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Morphology of *Ecklonia radiata* (Phaeophyta: Laminariales) along its geographic distribution in south-western Australia and Australasia

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Abstract *Ecklonia radiata* (C. Ag.) J. Agardh is a common macroalga on reefs in the warm-temperate parts of the southern hemisphere. It is a dominant habitat-former and as such has a strong structuring effect on associated algal assemblages. Morphological variation in *E. radiata* potentially affects its interactions with the surroundings and contributes to confusion about its taxonomy. We quantified the magnitude of morphological variation in fully developed *E. radiata* sporophytes across Australasia and tested the hypotheses that *E. radiata* has different morphology at different locations and that the degree of morphological difference depends on spatial distances among locations. A total of 11 morphological characters were sampled from 11 locations along the Australian coastline from Kalbarri in Western Australia to Sydney in New South Wales as well as from Doubtful Sound, New Zealand. Most morphological characters varied considerably from one location to another. For example, the average (\pm SE)

thallus length was 135.2 ± 12.5 cm in Kalbarri and only 69.7 ± 5.5 cm in Sydney. There were no consistent spatial patterns of variation among individual morphological characters, and, generally, variations among individual characters were poorly correlated ($-0.5 < R < 0.5$). This suggests that individual morphological characters develop independently of each other in response to processes operating at different spatial scales. Multivariate measures of morphology were found to be different among some locations and similar among others ($-0.37 \leq \text{Clarke's } R \leq 1$), but there was no correlation (Spearman's $R = 0.08$) between morphological similarity and distance between locations. Consequently, our results do not support clinal variation in *E. radiata* morphology. Rather, they suggest the presence of discrete morphologically different populations, in which the morphology at any one location reflects multiple forcing factors operating on different morphological characters at different spatial scales.

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Introduction

Ecklonia radiata (C. Ag.) J. Agardh is a small kelp reaching a maximum length of about 2 m. It has its main distribution in the southern hemisphere where it is common, often dominant, in the warm-temperate parts of South Africa (Field et al. 1980), Australia (Steinberg and Kendrick 1999) and New Zealand (Choat and Schiel 1982). *E. radiata* is also found in the northern hemisphere, but so far it has been described only from Oman on the Arabian Peninsula (Bolton and Anderson 1994). It is likely, however, that a revision of the genus *Ecklonia* would include one North African and several Japanese *Ecklonia* species under *E. radiata* (Bolton and Anderson 1994), increasing its northern hemisphere distribution considerably.

E. radiata is remarkably successful in terms of its ecological dominance and it is probably the most abundant macroalga in Australia (Steinberg and Kend-

rick 1999). It has a profound influence on associated algal assemblages (Kendrick et al. 1999; Melville and Connell 2001) because canopies of large macroalgae modify the physical environment (Eckman et al. 1989; Kennelly 1989; Critchley et al. 1990). The contribution of individual kelps to modification of the environment is a function of their morphology (Velimirov and Griffiths 1979; Kennelly 1989). Consequently, if *E. radiata* exhibits systematic spatial variation in morphology, it will likewise systematically exert spatially variable effects on algal assemblages. This may be a factor contributing to the large variability commonly encountered in comparisons of *E. radiata* assemblages across various spatial scales (Kennelly and Underwood 1992; Kendrick et al. 1999; Fowler-Walker and Connell 2002).

The objective of the present study was to quantify the morphological variation in *E. radiata* along its geographic range in Australasia. Geographic separation may cause morphological differences among populations of macroalgae as genetic exchange among populations becomes restricted (Kusumo and Druhl 2000) and they are exposed to grossly different environmental conditions. These differences may be continuously changing following major environmental clines in, for example, insolation, temperature or salinity (Russell 1986; Kalvas and Kautsky 1998). Consequently, we tested the hypotheses that *E. radiata* has different morphology at different locations and that the degree of morphological difference depends on spatial distances among locations.

