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The effect of wave exposure on the morphology of *Ecklonia radiata*

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Abstract

This study examined the consistency of the effect of wave exposure on the morphology of *Ecklonia radiata*, a small kelp, across a broad geographic range (>1100 km). Fifteen morphological characters were measured on individuals from sites of low (2.5 ± 0.8 S.E.) and high (12.2 ± 2.0 S.E.) wave exposure (Baardseth's index) within six locations in southwestern Australia. With the exception of lateral width ($P = 0.0001$), none of the morphological characters were consistently statistically different ($P > 0.06$) between high and low wave exposure and correlations with wave exposure were generally weak ($r < 0.60$). While 12 of the 15 characters were statistically different ($P < 0.008$) between sites of different exposure within at least one location, the direction of difference (significant or not) was opposite between some locations for all but one character (lateral width). ANOSIM was not able to separate thalli from high and low exposure when all locations were pooled (Clarke's $R = 0.127$), but within each location most sites showed better separation ($0.126 <$ Clarke's $R < 0.829$). Despite the lack of statistical differences, trends suggested that *E. radiata* responds to exposure by having drag-reducing (small size, narrow laterals and blades, low spinosity) and strength-increasing (relatively large holdfast, thick stipe and thick blades and lamina) morphological traits, as observed for several other kelps in small-scale studies. We conclude that while wave exposure does have an effect on kelp morphology, the effect is not independent of other location-specific processes.

Keywords: Kelp; *Ecklonia radiata*; Wave exposure; Morphological variation; Broad-scale pattern

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1. Introduction

Hydrodynamic gradients are ubiquitous in the marine environment and they have profound effects on most aspects of the biology of macroalgae (see reviews by Koehl, 1986; Wheeler, 1988; Hurd, 2000). Many studies have investigated the effect of wave exposure (hereafter referred to as 'exposure') on the morphology of macroalgae, and it has been demonstrated that exposure may affect a wide range of morphological characters (op. cit.). For example, morphological variation in response to sheltered environments may reflect constraints of mass transfer limitation (Wheeler, 1988) where drag-increasing features such as spines and corrugations break down boundary layers and increase nutrient uptake and waste removal rates. Responses to exposed environments, on the other hand, may reflect simple pruning and tattering (Cheshire and Hallam, 1988; Blanchette, 1997; Andrew and Viejo, 1998) or drag-decreasing and strength-increasing adaptation to reduce the probability of detrimental damage and dislodgement. These adaptations to exposed environments may include thallus streamlining (Gerard, 1987), increased stipe (Cheshire and Hallam, 1988; Klinger and DeWreede, 1988) and thallus thickness (Cheshire and Hallam, 1988; Molloy and Bolton, 1996; Kawamata, 2001) or increased holdfast biomass (Sjøtun and Fredriksen, 1995). Although morphological adaptation to the hydrodynamic environment may reduce mortality (Friedland and Denny, 1995; Blanchette et al., 2002) it may also have physiological consequences such as reduced capacity for photosynthesis, productivity and growth (Gerard and Mann, 1979; Jackelman and Bolton, 1990; Blanchette et al., 2002).

Our current knowledge of how hydrodynamic gradients affect macroalgal morphology comes largely from studies conducted at small geographic scales or from studies where a few sites of different exposures are compared (e.g. Gerard and Mann, 1979; Cousens, 1982; Cheshire and Hallam, 1988; Back, 1993; Molloy and Bolton, 1996), often confounding the exposure gradient by space. Broad-scale studies of morphological variation in algae have used exposure as an ad hoc explanation of large variation among sites rather than quantifying, replicating and testing this effect specifically (examples include Ralph et al., 1998; Blanchette et al., 2002; Wernberg et al., 2003b). Rarely has the consistency of effect been studied over large geographic scales or between locations with nested replication of exposure (exceptions include Rice et al., 1985; Jackelman and Bolton, 1990; Rice and Kenchington, 1990). This is particularly important if we are to understand morphological variation and its ecological consequences in relation to widespread species such as the small kelp *Ecklonia radiata* (C. Agardh) J. Agardh, a dominant habitat former on many temperate reefs in the southern hemisphere (Choat and Schiel, 1982; Wernberg et al., 2003a; Goodsell et al., 2004).

