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Morphological differences in *Fucus gardneri* between two shores with equal cartographic exposure values but different levels of wave action

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The morphology of *Fucus* species, such as *F. gardneri* (ex *F. distichus*), is known to respond strongly to wave exposure. Shore exposure can be described using cartographic methods in which a shore is given a numerical value. While two shores may have equal shore exposure values, they can receive different wave force due to off-shore meteorological conditions. We studied differences in *Fucus gardneri* morphology between two Californian shores with the same numerical exposure value but which — according to off-shore conditions — may receive different levels of wave force. Thalli were smaller and on average more fronds grew in the holdfasts of the shore considered to be subjected to stronger wave action. Although this result is consistent with earlier observations of decreasing thallus size with increasing wave exposure, we found cartographic methods used to describe shore wave force to be insufficient.

Key words: algae, exposure, *Fucus gardneri*, holdfast, morphology

Introduction

Morphological responses of marine macroalgae to wave action are well documented, and the thalli of perennial macroalgae have often been used as an indicator of prevailing wave exposure conditions (Jordan & Vadas 1972, Kalvas & Kautsky 1993, Scott *et al*. 2001). Although responses vary from species to species, individual morphological characteristics tend to decrease in size as wave exposure increases. Even small changes in wave force may be reflected in algal morphology, and a geographical distance of several tens of metres along an exposure gradient is sufficient to elicit considerable changes (Anderson & Scott 1998, Ruuskanen *et al*. 1999, Scott *et al*. 2001). On a large geographical scale, along latitudinal and longitudinal gradients, marked variation can be found (Rice *et al*. 1985).

Of the brown algae, the genus *Fucus* in particular has been closely studied, and the effects of wave exposure on the morphology of *F. vesiculosus*, *F. distichus* and *F. spiralis* have undergone detailed investigation. The algal phenotype is a product of numerous thallus characteristics that can be studied with multivariate analysis. For example, discriminant analysis has been used to demonstrate morphological intra-

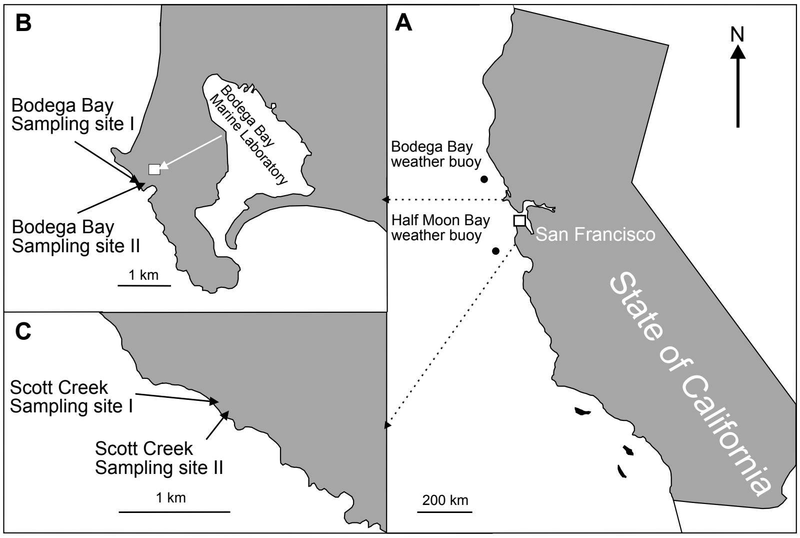

Fig. 1. Sampling sites and rough locations of NOAA weather buoys (filled dots).

and inter-species differences in the genus *Fucus* (Schonbeck & Norton 1981, Marsden *et al.* 1983a, 1983b, Rice & Chapman 1985, Rice *et al.* 1985, Bäck 1993, Kalvas & Kautsky 1993, Scott *et al.* 2001).

In morphological studies, a common procedure for studying algal response to environmental factors is the measurement of vegetative characteristics of individual fronds. However, defining an individual frond is sometimes difficult. In some cases, frond aggregations occur which can be described as several fronds emerging in the same holdfast. These are called holdfast/blade complexes, or clumps (Foster 1982) or tufts (Bäck *et al.* 1991). Frond aggregation may play a role in algal ecology in certain environments; the number of *F. vesiculosus* fronds per holdfast has been reported to increase with increasing wave exposure (Bäck *et al.* 1991, Malm & Kautsky 1999) and with decreasing salinity (Kalvas & Kautsky 1999, Ruuskanen & Bäck 1999a).