Materials and methods

Sampling

Sampling was carried out during summer from November 2000 to March 2001. Eleven locations were selected; eight along the south-west Australian coastline and three from other Australasian regions (Fig. 1; Table 1). Locations within Western Australia were selected on the basis of accessibility and proximity. Locations outside Western Australia were found by requesting collaboration via the ALGAL-L email list. These 11 locations span 18° north-south and 37° east-west, and they cover > 6,000 km of coastline including the

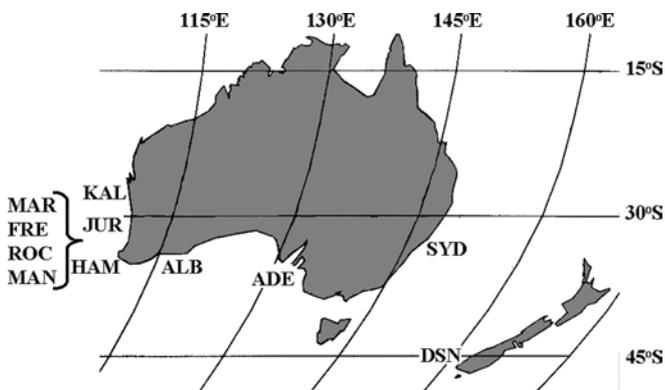


Fig. 1 The geographical position of sampling locations. Global positioning system co-ordinates and location codes are given in Table 1

geographic range of *Ecklonia radiata* from its northern limit in Western Australia (Kalbarri: Womersley 1987) and south around Australia to Sydney, and New Zealand. Three random sites were sampled within each location. Large, presumably fully developed, individuals were targeted during the sampling (Rice et al. 1985; Jackelman and Bolton 1990). Thus, in situ a SCUBA diver haphazardly collected large stage 3 sporophytes (sensu Kirkman 1981) by carefully dislodging the holdfast from the reef with a dive knife. Only solitary individuals where the holdfasts did not overlap were collected, and collections were generally made within an area of a few square metres. The collected specimens were kept moist and refrigerated until processing.

Within each site 11 morphological characters were sampled from $n=5-10$ individuals (Table 1). These morphological characters were chosen to cover most parts of the thallus (see illustrations in Bolton and Anderson 1994). The morphological characters and procedures for measurement are given in Table 2.

Data analyses

Firstly, we tested whether the morphology of *Ecklonia radiata* is different among locations along its geographic range in Australasia (H_0 : there are no differences in *E. radiata* morphology among locations separated by 10s–1,000s of kilometres). Each morphological character was tested with a one-way ANOVA (Zar 1996) where sites were nested within locations. Before testing, the data set was balanced by randomly removing individuals from each of the sites to meet the lowest common denominator ($n=5$; cf. Table 1) and checked for homogeneity of variances (Cochran's C -test: Winer et al. 1991). Because of the large number of tests (11 ANOVAs) Bonferroni corrected α -values ($\alpha/11$) were used to determine significance levels. Further, the total variation was decomposed and partitioned into the relative contribution from each level of nesting, and the relative magnitude of effect (ω^2) was calculated (Graham and Edwards 2001).

Multivariate analyses were performed in PRIMER v5 (Clarke and Gorley 2001). To test the independence of each character, product moment correlation was performed among all pairs of variables using the "Draftmans plot" routine. A normalised euclidean distance dissimilarity matrix was calculated from untransformed data using the full unbalanced data set on all morphological characters. Difference in morphology among locations was tested with a two-way nested ANOSIM (analysis of similarities) with sites nested in locations, followed by pairwise comparisons. The data were represented graphically in non-metric multidimensional scaling (nMDS) plots. SIMPER (similarity of percentages) was performed to identify which morphological characters contributed most to the observed patterns.

Secondly, we tested whether the magnitude of morphological difference was a function of distance between locations (H_0 : there is no correlation between distance and the degree of morphological similarity among locations). The matrix of pairwise R -values from the ANOSIM was correlated (Spearman rank correlation) to an among-location distance matrix generated from GPS (global positioning system) co-ordinates (cf. Table 1).

