



Variation in morphological traits over a wave-exposure gradient in one but not in another species of the brown alga *Carpophyllum* (Fucales)

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Environmental conditions can influence the morphology of local biota through phenotypic plasticity or local adaptation. Macroalgal morphologies are often associated with wave-exposure conditions. We investigated the relationship between morphology and wave exposure in two common endemic subtidal macroalgae, *Carpophyllum angustifolium* and *C. maschalocarpum*, from the East Cape of New Zealand. Morphological comparisons were made between individuals from two sites and four different wave-exposure zones, as defined by fetch and barnacle composition. Of the seven morphological traits measured in *C. angustifolium*, only total length varied, and individuals were longer in more wave-exposed environments between the two exposure zones where the species were found. In contrast, total length, stipe thickness and vesicle presence all varied significantly between exposure zones in *C. maschalocarpum*. *C. maschalocarpum* specimens were shorter with thinner stipes, and fewer individuals had vesicles in the more wave-exposed zones. Morphological traits of both species also varied between sites, suggesting that other influences are important for determining species morphology. Further study is needed to investigate the role of phenotypic plasticity and genetic variability for driving morphological variation in *C. angustifolium* and *C. maschalocarpum*.

Key Words: *Carpophyllum angustifolium*; *Carpophyllum maschalocarpum*; Fucales; morphology; Phaeophyceae; phenotypic plasticity; wave exposure

INTRODUCTION

Local environmental conditions can influence the morphology of organisms as a result of selection or phenotypic plasticity, which has been shown in a range of taxa and environments (Trussell 2000, Hochkirch et al. 2008, Mboumba and Ward 2008). In coastal environments, the morphology of local biota is significantly affected by wave exposure (Denny 2006, Stewart 2006). For example, Arsenault et al. (2001) found that leg length of the barnacle *Balanus glandula* Darwin declines with increasing wave exposure.

In Phaeophyceae, brown macroalgae are significantly

affected by wave exposure (Engelen et al. 2005, Wernberg and Thomsen 2005, Fowler-Walker et al. 2006, Tuya and Haroun 2006). Water motion around macroalgae affects their nutrient acquisition, creates mechanical fatigue, and can result in the loss of biomass or dislodgement of entire individuals (Hurd 2000, Kawamata 2001). Phaeophyceae are highly plastic organisms, with numerous examples of environmentally induced forms (Mathieson et al. 1981, 2006). Optimal morphologies exist for Phaeophyceae in different wave-exposure regimes. Traits that reduce drag (i.e., small size, streamlined shape, and flex-

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ibility) and increase strength (i.e., thickness and aggregation) are favoured in high wave-exposed areas (Stewart and Carpenter 2003, Puijalon and Bornette 2004, Thomsen et al. 2004, Ruuskanen and Nappu 2005, Wernberg 2005, Stewart 2006). Johnson and Koehl (1994) found that the blade morphology of the kelp *Nereocystis luetkeana* (K. Mertens) Postels & Ruprecht is longer and thinner in more wave-exposed areas and experienced less drag than that of the sheltered blade form.

Carpophyllum angustifolium J. Agardh and *Carpophyllum maschalocarpum* (Turner) Greville dominate the high subtidal zone of northeastern New Zealand (Schiel 1990). These two species have different morphologies and wave-exposure distributions. *C. angustifolium* is streamlined, flexible, with strong aggregating holdfasts and is distributed in very to moderate wave-exposed areas (Adams 1994, Hodge 2009). *C. maschalocarpum* has vesicles, is larger, has wide flat stipes and occurs in sheltered to moderately exposed areas (Adams 1994, Hodge 2009). Determining how the morphology of these species is affected by wave exposure will provide insight into environmental selection and plasticity in *Carpophyllum* species. It will also allow hypotheses to be generated about the fitness and distribution of their morphologically intermediate hybrids (Hodge et al. 2010) relative to wave exposure.