A recent study of *E. radiata* demonstrated that there was considerable morphological variation among Australasian populations of this species, but that the magnitude of this variation was unrelated to spatial separation of populations as it would have been expected from a genotypic or environmental cline (Wernberg et al., 2003b). Because the morphology of kelp populations separated by only 10's of kilometers was just as different as populations separated by 100's or 1000's of kilometers these results suggest a strong non-clinal phenotypic component in the origin of this morphological variation. Moreover, Wernberg et al. (2003b) demonstrated that variation in individual morphological characters did not correlate and that variation in different characters was associated with different spatial scales, suggesting that some characters may reflect the phenotype whereas others may be determined by the genotype. This implies that, in order to understand morphological variation we must acknowledge that morphology is a composite measure and attempt to understand how each component is affected. In this study we examine the effect of wave exposure on the morphology of *E. radiata*: we test the hypothesis that wave exposure has a significant effect on the morphology of *E. radiata* thalli from southwestern Australia, and detail its effects on individual morphological characters.

2. Materials and methods

E. radiata thalli were collected from six locations along 1100 km of the southwest Australian coastline (Table 1). Within each location, one wave sheltered (L = low exposure) and one wave exposed (H = high exposure) site was selected based on their position in shore or off shore of reef structures and islands. Wave exposure is the only major source of water motion because the region is micro-tidal. The wave exposure of each site (Table 1) was calculated by counting the number of 10° sectors with a 7.5 km open fetch (Baardseth, 1970), where anything shallower than 5 m (e.g. submerged reefs) was considered an obstacle (e.g., Phillips et al., 1997; Wernberg, 2003). Thus, the exposure scale range from 0 = fully protected to 36 = fully exposed. Measurements were made on marine charts ranging in scale from 1:25,000 to 1:100,000 depending on location. Sites

Table 1
Locations with GPS position and calculated wave exposure (Baardseth's index) for each site

Location	GPS position	Wave exposure
Jurien Bay		
Exposed (H)	S 30°18′38″ E 114°58′24″	12
Sheltered (L)	S 30°17′26″ E 114°58′24″	1
Marmion Lagoon		
Exposed (H)	S 31°51′05″ E 115°42′24″	19
Sheltered (L)	S 31°50′29″ E 115°44′53″	5
Fremantle		
Exposed (H)	S 32°03′58″ E 115°38′33″	4
Sheltered (L)	S 32°10′04″ E 115°40′52″	0
Rockingham		
Exposed (H)	S 32°21′07″ E 115°41′13″	15
Sheltered (L)	S 32°19′49″ E 115°41′31″	2
Hamelin Bay		
Exposed (H)	S 34°12′46″ E 115°00′15″	12
Sheltered (L)	S 34°12′57″ E 115°01′13″	3
Albany		
Exposed (H)	S 35°03′59″ E 118°02′35″	11
Sheltered (L)	S 35°02′29″ E 118°02′31″	4

within locations were separated by a few kilometers and, with the exception of Albany which was granite, all were limestone reefs in the depth range 5–12 m. The locations are described in Wernberg et al. (2003b), and Searle and Semeniuk (1985) provides a broad account of the geology and wind and waves in the region. Ten grown (>30 cm) thalli, fully differentiated into branching laterals (‘stage 3’ as defined by Kirkman, 1981), were haphazardly collected from within a few square metres at each site. Fifteen morphological characters were measured on each thallus (cf. Table 2), 11 characters as described in Wernberg et al. (2003b) and four additional characters: (a) lamina and (b) lateral thickness measured with callipers midway along the lengthwise axis, (c) rugosity measured as the number of corrugations per centimetre across the width of a lateral and (d) holdfast ash free dry weight.