Results

Spatial variability of individual morphological characters

Most morphological characters of *Ecklonia radiata* showed considerable variation among locations (Tables 3, 4). For example, total thallus length differed by > 65 cm between the individuals in Kalbarri and the individuals in Sydney. Similarly, there was > 130 g dry weight difference between the thallus biomass of indi-

Table 1 Sampling locations. Three sites were sampled within each location. Ten individuals were sampled at each site, except ADE3 ($n=6$) and DSN1–3 ($n=5$)

Location	Code	Habitat
Western Australia		
Kalbarri (27°45'S; 114°08'E)	KAL	8–14 m, low relief sand stone reef, extensive dense beds
Jurien Bay (30°17'S; 114°58'E)	JUR	8–12 m, low relief limestone reef, extensive dense beds. Reef structures
Marmion Lagoon (Perth north) (31°50'S; 115°42'E)	MAR	8–10 m, low–medium relief limestone reef, extensive dense beds. Reef structures
Fremantle (Perth south) (32°06'S; 115°39'E)	FRE	5–8 m, medium–high relief limestone reef, scattered individuals–small patches. Reef structures
Rockingham (32°20'S; 115°41'E)	ROC	5–8 m, low–high relief limestone reef, scattered individuals–small patches. Reef structures
Mandurah (32°32'S; 115°41'E)	MAN	5–7 m, fragmented low relief limestone reef, scattered individuals
Hamelin Bay (34°14'S; 115°01'E)	HAM	8–12 m, low–high relief limestone reef, dense extensive beds. Reef structures
Albany (35°03'S; 118°02'E)	ALB	8–10 m, high relief granite reef/boulders, dense extensive beds. Reef structures
Other states		
Adelaide (35°34'S; 138°38'E)	ADE	7–8 m, medium relief boulder reefs, dense patches
Sydney (33°55'S; 151°17'E)	SYD	5–10 m, low relief rocky reef with small patches of sand
Doubtful Sound, New Zealand (45°20'S; 167°02'E)	DSN	18–20 m, rocky reef

Table 2 Morphological characters measured

Morphological character	Code	Description
Total length (cm)	TL	From stipe, immediately above holdfast, to the distal end of the frond
Total DW thallus (g)	DW	Fresh weight converted to dry weight (DW) by applying WW:DW obtained from small batches and averages
Stipe length (mm)	SL	From immediately above the holdfast to where the stipe widens and flattens into the frond
Stipe diameter (mm)	SD	Immediately above the holdfast. Widest direction if not circular
Lamina length (cm)	LL	From where the stipe widens and flattens into the frond to the distal end of the central lamina
Lamina width (cm)	LW	Width measured at an arbitrarily selected place on the mid-1/3 of the central lamina
Lamina twists (count)	LT	Number of full rotations of the central lamina
Number of laterals (count)	NL	Count of secondary laterals (> ca. 5 cm, except were heavily eroded) protruding from the central lamina
Lateral length (cm)	LAL	Length of an intact secondary lateral arbitrarily selected from the mid-1/3 of the central lamina
Lateral width (cm)	LAW	Width of the selected (cf. lateral length) secondary lateral at its widest place
Lateral spinosity (spines mm ⁻²)	LS	Count per mm ² of pointed protrusions from the surface (both sides) of a small (~4 cm ²) section taken from where lateral width was measured

viduals from Kalbarri and individuals from Mandurah. Lateral spinosity was the most variable character (CV = 48%), whereas stipe diameter was the least variable (CV = 3%).

Five of the 11 morphological characters were significantly different ($P < 0.05/11$) among locations (Table 4). All morphological characters, except lateral spinosity, were also significantly different ($P < 0.05/11$) among sites within locations (Table 4). Although sites within locations in most cases were highly significantly different ($P < 0.001/11$), the variation at this level generally contributed < 30% to the total variation, as indicated by the magnitudes of effect in Table 4. Location was the

dominant contributor to variance in lamina width, numbers of laterals and in lateral spinosity. Variation among individuals within a site (i.e. the error term) generally had a high, often > 40%, contribution towards the total variation, particularly in the number of lamina twists per plant.

Most morphological characters were poorly to moderately correlated to each other ($-0.5 < R < 0.5$; Table 5). Exceptions were thallus length versus stipe length ($R = 0.53$), lamina length ($R = 0.85$) and number of laterals ($R = 0.74$), and number of laterals versus lamina length ($R = 0.70$). These correlations could however be expected as some of these characters are

Table 3 *Ecklonia radiata*. Summary statistics of morphological characters. Each location: data given are means (standard errors) of $n = 11$ locations. Location codes are given in Table 1