One of the major barriers when studying the relationship between morphology and wave exposure is measuring the wave exposure component. Measuring wave exposure on rocky shores is difficult due to spatial and temporal variability (Denny 1988, Eckman et al. 2003). Water motion can be directly measured using a range of equipment including dynamometers and plaster of Paris clod cards (Carrington Bell and Denny 1994, Thompson and Glenn 1994). But, these methods have limitations (Porter et al. 2000, Lindegarth and Gamfeldt 2005). One serious obstacle when deploying sensitive and expensive equipment is its attachment and survival in high wave-exposed environments. Consequently, direct measurements often rely on short-term data collected in calm water (Arsenault et al. 2001, Stewart and Carpenter 2003). For example, Coleman and Muhlin (2008) only measured water motion on days of 'low to moderate water motion.' However, short-term measurements can be misleading if extrapolated over long periods with varying environmental conditions (Gaylord 1999).

The difficulties associated with direct measurements have led many researchers to infer water motion from fetch or biological information (Ballantine 1961, McQuaid et al. 2000, Engelen et al. 2005). In two major

journals, approximately half of the wave-exposure studies over a recent 10 year period developed categorical definitions of exposure using fetch or local biota (Lindegarth and Gamfeldt 2005). Fetch and local biota provide information about wave exposure over a relatively long time frame; however, both have their limitations. Fetch data have low spatial resolution, whereas geographically specific information on the distribution or morphology of local biota may not be available (Gaylord 1999, Arsenault et al. 2001, Lindegarth and Gamfeldt 2005). Barnacle distribution and its relationship to wave exposure in New Zealand have been well described (Foster 1967, 1978). Barnacles are one of the first taxa to be considered when defining wave exposure and are a useful guide due to their immobility and dominance on rocky shores (Ballantine 1961, Heaven and Scrosati 2008).

In this study, we compared the morphology of *C. angustifolium* and *C. maschalocarpum* between four wave-exposure zones defined by fetch and barnacle distribution. We were interested in determining whether the morphology of *C. angustifolium* and *C. maschalocarpum* individuals changes in areas of different wave exposure. Furthermore, we evaluated whether the relationship between wave exposure and morphology was the same in both species.

MATERIALS AND METHODS

Sampling locations

Samples were collected from two sites on the East Cape of the North Island, New Zealand. The two sites were both within greater Whanarua Bay, which faces northwest and contains a number of smaller sandy bays divided by large rocky islands or outcrops. The first site was located at the southeastern end of Maraehako Bay (37°40.4' S, 177°47.8' E), and the second site was on the rock walls located at Uncles Bay (37°40.0' S, 177°48.0' E), which is the adjacent bay to the northeast. The two sites are approximately 500 m apart and are separated by Motu Kaimeanui Island and two deep inlets. Sampling was conducted during the 2007-2008 austral summer.

Assessing wave exposure

Four wave-exposure zones were selected from each of the two sites. These zones were determined based on fetch and barnacle distribution. The first sites were divided using an estimate of fetch based on the modified