Cartographic methods provide a simple means of assessing wave exposure of seashores (Baardseth 1970, Håkansson 1981) but are subject to many kinds of errors. Shores with the same cartographic index may, for instance, experience differences in wave exposure as a result of different vertical positions on the intertidal shore with tide (Schonbeck & Norton 1981, Sideman & Mathieson 1983, Scott *et al.* 2001). In addition, shores with particularly intricate geomorphologies may have complex wave patterns, resulting in inaccurate cartographic measurements. Finally, on tideless shores, wave action decreases with depth at any given site and needs to be taken into consideration in morphological studies (Kalvas & Kautsky 1993). Cartographic methods were developed to describe wave action under ideal conditions. With increasing fetch, conditions becomes less ideal, and error with cartographic measurements increases.

In comparative studies in which changes in environmental factors, such as salinity, are connected to changes in morphology, cartographic methods have an important role. Cartographic methods are useful for describing algal morphology in enclosed sea areas (Ruuskanen *et al.* 1999), such as the Baltic Sea, in conditions where geographical dimensions (fetch) are relatively small, and in areas where tidal activity is low. To exclude the effect of wave action on morphology between two shores, the shores must fall into the same numerical cartographic category (Ruuskanen & Bäck 1999a, 1999b). The question then arises that if numerical values of the shores are the same are wave forces also identical?

The aim of this study was to describe and compare the morphologies and blade/holdfast complexes of *Fucus gardneri* (ex *F. distichus*), of two Californian intertidal shores with equal cartographic wave exposure values but assumed to be subjected to different wave forces due to off-shore meteorological conditions. In addition the relationship between the numerical value of wave exposure and morphological response of algae to wave action was examined.

Material and methods

Study sites and sampling

Fucus gardneri samples were collected during low tide from two flat rocky shores on the coast of California in July 1999 (Fig. 1). The northern shore, Bodega Bay, is located about 100 kilometres north, and the southern shore, Scott Creek, 77 kilometres south of San Francisco. These shores were chosen because of their vicinity to the off-shore weather stations and because environmental factors were equal. Estimated subjectively, both shores have the same bottom slope, topography, distance to tide/tidal range and percentage of alga cover. From each shore, two sites (SCI and SCII; BBI and BBII), located about 500 meters apart, were chosen. From each site, 15 holdfasts plus all fronds growing in it were collected randomly at low tide. From each holdfast, one mature frond was randomly chosen for morphological analysis. To avoid ontogenetic differentiation and differences caused by age structure, only fronds bearing mature receptacles were accepted (Knight & Parke 1951, Schonbeck & Norton 1981, Bäck 1993).

Shore exposure

Shore wave exposure was measured using the Baardseth (1970) index. To calculate the Baardseth index, the centre of a transparent circular disc with a radius of 7.5 kilometres was placed on a nautical chart. The circle was divided into 40 equal sectors, each with an angle of 9°. A sector was ignored if it contained skerries, islands or parts of the mainland shore. The Baardseth index is the sum of free sectors.

The Baardseth index of the studied shores was 19, and both shores faced the open sea, thus receiving full wave force (Fig. 1B and C).

Wave height data for the shores were derived from weather station (weather buoy) data of the National Data Buoy Centre, NOAA. The wave height for Bodega Bay was derived at the Bodega Bay weather buoy, and for Scott Creek at the Half Moon Bay weather buoy (Fig. 1). The measurement period was from June 1998 to May 1999. This period is assumed to have the most significant effect on morphology during the algal growth period (before collecting). At Bodega Bay, the yearly average significant wave height was 2.47 metres, and at Scott Creek 2.19 metres. However, the total energy in a wave is proportional to the square of the wave height, i.e., doubling the wave height increases its energy by a factor of four (Gross 1977), a difference in wave energy comes more evident between Bodega Bay and Scott Creek.

Analysis

For morphological analysis, the following six vegetative characteristics known to be responsive to wave exposure were measured from each plant (Schonbeck & Norton 1981, Rice *et al*. 1985):

1. Frond length (mm), from the base of the holdfast to the tip of the most distal apex (longest part of the frond).
2. Frond width (mm) (average of five), at a point midway between the youngest and the next youngest dichotomy.
3. Number of dichotomies, from the longest part of the frond.
4. Distance of dichotomies (mm), average of all distances from the base to the top along the longest part of the frond.
5. Stipe width (mm), at the middle of the stipe.
6. Stipe length (mm), from the base to the oldest dichotomy.

To compare characteristics of the algae on the two shores and reveal any co-effects between them, data were analysed with discriminant analysis (Bäck 1993, Kalvas & Kautsky 1998, Scott *et al*. 2001).

For blade/holdfast complexes, the number of fronds growing in the same holdfast was tested with the *t*-test.