Morphological character	KAL	JUR	MAR	FRE	ROC	MAN	HAM	ALB	ADE	SYD	DSN	Total
Total length (cm)	135.2 (12.5)	84.1 (8.1)	83.5 (4.5)	72.1 (3.3)	91.7 (6.5)	77.2 (8.3)	115.0 (7.5)	90.2 (10.1)	108.8 (16.1)	69.7 (5.5)	87.3 (16.0)	93.3 (6.0)
Total DW thallus (g)	135.5 (6.0)	106.6 (12.0)	185.5 (25.2)	150.4 (44.8)	172.2 (7.6)	50.5 (7.3)	142.0 (14.7)	113.8 (13.0)	139.3 (29.3)	143.3 (4.8)	134.9 (21.2)	134.0 (10.7)
Stipe length (mm)	26.1 (5.4)	7.0 (0.7)	6.4 (0.7)	7.7 (0.6)	12.1 (0.9)	9.4 (3.1)	14.2 (2.4)	9.5 (1.8)	11.8 (3.7)	16.0 (3.9)	20.6 (6.7)	12.8 (1.8)
Stipe diameter (mm)	15.3 (0.3)	12.5 (0.6)	12.9 (0.6)	13.7 (0.2)	15.0 (0.5)	14.1 (1.1)	12.6 (0.4)	12.4 (0.2)	12.8 (0.5)	13.3 (0.9)	10.8 (2.4)	13.2 (0.39)
Lamina length (cm)	89.8 (10.7)	63.9 (12.0)	65.8 (2.8)	58.2 (2.9)	72.5 (4.5)	60.3 (5.9)	89.5 (13.9)	65.4 (9.7)	81.7 (24.0)	49.0 (5.3)	66.8 (18.5)	69.4 (3.9)
Lamina width (cm)	5.3 (0.04)	6.0 (0.25)	7.5 (0.58)	6.4 (0.34)	6.6 (0.25)	5.5 (0.16)	6.1 (0.52)	7.5 (0.30)	8.3 (1.04)	9.2 (1.11)	22.4 (2.54)	8.3 (1.5)
Lamina twists (count)	2.67 (0.38)	1.55 (0.76)	2.67 (0.59)	1.07 (0.3)	1.40 (0.32)	1.43 (0.75)	1.27 (1.02)	0.57 (0.15)	1.07 (0.55)	0.43 (0.12)	0 (0)	1.30 (0.23)
Number of laterals (count)	83.47 (8.7)	42.43 (7.36)	48.8 (4.1)	41.4 (4.07)	47.87 (3.61)	48.14 (3.69)	75.07 (12.6)	56.57 (4.84)	58.49 (12.5)	30.83 (2.04)	28.13 (3.43)	48.31 (5.37)
Lateral length (cm)	44.67 (3.08)	36.8 (2.62)	39.03 (0.93)	33.25 (1.08)	42.54 (2.46)	26.93 (0.19)	47.31 (3.85)	39.2 (4.56)	44.59 (6.8)	32.55 (2.67)	26.63 (5.91)	36.27 (2.36)
Lateral width (cm)	3.38 (0.14)	7.65 (0.72)	7.94 (0.62)	6.42 (0.50)	6.33 (0.37)	5.65 (0.26)	6.88 (0.66)	8.91 (0.84)	6.94 (1.16)	6.71 (0.22)	9.80 (0.48)	6.70 (0.53)
Lateral spinosity (spines mm ⁻²)	0 (0)	0.04 (0.01)	0.15 (0.14)	14.07 (1.59)	9.69 (1.48)	1.47 (0.13)	0 (0)	1.00 (0.96)	0 (0)	2.83 (0.35)	0 (0)	2.74 (1.31)

defined from each other. For example, total length is the sum of stipe length, lamina length and the length of laterals that extend beyond the tip of the central lamina. Contrary to what would be expected from simple allometric scaling (Larkum 1986; Wernberg et al. 2001), there was no correlation between thallus dry weight and thallus length ($R=0.11$) or the number of laterals ($R=0.11$).

Spatial variability of multivariate morphology

The ordination based on all morphological characters (Fig. 2) showed large separation (high dissimilarity) among some locations (e.g. DSN and KAL) and very small separations (high similarity) among other locations (e.g. JUR and ALB). Sites within locations also exhibited large separation within some locations (e.g. FRE and DSN). The ANOSIM revealed a moderate, but highly significant, separation of locations (Clarke's $R=0.512$, $P<0.001$). There was also a marked, although smaller, separation of sites nested within locations (Clarke's $R=0.326$, $P<0.001$).