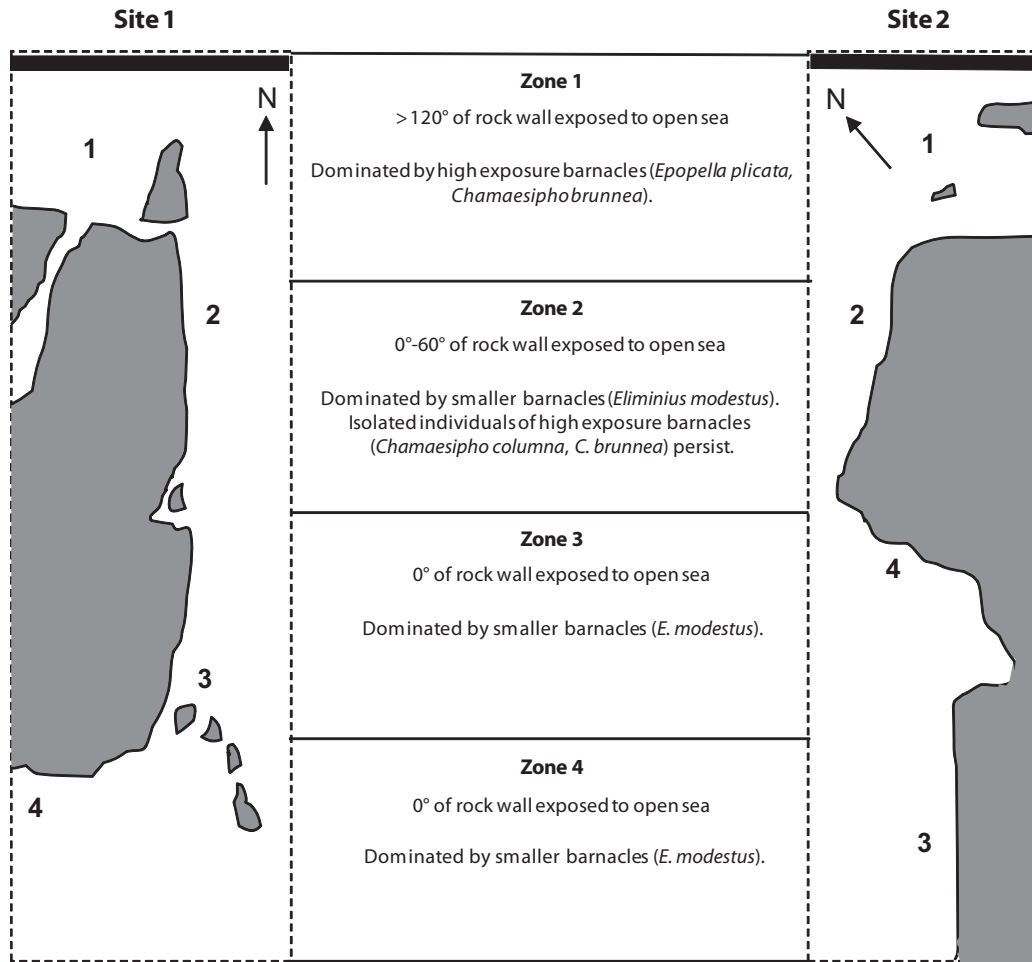


Fig. 1. Wave-exposure zones were defined by the degree of exposure to the open sea, orientation of the rock walls and the barnacles in the inter-tidal portion of the rock wall. Simplified illustrations of the two study sites are shown on the left and right with the general locations of the zones marked. The open sea is to the north.

Baardseth index. The Beardseth index is calculated by placing a transparent circular disc with a radius of 7.5 km on a map point and determining the number of 9° segments containing no land or islands (Baardseth 1970). In this study, the angle of open segments was summed *in situ* to incorporate small-scale disruptions to oncoming waves such as rocky outcrops. This sum was > 120° for the most exposed zone (zone 1), up to 60° for the second most exposed zone (zone 2), and 0° in the two most sheltered zones. The two most sheltered zones were distinguished by the direction the rock walls were facing. The rock walls in the moderately sheltered exposure zone (zone 3) faced the opposite side of the bay, whereas those in the most sheltered exposure zone faced the shore (zone 4) (Fig. 1).

A single transect line was laid in each exposure zone at each site, and quadrat locations were selected randomly from the top 0.5 m of the *Carpophyllum* depth distri-

bution. The inter-tidal barnacle fauna was checked for consistency with wave exposure prior to sampling each quadrat. The expected barnacle fauna for the four exposure zones was determined based on work by Foster (1967, 1978), and is summarised in Fig. 1. Quadrats were rejected if barnacles did not match the expected fauna in the exposure zone, the rock face was not vertical, fewer than three algal individuals were present, or the quadrat was less than 0.5 m from a previously sampled quadrat. All *Carpophyllum* individuals with holdfasts inside the 20 × 20 cm quadrats were collected. Sixty-nine quadrats (approximately eight quadrats per transect per exposure zone) were sampled at the two sites, with 280 *C. angustifolium* and 152 *C. maschalocarpum* adults collected in total. Collected material was frozen at -4°C within 1 week of collection and thawed in seawater prior to morphometric analysis.

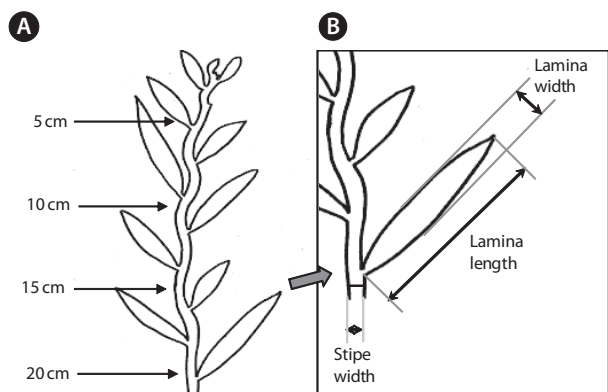


Fig. 2. The location of the measurements taken from each individual at 5, 10, 15, and 20 cm are shown with arrows on a stylised axis in (A). (B) Stipe width, lamina length and width are illustrated at 20 cm from the apex.