Results

The Scott Creek (SCI and SCII) and Bodega Bay (BBI and BBII) sampling sites were combined for comparison of southern and northern populations (Table 1). Most measurements of *F. gardneri*, including frond length, the number of dichotomies and the distance of dichotomies were smaller at Bodega Bay (northern, more exposed shore) than at Scott Creek (southern, less exposed shore). Frond width, stipe width and stipe length did not differ between the north and the south.

The distribution of the plants according to the co-effect of measured morphological characteristics on the first two discriminant functions (scores 1 and 2) is shown in Fig. 2. The first axis (score 1) explains 86% and the second axis (score 2) 11% of the morphological variation. Number of dichotomies and frond length give the highest loading on the first axis, and stipe width and distance of dichotomies yield the highest loading on the second axis. In general, plants located on the right-hand side of Fig. 2 have fewer dichotomies and their fronds are narrower and shorter than plants located on the left side.

The Scott Creek sampling points (SCI and SCII) are situated on the left-hand side and the two from Bodega Bay (BBI and BBII) on the right-hand side of the diagram. An intra-shore but not inter-shore overlap was found for the Scott Creek and Bodega Bay sampling points (Fig. 2).

In Jackknife classification, 40%–47% of individual plants from each sampling point could be classified in their own groups (Table 2). The remaining plants were classified mainly under a neighbouring group, located on the same shore.

Fucus gardneri holdfasts consisted of an average of 2.5 fronds per holdfast at Scott Creek (less exposed) and 3.12 fronds per holdfast at Bodega Bay (more exposed) (Fig. 3). There is no statistical difference between Scott Creek and Bodega Bay.

Discussion

This section of the Californian coast lacks islands and other geomorphological complications so that the shoreline receives the full wave force. Rougher meteorological conditions in the northern Pacific Ocean generate a stronger wave force on the northern than the southern coast of California. Whether large-scale meteorological changes occur within a geographical distance of approximately 200 kilometres is uncertain. However, according to the weather buoy data, offshore conditions in Bodega Bay and Scott Creek do differ in terms of significant wave height. In addition, although the theoretical difference of 21% in wave force between Bodega Bay and Scott Creek may not seem large, Baltic *F. vesiculosus* and Atlantic *F. spiralis* are sensitive to changes in wave force, and even a small change in fetch is sufficient to induce morphological variation (Ruuskanen *et al.* 1999, Scott *et al.* 2001). According to nautical maps, the seabed consists mainly of sand and both shores have a similar bottom slope; however, in the distance from the buoy to the shore, waves might change in different ways due to local geomorphological conditions.

Comparing averages of wave height does not necessarily yield a realistic figure of wave

Table 1. Comparison of mean values (± SEM) of characteristics for Scott Creek and Bodega Bay populations (intra-shore sampling sites are combined).

Characteristics	Scott Creek (less exposed) *n* = 30	Bodega Bay (more exposed) *n* = 30
Frond length (mm)	189.6 (9.67)	149.8 (6.8)
Frond width (mm)	9.9 (0.2)	9.2 (0.3)
Number of dichotomies	8.2 (0.4)	5.4 (0.2)
Distance of dichotomies (mm)	16.7 (0.4)	14.7 (0.4)
Stipe width (mm)	3.6 (0.1)	3.5 (0.1)
Stipe length (mm)	10.1 (0.9)	9.1 (0.5)

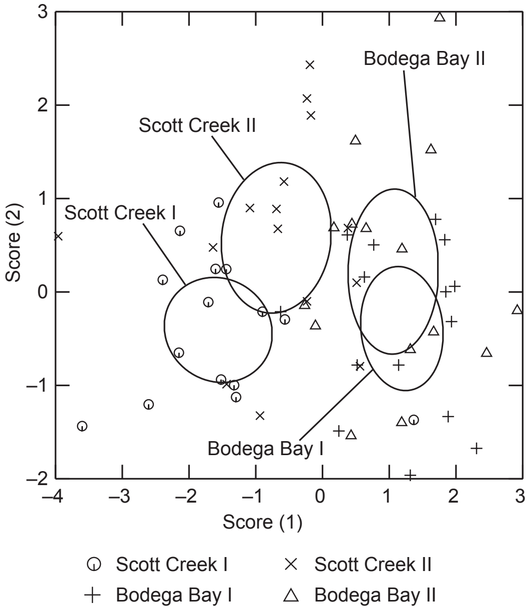

Fig. 2. *Fucus gardneri* individuals from four sampling sites (Bodega Bay I, Bodega Bay II, Scott Creek I, Scott Creek II) positioned on the first two canonical variables (scores 1 and 2; *see* explanation in text) in discriminant analysis. Confidence ellipses are included to help in interpreting the results. Ellipses are confidence intervals on the centroid that are centred around the means of the variables. The probability value was set at 0.95.