The multivariate pairwise comparisons among locations (Table 6) yielded very small or even negative Clarke's R values among ADE–JUR–HAM–ALB, suggesting that *E. radiata* from sites within these locations were particularly similar. ADE had relatively small Clarke's R values in comparisons with all locations. Conversely, MAN and DSN were different to most other locations.

Thallus dry weight was by far the most important morphological character, on average accounting for >30% of the dissimilarity in *E. radiata* morphology between location pairs (Table 7). Thallus dry weight also had the most consistent contribution to location dissimilarity.

There was no correlation between distance and location dissimilarity (Spearman's $R=0.08$, $P=0.57$, $n=55$; Fig. 3). Some *E. radiata* populations separated by <200 km were just as different from each other as they were from populations >3,000 km away. There was a trend of populations separated by >3,000 km to be relatively different (Clarke's $R\geq 0.37$), although this must be interpreted conservatively because of the lack of closely located regions outside Western Australia and the potentially confounding effects of sampling depths (cf. Table 1).

Discussion

The morphological variation within and among 11 populations of *Ecklonia radiata* in Australasia was determined to be highly variable. There were no consistent patterns of spatial variation in individual morphological characters: variation among locations, sites within locations and individuals within sites were all main contributors to total variation in one character or

Table 4 *Ecklonia radiata*. Results from ANOVA on individual morphological characters [$df=10, 22$ and 132 for location, site(location) and individuals within site]. No transformations were necessary to homogenise variances (Cochran's C -test: $P>0.05$). [$Var. Comp.$ and ω^2 are the variance components and magnitude of effect (Graham and Edwards 2001), respectively] ***, $P<0.001/11$; **, $P<0.01/11$; *, $P<0.05/11$; n.s., $P>0.05/11$

Morphological character	Cochran's C	MS	F	P	Var. comp.	ω^2
Total length	0.12					
Location		5,407	3.21	n.s.	248.3	33.3
Site(location)		1,683	8.34	***	296.2	39.7
Individuals within site		201.7			201.7	27.0
Total DW thallus	0.11					
Location		2,0318	2.93	n.s.	891.7	23.3
Site(location)		6,942	3.58	***	1,001	26.1
Individuals within site		1,939			1,939	50.6
Stipe length	0.28					
Location		578.5	2.62	n.s.	23.80	20.2
Site(location)		221.5	3.58	***	31.91	27.1
Individuals within site		61.96			61.96	52.7
Stipe diameter	0.22					
Location		26.79	2.32	n.s.	1.016	17.5
Site(location)		11.55	3.71	***	1.688	29.0
Individuals within site		3.115			3.115	53.5
Lamina length	0.10					
Location		2,323	1.02	n.s.	2.496	0.37
Site(location)		2,285	8.77	***	404.9	60.6
Individuals within site		260.8			260.8	39.0
Lamina width	0.21					
Location		352.3	24.5	***	22.53	81.3
Site(location)		14.36	4.98	***	2.295	8.28
Individuals within site		2.883			2.883	10.4
Lamina twists	0.39					
Location		14.39	1.07	n.s.	0.065	0.90
Site(location)		13.41	2.38	*	1.554	21.4
Individuals within site		5.636			5.636	77.7
Lateral no.	0.17					
Location		4,993	6.09	**	278.2	47.8
Site(location)		819.2	4.69	***	128.9	22.2
Individuals within site		174.7			174.7	30.0
Lateral length	0.25					
Location		930.8	4.36	*	47.82	34.4
Site(location)		213.5	3.53	***	30.59	22.0
Individuals within site		60.52			60.52	43.6
Lateral width	0.11					
Location		352.3	24.5	***	2.431	41.7
Site(location)		14.36	4.98	***	0.4679	8.0
Individuals within site		2.883			2.927	50.2
Lateral spinosity	0.36					
Location		308.0	59.2	***	20.18	79.4
Site(location)		5.200	0.99	n.s.	-0.012	-0.05
Individuals within site		5.259			5.259	20.7

Table 5 *Ecklonia radiata*. Correlation coefficients (Pearson product moment correlation) among the morphological characters on all the sampled individuals ($n=311$). Morphological codes are given in Table 2