Morphometrics

Adults were morphologically identified and cleared of any epiphytes. Individuals longer than 20 cm were considered adults. Only those individuals with complete haptera were used in the morphometric analysis to avoid pseudo-replication (i.e., the doubling up of measurements from the same individual). Individuals were measured using digital callipers and a metre rule.

The morphometric characteristics selected for measurement were stipe width and thickness; as well as lamina length, width and thickness (Fig. 2). We focused on the stipe and lamina characteristics of the primary axes (defined as the dominant axis that arises directly from the holdfast). The stipe and lamina measurements were taken approximately 5, 10, 15, and 20 cm from the apex of the primary axis. Lamina length was measured from the edge of the stipe where the lamina forms a tip. Lamina and stipe width were measured at the widest point, perpendicular to an imagined mid-line. Thicknesses were measured at the thickest point. In some places, herbivory had altered morphology of the stipe and lamina; these could be detected by sudden and distinct changes in the lamina or stipe outline. Stipe and lamina measurements that were affected by herbivory were excluded and replaced by measurements of the nearest intact equivalent within 3 cm, if possible. The total length of the individual, presence of vesicles longer than 8 mm and presence of secondary branches longer than 20 cm, were also recorded.

Data analysis

The morphometric data contained missing values due

to herbivory and wave exposure damage on parts of some individuals. No observable difference was found between the measurements taken at the different locations down the apex of individuals, when these values were graphed on a scatter plot. Consequently, these measurements were averaged for each individual. This resolved the missing values problem, as most individuals had at least one measurement for each morphological trait. For example, stipe width of an individual was an average from measurements at 5, 10, 15, and 20 cm from the apex.

Morphological characters from individuals in different wave-exposure zones were compared for each species. Data from the two sites were combined. An analysis of variance (ANOVA) and Tukey's post-hoc comparisons were conducted when data were normally distributed and the variances were equal. Data were log transformed when the ANOVA assumptions were not met. Log transformed data that still did not meet the assumptions of normality was analysed non-parametrically with the Kruskal-Wallis test. The chi-square test was used to investigate the presence data on vesicles and branching. The level of significance for all statistical tests was $\alpha = 0.05$.

RESULTS

Wave exposure and morphology

C. angustifolium was found only in the two most wave-exposed zones ($n_{\text{zone 1}} = 165$, $n_{\text{zone 2}} = 115$), whereas *C. maschalocarpum* was found in all four wave-exposure zones ($n_{\text{zone 1}} = 7$, $n_{\text{zone 2}} = 31$, $n_{\text{zone 3}} = 62$, $n_{\text{zone 4}} = 52$). Some morphological traits differed between exposure zones (Table 1). Total length of both species varied by wave-exposure zone (Fig. 3). However, the two species showed opposite trends for total length, as *C. angustifolium* individuals were longer in the more exposed zone. By comparison, *C. maschalocarpum* tended to be longer in the more sheltered zones, with individuals in exposure zones 3 and 4 significantly longer than those in zone 2 (Tukey's test: $p_{\text{zone 3}} < 0.001$, $p_{\text{zone 4}} = 0.024$). No significant difference was observed for *C. maschalocarpum* length between the two most sheltered zones (zones 3 and 4) (Tukey's test: $p = 0.344$). Furthermore, the seven *C. maschalocarpum* individuals in the most exposed zone (zone 1) had highly variable total lengths and, subsequently, could not be differentiated from any other zone (Tukey's test: $p_{\text{zone 2}} = 0.807$, $p_{\text{zone 3}} = 0.452$, $p_{\text{zone 4}} = 0.902$).