Paired *t*-tests between sites of low and high exposure within each location were used to test for differences in calculated wave exposure and means of all morphological characters. These tests adjust for regional-scale spatial effects by focusing on differences between paired sites within locations while, most importantly, locations provides true replication of wave exposure. Multivariate analyses, based on a normalised euclidian distance dissimilarity matrix calculated from standardised untransformed data, were used to assess patterns when taking all morphological characters into consideration. Samples were graphically represented in non-parametric multidimensional scaling (nMDS) plots and the separation of low versus high exposure tested with one-way analysis of similarities (ANOSIM, Clarke and Green, 1988) of thalli from sites of low and high exposure, both pooled among all locations and within individual locations. Product moment correlation tested the relationship between the calculated wave exposure and the mean of every morphological character.

Table 2
List of morphological characters measured and their mean values (±S.E., $n = 6$ locations) at low and high exposure sites

Morphological character	Low exposure	High exposure	*P*	$r(n = 12)$
Thallus length (cm)	84.2 ± 5.7	96.5 ± 8.4	0.143	0.41
Thallus dry weight (g)	165.6 ± 19.1	129.8 ± 21.1	0.284	0.05
Stipe length (cm)	9.1 ± 1.5	9.7 ± 0.8	0.629	0.08
Stipe diameter (mm)	12.7 ± 0.5	13.6 ± 0.4	0.081	0.39
Lamina length (cm)	59.2 ± 4.4	79.8 ± 7.4	0.068	0.60
Lamina width (cm)	6.9 ± 0.3	6.3 ± 0.3	0.191	−0.13
Lamina thickness (mm)	1.9 ± 0.1	2.0 ± 0.1	0.089	0.17
Lamina twists (number)	1.2 ± 0.3	1.8 ± 0.5	0.335	0.47
Lateral numbers (number)	44.2 ± 2.9	60.2 ± 8.3	0.060	0.59
Lateral length (cm)	41.8 ± 2.8	39.0 ± 2.4	0.599	−0.02
Lateral width (cm)	8.2 ± 0.4	6.3 ± 0.3	0.0001	−0.49
Lateral thickness (mm)	0.4 ± 0.03	0.5 ± 0.02	0.180	0.12
Rugosity (corrugations/cm)	1.1 ± 0.3	1.4 ± 0.2	0.235	0.20
Spinousity (spines/cm^2)	4.8 ± 2.8	3.7 ± 2.5	0.097	−0.40
Holdfast ash free dry weight (g)	6.2 ± 0.5	5.8 ± 0.4	0.391	0.02

P-values indicate level of significance from paired *t*-test between low and high exposure from each location. *P*-values have not been corrected for multiple testing because the test of each character represents an independent hypothesis.

3. Results

The calculated wave exposure of low exposure sites (2.5 ± 0.8 S.E.) was highly significantly ($P = 0.002$) lower than the calculated wave exposure of high exposure sites (12.2 ± 2.0 S.E.). There were no statistical differences ($P > 0.060$) between low and high wave exposure in most morphological characters, the only exception being lateral width ($P = 0.0001$) where thalli from low exposure had wider laterals (Table 2). Not surprisingly, therefore, most morphological characters were weakly correlated to calculated wave exposure ($r < 0.60$; Table 2). Although most morphological characters did not show statistical differences between levels of exposure there were indications that thalli from exposed sites were stronger, more slender and less bushy. For example, the trend was that thalli from high exposure were longer, lighter and had thicker stipes than thalli from low exposure. When all morphological characters were considered across all locations, thalli from exposed sites were not distinguishable from thalli from sheltered sites (Global test, Clarke's $R = 0.127$). Within each location there was a wide spread in the effect of exposure (Fig. 1) as the separation of thalli from sites of high and low exposure varied from not distinguishable (Rockingham, Clarke's $R = 0.126$) to highly distinct (Fremantle, Clarke's $R = 0.829$). This suggests that the effect of wave exposure on individual morphological characters was inconsistent from location to location. These inconsistencies are evident from Table 3, which show that the direction of difference between sites of high and low exposure was opposite at some locations for all but one morphological character (lateral width). For example, relative to low exposure, thalli from high exposure had shorter laterals in Jurien Bay and Hamelin Bay but longer in Albany.