	DW	SL	SD	LL	LW	LT	NL	LAL	LAW	LS
TL	0.11	0.53	0.17	0.85	-0.10	0.15	0.74	0.29	-0.34	-0.30
DW		-0.05	0.08	0.09	0.19	0.16	0.11	0.35	0.16	0.16
SL			0.38	0.27	0.12	-0.00	0.28	-0.00	-0.25	-0.13
SD				0.04	-0.26	0.07	0.20	0.12	-0.27	0.20
LL					-0.07	0.14	0.70	0.08	-0.29	-0.18
LW						-0.20	-0.33	-0.18	0.38	-0.11
LT							0.37	0.02	-0.12	-0.06
NL								0.17	-0.34	-0.22
LAL									-0.03	-0.10
LAW										-0.07

another. When all morphological characters were considered concomitantly, distinctly different *E. radiata* morphologies were found among some locations. Yet, there was no relationship between the degree of morphological difference and the linear distance between locations. We thus reject our first null hypothesis of no

differences in morphology among locations, but retain our second null hypothesis that there is no relationship between distance and degree of morphological difference. Consequently, our results do not support a model of geographic clines in *E. radiata* morphology. Instead we propose that the "total-morphology" at any one site

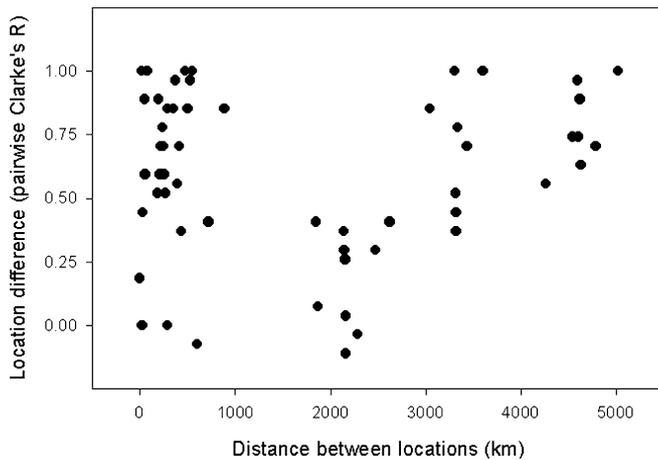


Fig. 3 *Ecklonia radiata*. Location dissimilarity (pairwise Clarke's *R*) versus linear distance between locations

Kautsky 1993). However, morphological characters are not necessarily affected only by processes operating at one scale: lateral spinosity could, at the same time, reflect a protective adaptation to large-scale differences in grazing pressure as well as a physiological adaptation to reduce the thickness of diffusion boundary layers (Hurd 2000) under small-scale differences in hydrodynamic regimes (Bell and Denny 1994). Indeed, the large importance of the smallest scale, among individuals within site, to variation in all morphological characters suggests wide genotypic plasticity. The differences in scales of variation also emphasise the potential bias in only looking at a few arbitrarily selected morphological characters.

Thallus dry weight was identified as the morphological character contributing most to differences in kelp morphology among locations. The poor correlation between dry weight and other size-related measures (e.g. total length, number of laterals) suggests that the influence of differences in dry weight among locations is more than simple allometric scaling, whereby, for example, dry weight increases because the length increases (Larkum 1986; Wernberg et al. 2001). Dry weights integrate aspects from many morphological characters, and the independent variation in several characters concomitantly may result in unpredictable variation in dry weight depending on whether variations in one character compensate or exacerbate the effect of variation in other characters. Biomass, including dry weight, may be affected directly by tattering (Blanchette 1997) or grazing (Steinberg 1995) or indirectly through the effect of external factors on the development of individual morphological characters such as thallus thickness (depth and wave exposure: Molloy and Bolton 1996) and stipe elongation (light and wave exposure: Sjøtun et al. 1993; nutrient concentrations and wave exposure: Gerard and Mann 1979).

Studies on intertidal algae have demonstrated considerable morphological variation among locations separated by a few kilometres to 1,000s of kilometres (Rice et al. 1985; Kalvas and Kautsky 1993; Ralph et al.