None of the other morphological traits varied significantly. Some non-significant trends were identified in *C.*

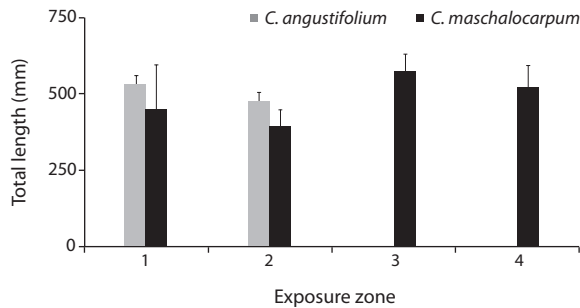


Fig. 3. The average length of individuals in each sample differed between wave-exposure zones in both species. The bars show average total length. Error bars indicate 95% confidence intervals.

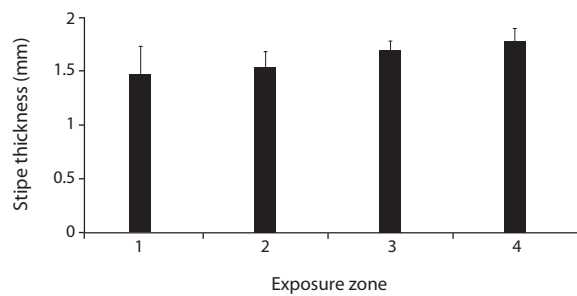


Fig. 4. Variation in stipe thickness in *Carpophyllum maschalocarpum* between wave-exposure zones. Error bars indicate 95% confidence intervals.

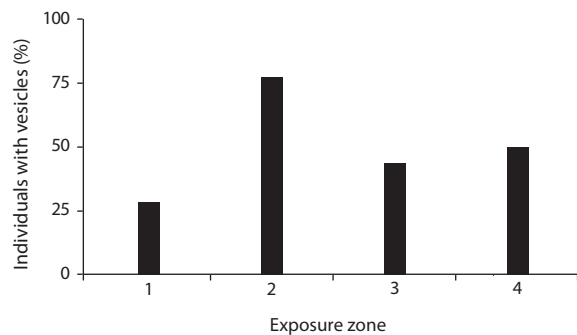


Fig. 5. The variation in vesicle presence in *Carpophyllum maschalocarpum* between wave-exposure zones. Error bars indicate 95% confidence intervals.

maschalocarpum, such as lamina thickness (thinner in exposed zones) and the presence of branching (less in exposed zones). Also, non-significant trends were seen in *C. angustifolium* (e.g., stipe width, stipe thickness, lamina length, lamina width, lamina thickness, and the presence of vesicles) (Table 1).

The average *C. maschalocarpum* stipe thickness increased as wave exposure decreased (Fig. 4). Stipes were significantly thinner in exposure zone 2 than those in

zones 3 and 4 at both sites (Tukey's test: $p = 0.026$). The presence of vesicles in *C. maschalocarpum* individuals varied between the different exposure zones. The proportion of individuals with vesicles was lowest in the most exposed zone, highest in the moderately exposed zone and intermediate in the two most sheltered zones (Fig. 5).

A non-significant trend in lamina thickness of *C. maschalocarpum* was observed between exposure sites; they were thinner in more exposed zones. Another non-significant trend in *C. maschalocarpum* was in the branching, as there appeared to be fewer individuals with major branches in more exposed zones (Table 1).

Site effects

Carpophyllum species morphological traits also varied between sites (Table 2). Stipe thickness and lamina thickness of *C. angustifolium* and *C. maschalocarpum* were significantly different between the two sites. *C. angustifolium* stipe width and lamina width also varied between the two sites. *C. maschalocarpum* lamina length varied between the two sites.

DISCUSSION

Some morphological traits differed between exposure zones, suggesting that *C. angustifolium* and *C. maschalocarpum* morphologies were affected by wave exposure. Previous studies have found that algae in more wave-exposed areas tend to be shorter with narrower and thicker lamina and stipes and fewer or no vesicles (Johnson and Koehl 1994, Kawamata 2001, Stewart and Carpenter 2003, Fowler-Walker et al. 2006). These patterns have also been detected in *Carpophyllum flexulosum* (Esper) Greville (Cole et al. 2001). Some of these patterns were found in *C. maschalocarpum*; individuals were shorter, and a lower proportion had vesicles in the more wave-exposed zones. A non-significant trend of *C. maschalocarpum* was being less branched in the more wave-exposed zones. However, opposing patterns were also found, with *C. angustifolium* being longer, and *C. maschalocarpum* stipes being thinner in more wave exposed zones. A non-significant trend was also found for *C. maschalocarpum* lamina being thinner in more wave-exposed zones.