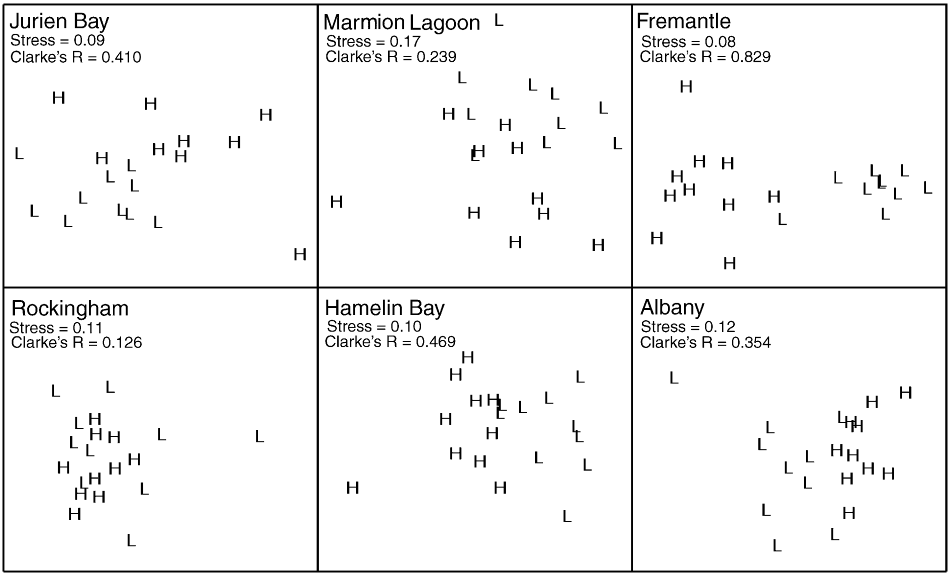

Fig. 1. nMDS plot of *Ecklonia radiata* thalli from low exposure (L) and high exposure (H).

Table 3
Differences in means of morphological characters from high and low wave exposure sites within each location ('High' minus 'Low exposure', i.e. a negative value indicate higher value in the sheltered environment)

Morphological character	Jur	Mar	Fre	Roc	Ham	Alb
Thallus length (cm)	26.0*	9.1 ns	−4.6 ns	−11.3 ns	25.3*	29.5**
Thallus dry weight (g)	−10.8 ns	−29.1 ns	−143.8***	18.3 ns	−48.3 ns	−1.2 ns
Stipe length (cm)	2.38***	2.44***	2.11 ns	−3.06 ns	1.97 ns	−2.55 ns
Stipe diameter (mm)	1.82*	1.94 ns	−0.08 ns	0.66 ns	1.47 ns	−0.43 ns
Lamina length (cm)	41.0**	9.0 ns	−3.7 ns	−0.7 ns	45.6***	31.9**
Lamina width (cm)	0.84 ns	−1.67 ns	−1.08 ns	0.43 ns	−1.73**	−0.78 ns
Lamina thickness (mm)	0.20 ns	0.22 ns	−0.01 ns	−0.08 ns	0.26 ns	0.12 ns
Lamina twists (count)	1.80 ns	−0.60 ns	−0.70 ns	0.70 ns	3.00 ns	−0.30 ns
Lateral numbers (count)	23.7**	11.1 ns	−6.9 ns	12.0*	42.0**	14.0*
Lateral length (cm)	−7.8*	0.6 ns	−2.5 ns	−7.1 ns	−12.3*	12.3*
Lateral width (cm)	−2.37 ns	−2.06 ns	−1.64 ns	−1.28 ns	−2.28*	−1.68 ns
Lateral thickness (mm)	0.12*	0.01 ns	0.02 ns	−0.05 ns	0.09*	0.06 ns
Rugosity (corrugations/mm)	−0.22 ns	0.51 ns	1.36***	0.17ns	0.09 ns	−0.11 ns
Spinousity (spines/cm^{2})	−0.04 ns	−0.44 ns	−2.72 ns	−0.57 ns	0.00 ns	−2.92*
Holdfast ash free dry weight (g)	0.30 ns	0.64 ns	−1.21 ns	0.77 ns	−1.75 ns	−1.33 ns