1998), but there is little evidence to suggest that these differences are continuously distributed in space or follow major clines (Rice et al. 1985; Ralph et al. 1998; Scott et al. 2001; but see Rice and Kenchington 1990). Also, variation among sites within locations is often of similar magnitude (or larger) to variation among locations, and a large proportion of the total variation is generally present at the lowest level of analysis: among individuals within sites (Rice et al. 1985; Kalvas and Kautsky 1998; Ralph et al. 1998; Scott et al. 2001). Morphological variation in macroalgae is often explained in terms of adaptation to hydrodynamic environments (see review by Hurd 2000). As pointed out by Rice et al. (1985) these environments are not continuously distributed in space over large geographic scales. Rather, microtopography (Carpenter and Williams 1993; Bell and Denny 1994) along with reef and coastline topography (Phillips et al. 1997; Gaylord 1999) causes hydrodynamic environments to vary discretely on scales from centimetres to several kilometres. Thus, variation in the hydrodynamic environment is a plausible cause of mosaics of morphs on several spatial scales, if *E. radiata* morphology varies consistently with the hydrodynamic regime.

Morphological differences among locations are not necessarily caused by either pheno- or genotypical variation. Unless the age distributions of the investigated populations are known to be similar, ontogenetic differences cannot be ruled out (e.g. Kalvas and Kautsky 1993) as many morphological characters are known to correlate with age within several laminarian algae (Novaczek 1981; Hymanson et al. 1990; Sjøtun and Fredriksen 1995). Differences in age structure, for example caused by difference in wave exposure (Sjøtun et al. 1993) or grazing (Andrew and Jones 1994), could contribute towards regional differences in morphology because *E. radiata* from northern New Zealand has been reported to attain ages of > 15 years (Novaczek 1981) whereas *E. radiata* from Fairlight Bay in New South Wales (Larkum 1986) and Marmion Lagoon in Western Australia (T. Wernberg, unpublished data) are considerably younger, with maximum ages of 2–4 years. Thus, in this study the large, fully developed individuals sampled from Doubtful Sound, New Zealand, might have been considerably older than those from other locations, leading to among-location differences that are unrelated to factors associated with geographic separation. Similarly, if kelp beds are composed of individuals from several cohorts (Dayton et al. 1984; Sjøtun et al. 1993), age differences among individuals within sites could possibly explain the large morphological variation among individuals within sites.

Taxonomic issues

The morphology of *Ecklonia radiata* is highly variable and this has led to the formation of an intractable suite of names for the various morphotypes, covering several

levels in the taxonomic hierarchy (Bolton and Anderson 1994). An example of this is *E. radiata* v. *biruncinata* or *E. biruncinata* (Bory) Papenf., a morph in which the surface of the thallus is covered with small spines. No studies have systematically tested whether the differences in morphological characters justify taxonomic distinction, and it is unknown whether these morphological variants are geno- or phenotypes. Because of the confusion and inconsistency in the systematics of the various geographical and morphological varieties of “*E. radiata*”, Bolton and Anderson (1994) found it more appropriate to group them under “*E. radiata* complex” rather than classifying them as distinct species or subgroups under *E. radiata*.

Substantial morphological variation is a common phenomenon in marine macroalgae (Rice et al. 1985; Jackelman and Bolton 1990; Molloy and Bolton 1996; Ralph et al. 1998) that has led to taxonomic confusion and debate about the nature of such variation and the level at which it should be recognised (Bolton and Anderson 1994; Ralph et al. 1998). We have found no evidence of distinct morphotypes among the 11 populations of *E. radiata* sampled. This study, however, did not include the large stipitate forms, with stipe lengths in excess of 1 m known from northern New Zealand and Queensland (Novacek 1984; Cole and Syms 1999), nor did it include the peculiar form of *E. radiata* from Hamelin Bay, with haptera forming at the lateral apices, tentatively identified as *E. brevipes* J. Agardh by Huisman (2000). Our findings support the very wide species definition suggested by others (Bolton and Anderson 1994, and references herein). However, as there are relatively large variations within location that appear to be phenotypic, morphological distinctness (“ecotypes”) may warrant the recognition of types on some level below species. This, however, needs further experimental research directed at the influence of specific environmental factors such as light, temperature, grazing pressure and hydrodynamic regime. Also, genetic analyses (e.g. Kusumo and Druehl 2000) would be a very strong tool to elucidate the nature of differences among *E. radiata* populations and their morphology.

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