C. angustifolium individuals were marginally but significantly longer in the most wave-exposed zone, which is contrary to the trend found in other macroalgae. High wave exposure can prevent macroalgae from reaching

large sizes, due to dislodgement or breakage, and smaller sized macroalgae experience less drag and wave damage (Blanchette 1997, Hurd 2000). The results of this study could reflect different strategies for tending to the mechanical stress of wave exposure. *C. angustifolium* grows in higher densities than those of *C. maschalocarpum*. The wave exposure that individuals are subjected to can be modified and reduced in dense macroalgal stands (Eckman 1983), potentially reducing the selection pressure on morphology. Flexibility allows for morphological re-configuration *in situ*, which can reduce the drag forces a macroalga is exposed to (Carrington 1990, Denny 2006).

Flexibility in some macroalgae results in reduced drag in higher flows (Carrington 1990, Gaylord et al. 1994).

Another opposing trend to that found in other macroalgae was in the thickness of the *C. maschalocarpum* stipes and lamina. Stipes were significantly thinner in *C. maschalocarpum* from more exposed zones, and *C. maschalocarpum* laminae showed a similar non-significant trend. This pattern could be a reflection of the relationship between age and thickness. Laminae and stipes get thicker with age, and individuals within a population are often younger in more exposed areas due to wave damage and loss (Dudgeon and Johnson 1992). *C. mascha-*

Table 1. Variation in morphological traits between *Carpophyllum angustifolium* and *C. maschalocarpum* in the wave-exposure zones

Species	Significance	Character trait	Statistics
<i>C. angustifolium</i>	Significant	Total length	$X_2 = 5.980$, $df = 1$, $n = 280$, $p = 0.014$
	Not significant	Stipe width	$F = 0.883$, $df = 1$, $n = 280$, $p = 0.348$
		Stipe thickness	$F = 1.944$, $df = 1$, $n = 280$, $p = 0.164$
		Lamina length	$X_2 = 0.009$, $df = 1$, $n = 280$, $p = 0.927$
		Lamina width	$F = 1.137$, $df = 1$, $n = 173$, $p = 0.288$
		Lamina thickness	$X_2 = 0.010$, $df = 1$, $n = 173$, $p = 0.919$
		Proportion with vesicles	$X_2 = 0.529$, $df = 1$, $n = 280$, $p = 0.467$
<i>C. maschalocarpum</i>	Significant	Total length	$F = 6.063$, $df = 3$, $n = 152$, $p = 0.001$
		Stipe thickness	$F = 6.981$, $df = 4$, $n = 149$, $p < 0.001$
		Proportion of individuals with vesicles	$X_2 = 11.491$, $df = 3$, $n = 152$, $p = 0.009$
	Non-significant trends	Lamina thickness	$F = 2.689$, $df = 2$, $n = 49$, $p = 0.079$
		Proportion with branches	$X_2 = 6.159$, $df = 3$, $n = 152$, $p = 0.104$
	Not significant	Stipe width	$F = 1.874$, $df = 1$, $n = 149$, $p = 0.137$
		Lamina length	$F = 1.461$, $df = 3$, $n = 49$, $p = 0.289$
Lamina width		$F = 0.458$, $df = 3$, $n = 49$, $p = 0.713$	

Table 2. Relative differences and statistics for character traits that significantly differed between the two sites (at the 5% significance level)

Species	Character trait	Maraehako Bay	Statistics
<i>Carpophyllum angustifolium</i>	Stipe width	Wider	$F = 23.917$, $df = 1$, $n = 280$, $p < 0.000$
	Stipe thickness	Thicker	$F = 6.848$, $df = 1$, $n = 280$, $p = 0.009$
	Lamina width	Wider	$F = 1.137$, $df = 1$, $n = 173$, $p < 0.000$
	Lamina thickness	Thinner	$F = 7.371$, $df = 1$, $n = 173$, $p = 0.007$
<i>C. maschalocarpum</i>	Stipe thickness	Thinner	$F = 42.163$, $df = 1$, $n = 149$, $p < 0.000$
	Lamina length	Thinner	$F = 4.782$, $df = 1$, $n = 49$, $p = 0.034$
	Lamina thickness	Longer	$F = 23.979$, $df = 1$, $n = 49$, $p < 0.000$

locarpum stipes and laminae might be thinner in more exposed areas because they are younger.