Asterisks indicate significance level of t-test (P-values Bonferroni-corrected for multiple testing across locations). ns = not significant.

* $P < (0.05/6)$.

** $P < (0.01/6)$.

*** $P < (0.001/6)$.

4. Discussion

Wave exposure is probably the most commonly identified cause of morphological variation in macroalgae (e.g. Gerard and Mann, 1979; Cousens, 1982; Cheshire and Hallam, 1988; Molloy and Bolton, 1996; Ralph et al., 1998; Blanchette et al., 2002; Roberson and Coyer, 2004; see also review by Hurd, 2000). This study found morphological differences between thalli from sites of high and low exposure within most locations. There was however only little evidence to suggest that wave exposure has a consistent effect on morphological variation in *E. radiata* across locations in southwestern Australia.

At first impression, our results are at odds with the prevailing paradigm that hydrodynamic gradients exert a unidirectional influence on macroalgal morphology, with drag-increasing morphologies at low exposure levels (to break down boundary layers) and drag-decreasing and strength-increasing morphologies at high exposure levels (to decrease dislodgement rates) (Hurd, 2000).

We found consistent effects in only one character, lateral width, where kelps at high exposure had narrow laterals relative to kelps from low exposure. Narrowing of fronds in response to increased exposure has also been reported for several other kelps including *Laminaria longicruris* (Gerard and Mann, 1979), *L. japonica* (Kawamata, 2001), *Nereocystis leutkeana* (Johnson and Koehl, 1994) and *Eisenia arborea* (Roberson and Coyer, 2004), and the fucoid *Fucus vesiculosus* (Back, 1993). Most other morphological characters were significantly different between sites of high and low exposure at at least one of the locations. Interestingly, for all but one of the morphological characters (lateral width) the direction of difference (significant or not) was opposite among locations, underpinning the location-specific nature of morphological variation as emphasised by Wernberg et al. (2003a). Lamina twists, lamina thickness and holdfast biomass showed no differences at all. Particularly the absent effect of exposure on holdfast biomass is surprising. Holdfast size has been shown to be positively correlated to wave exposure in *L. hyperborea* (Sjøtun and Fredriksen, 1995) and *E. arborea* (Roberson and Coyer, 2004), presumably as an adaptation to increase attachment capacity. However, thalli from high exposure sites were commonly lighter than thalli from low exposure sites, implying that high exposure sites does have larger holdfasts relative to thallus size. This also highlights the usefulness of evaluating ecologically important morphological ratios in addition to raw characters. While not statistically significant, other characters showed trends of morphological differences between sites of low and high wave exposure: kelps were longer (most predominant in lamina length) and lighter with thicker stipes, laminae and laterals and had less spines at high exposure. These morphological trends are consistent with increased strength and reduced drag, and they correspond to similar responses to exposure observed in other kelps (smoothness: Armstrong, 1989; Roberson and Coyer, 2004; thickness: Molloy and Bolton, 1996; Kawamata, 2001).

