; Underwood 1997) to provide an estimate of the contribution of each scale to the total variation across regions. By understanding the proportion of total variation that is attributable to each scale, we are in a stronger position to identify the scales at which general patterns, rules and laws may emerge (Noda 2004).

Morphological variation in macroalgae is often explained as an adaptive response to the hydrodynamic environment (see review by Hurd 2000), particularly that of water velocity (flow) and wave exposure that can vary over both small and large spatial scales (Gerard and Mann 1979; Hurd 2000). Specimens of *E. radiata* were generally larger (i.e. heavier, taller, thicker, greater surface area, and had more laterals) in monospecific stands than in mixed stands. Such morphological variation may indicate an adaptation to environmental conditions that vary between stands, such as the intensity of water movement (Gerard and Mann 1979) and the light environment (Sjötun and Fredriksen 1995), or differences that are associated with intra- and inter-specific competition (e.g. Barnes et al. 1990). Regional scale differences in morphological characters (WA = SA ≠ EA) may also reflect a response to the hydrodynamic environment that can change over geographic regions due to currents (Hurd 2000). Our results showed that plants in EA, compared with WA and SA, were smaller in thallus size but thicker in width, with larger medulla/cortex ratios. Such morphological differences have previously been associated with an increase in strength to accommodate high wave forces (e.g. Cheshire and Hallam 1988; Molloy and Bolton 1996; Blanchette et al. 2002). Hence, morphologies in EA may be responding to the force of the currents themselves, or alternatively to factors associated with currents, such as sea water temperature (Kalvas and Kautsky 1998) or nutrient concentrations (Gerard 1982), that can be affected by upwellings in the region (Rochford 1972; Tranter et al. 1986).

The regional patterns detected (WA = SA ≠ EA) reflect similar patterns observed for assemblages of understory algae (Fowler-Walker and Connell 2002; Irving et al. 2004) and holdfast invertebrates (Goodsell, unpublished data), and for species of mollusc (Kassahn et al. 2003) and fish (Cappo et al. 2000). This concordance is unlikely to be accidental. Temporal variation over long periods, that divides and reconnects populations and drives evolutionary change, may be key to understanding these patterns and what appear to be distinct ecologies across coastal Australia. The repeated formation and loss of a large south-eastern land bridge (between eastern-Australia and Tasmania) is thought to have been a significant barrier to dispersal for many taxa (Womersley 1981; Poore 1994; Cappo et al. 2000). An important step, therefore, is to establish whether the population structure of *E. radiata* is also concordant. This work would have profound implications if it establishes a link between genetic variation and ecological variation, particularly in characters (e.g. morphology of habitat forming plants) key to shaping the distribution and abundance of widespread taxa (e.g. communities of understory taxa).

Our key biological conclusion is that differences exist in the morphology of kelp between monospecific and mixed stands of canopy-forming forest and among regions. Despite substantial small scale variability, differences between stands could be detected and became

increasingly clear at broader spatial scales. This study, therefore, lends weight to the concept that large scale patterns can emerge from heterogeneity at small scales. These findings highlight trouble with the view that sufficient small scale observation and experimentation will lead to more general or large scale understanding of ecological patterns and processes. Indeed, there is little to no evidence that the accumulation and synthesis of numerous local studies is a valid method for interpreting general or broad scale patterns (Underwood and Pe-traitis 1993). We hope, therefore, that these results encourage more broad scale studies focused on understanding whether patterns (similarities or dissimilarities) at intensely studied locations are representative of larger areas of coast. We do not advocate comparisons of a few sites that are widely separated, but encourage replication to span entire regions. This way we may be in a better position to understand the spatial extent and nature of generalities (similarities).

In conclusion, we are becoming increasingly aware that ecologists are working at scales (i.e. local) where complexity is often greatest (Underwood and Chapman 1996; Fowler-Walker and Connell 2002; Anderson et al. 2005). At these scales, patterns are likely to represent special and unique events that incorporate variation from broad to local scales. For those interested in the existence of broad scale patterns, it is encouraging to observe that patterns can emerge from complexity at local scales. This realisation, together with the need for a renewed effort for carefully planned sampling across broad scales suggests that there are opportunities to test some of the more interesting questions about the relative importance of processes across the vast parts of the world's coast.

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