Interestingly, the relationships between wave exposure and morphology differed between the two species. The only trait that varied with wave exposure in both species was total length, which showed opposing trends in the two species. Furthermore, more morphological traits differed significantly with differences in wave exposure in *C. maschalocarpum* than those in *C. angustifolium*, which could be due to their different wave exposure distributions. High levels of phenotypic plasticity have been hypothesised to be associated with generalist species as opposed to specialist species (Sultan 2000). *C. maschalocarpum* had a much broader wave-exposure distribution than that of *C. angustifolium*. *C. angustifolium* was only found in the two most exposed zones, suggesting specialisation for high wave exposure. *C. maschalocarpum* was found in all four wave exposure zones, indicating that it is a generalist species (see also Dromgoole 1973).

Differences in wave exposure-morphological relationships between the species could also be a reflection of different strategies for reacting to wave exposure. The consequences of wave exposure on an individual are influenced by drag and attachment strength (Kawamata 2001). Changes in length, stipe and lamina dimensions can alter drag but not attachment strength. Higher attachment strengths have been found in individuals with aggregating or larger holdfasts and in individuals from exposed locations (Dudgeon and Johnson 1992, Thomsen et al. 2004, Wernberg 2005). The relative importance of reducing drag and increasing attachment strength could differ between the two species, with a greater emphasis on reducing drag in *C. maschalocarpum* and increasing attachment strength in *C. angustifolium*. Attachment strength, holdfast biomass and holdfast aggregation were not measured in this study but are hypothesised to vary between wave exposure zones and species. During sampling, it was noted that individuals were strongly attached in the most exposed zone, often having to be cut off or prised off the rocks with scissors. Empirical testing of attachment strength could help to interpret the relationship between morphology and wave exposure found in this study. Differing emphasis on drag and attachment strength was concluded in a similar study that found a lack of a correlation between morphological changes in two aquatic angiosperm species, *Berula erecta* (Huds.) Coville and *Mentha aquatica* L., along a water flow gradient (Puijalon and Bornette 2004).

The relationship between morphology and wave exposure was consistent between the two sites, but morphol-

ogy differed between the sites. Morphological variation between sites was found in a previous study on *Fucus* (Coleman and Muhlin 2008). Morphological variation could be due to environmental variability between the two sites, although these were thought to be very similar, as they were only 500 m apart. Alternatively, the structural variability could be due to genetic differences between the two populations. *Carpophyllum* species have low dispersal capacity; the majority of recruits settle within metres of parental plants (Schiel 1980). Such low dispersal capacity could allow genetic differentiation between the two populations. Previous studies have found fucoid algae to be genetically differentiated at very low spatial scales; populations just 10 m apart show genetic differentiation in *Fucus vesiculosus* (Williams and Di Fiori 1996, Coyer et al. 1997, Engelen et al. 2001, Tatarenkov et al. 2007).

It should be noted that we investigated wave exposure categorically, which has disadvantages. First, relationships between wave exposure and morphology can be obscured or confused by small-scale wave exposure variability (Kitzes and Denny 2005). In a study that compared algal morphology in exposed, semi-exposed and protected sites, Eckman et al. (2003) found that 30-50% of the variation in water flow occurred between replicates at the same site.

Further investigation of *C. angustifolium* and *C. maschalocarpum* is needed to understand the pattern of morphological variation found in this study. In particular, analysis of morphology relative to a continuous measure of wave exposure could reveal finer scale trends, and non-linear relationships. Also, an investigation of attachment strength and flexibility is required to determine the importance of morphology on the effects of wave exposure on the two species. The drivers for the morphological variations observed in this study are unknown. Therefore, exploring the role of the environment and genetic variation is required. Transplant experiments and an understanding of the genetic structuring of *Carpophyllum* populations could provide further insight.

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