Our findings of relatively few consistent morphological differences between sites of high and low exposure contrasts the study of Molloy and Bolton (1996) who found all of their nine characters to be different in *Laminaria schinzii*. However, as the physiological and ecological significance of individual morphological characters vary (see review by Hurd, 2000 and discussion by Wernberg et al., 2003b), there is no basis to assume a common geno or phenotypic origin of every character and therefore no reason to expect all morphological characters to show responses to exposure. In particular, wave exposure is a very complex factor with many attributes (e.g. speed, acceleration, lift, period, duration and direction) and it seems likely that different morphological characters respond differently to each of these attributes of the hydrodynamic environment. To our knowledge no studies have ever attempted to separate the effects of these attributes. Furthermore, recent biomechanical studies of *E. radiata* in Western Australia have shown that in more than 70% of the cases, the predominant limestone reefs will break before the kelp tissues (Thomsen et al., 2004) and, therefore, selective pressures may not be strong at the tissue level, potentially explaining the weak response in these characters (e.g. frond thickness). Interestingly, within the Laminariales, there appear to be some diversity in which characters are under phenotypic and which are under genotypic control; for example, Serisawa et al.'s (2003) transplant experiments indicated that stipe length is a genotypic character in different ecotypes of *Ecklonia cava* whereas findings of increased stipe length for a number of other kelps in response to crowding (Hymanson et al., 1990; Holbrook et al., 1991; Sjøtun and Fredriksen, 1995), suggests that in these species, stipe length is a phenotypic character that may be controlled by light.

In reconciling our results with the literature (op. cit.), it is important to recognise that most previous studies of morphological variation in response to the hydrodynamic environment, have been done at a spatial scale similar to each of our locations. When looking at the individual locations, we also found substantial morphological differences among several low and high exposure populations. Nevertheless, the large variation in response among locations suggests that non-clinal (cf. Wernberg et al., 2003b) location-specific processes such as depth (Molloy and Bolton, 1996), grazing pressure (Kalvas and Kautsky, 1993) or nutrient levels (Blanchette et al., 2002) have an overriding effect on *E. radiata* morphology, influencing various morphological characters differently. The implication is therefore that wave exposure cannot be seen entirely separate from other local processes and caution is warranted before extrapolating causality between wave exposure and morphology from studies done at restricted spatial scales.

We are confident that our sites of high and low exposure represent a substantial gradient within all locations, as demonstrated by the calculated Baardseth (1970) indices. In Marmion Lagoon, for example, previous measurements have shown significantly more wave energy (Phillips et al., 1997) and higher drag forces (Wernberg, 2003) at the exposed compared to the sheltered sites. Nevertheless, our tests assume a monotonic response where the direction of morphological change is the same whether going from low to intermediate or from intermediate to high wave exposure and this assumption may not be valid (Cousens, 1982; Cheshire and Hallam, 1988; Jackelman and Bolton, 1990). In *E. radiata*, for example, size measured either as biomass or length could be restricted at low exposure due to physiological constraints imposed by mass transfer limitation (Wheeler, 1988) and at high exposure by pruning (Cheshire and Hallam, 1988; Blanchette, 1997; Andrew and Viejo, 1998).

In conclusion, it should be emphasised that our results did not indicate that wave exposure is unimportant to *E. radiata* morphology. On the contrary, as most sites showed reasonable separation with wave exposure (cf. Fig. 1) we clearly reject this null-hypothesis, but note that the effect may not be consistent in space (cf. Table 3). This implies that it may not be possible to generalise the effect of exposure across broad geographic scales, or that the effects of exposure are confounded by other local processes such as grazing, sediment load, reef geology and geomorphology. Broad-scale studies that address the interactions between wave exposure, morphology and these localised ecological processes are sorely needed. However, only through fully nested sampling designs with multiple sites within exposure levels, replicated within locations, can this hierarchy of processes be unconfounded and understood.

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