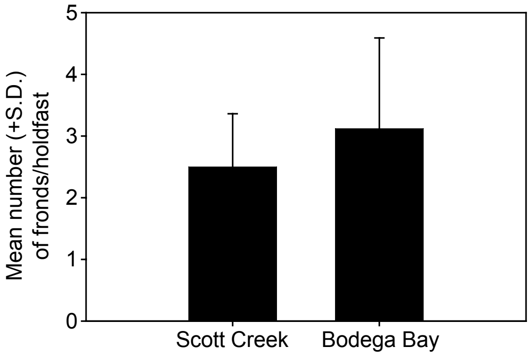

Fig. 3. Mean number (± SD) (n = 30) of *Fucus gardneri* fronds growing in the same holdfast at Bodega Bay and Scott Creek.

conditions of studied shores. According to the data, Bodega Bay has more and stronger wave peaks than Scott Creek, especially in wintertime. Phenotypic acclimation occurs during the entire lifespan of algae, and these peak periods in wave force may have an important role in this process.

Discriminant analysis and Jackknife classification show that, based on general habitus of algae, the algae of one shore can generally be distinguished from those of the other shore, but some inter-shore mixing has occured. This suggests that some larger environmental factors have an effect on plant morphologies of the two shores. However, some small-scale local factors are present as well, and their effect can be seen in the overlapping between the two sampling sites of each of the shores.

When studying individual morphological characteristics separately, inter-shore morphological variation is evident when the sampling sites are combined and only shores are compared (Table 1). A clear difference lies in the smaller frond length and decreased number of dichotomies under more exposed conditions. Schonbeck and Norton (1981) describe the morphological responses of the northeast Pacific *F. distichus* (same species?) to wave exposure on the San Juan Islands of Washington State, USA. Our findings of decreasing thallus size with increasing exposure are consistent with their results. These changes in vegetative morphological characteristics of Pacific *F. gardneri* along the wave

Table 2. Jackknife classification, using a discriminant function, of *Fucus gardneri* from the Scott Creek and Bodega Bay sampling sites (n = 15).

		Number of plants			
Group	Correct (%)	Scott Creek I	Scott Creek II	Bodega Bay I	Bodega Bay II
Scott Creek I	47	7	6	1	1
Scott Creek II	47	3	7	3	2
Bodega Bay I	40	0	1	6	8
Bodega Bay II	40	0	4	5	6
Total	43	10	18	15	17

exposure gradient correspond to changes in vegetative morphological characteristics of Atlantic and Baltic Sea *Fucus* species; at stronger wave exposure, *F. distichus*, *F. vesiculosus* and *F. spiralis* become smaller in most of the measured size characteristics (Rice *et al*. 1985, Bäck 1993, Kalvas & Kautsky 1993, 1999, Ruuskanen & Bäck 1999b, Ruuskanen *et al*. 1999, Scott *et al*. 2001).

A study unit here was the whole holdfast complex, consisting of both mature and juvenile fronds. The effect and origin of frond proliferation on algal ecology is unclear. Small juvenile fronds growing in the same holdfast might derive from settlements of neighbouring plants during previous years (Anderson *et al*. 1997), or frond proliferation may be regulated endogenously since all fronds growing in the same holdfast can be of the same sex (Bäck *et al*. 1991). Increased proliferation of *Fucus vesiculosus* seems to be connected to rougher environmental conditions such as decreasing salinity (Ruuskanen & Bäck 1999a) and increasing shore exposure (Bäck *et al*. 1991). Although cartographic methods give equal wave exposure values for the studied shores, we suggest that Bodega Bay and Scott Creek differ in terms of growth conditions. However, all *Fucus* species do not necessarily respond to wave exposure in the same way. Malm and Kautsky (1999) demonstrated that no difference was present in the number of fronds per holdfast in *F. serratus* collected along a wave exposure gradient, whereas a difference was seen in *F. vesiculosus*. More studies are needed to determine whether the number of fronds per holdfast can be used as an indicator in the same way as other morphological characteristics presented in this study, or if holdfasts are refuges for recruitment against grazing (Anderson *et al*. 1997). In conclusion, our findings support earlier observations on effects of wave exposure on morphology: with increasing wave exposure algae size decreases and frond proliferation increases.

The north–south geographical sampling distance of 200 km in our study may be insufficient to match the variation in *F. gardneri* described by Rice *et al*. (1985), who studied morphological variation of North Atlantic *F. distichus* along large-scale latitudinal and longitudinal gradients. In contrast to our results, Rice *et al*. (1985) found that frond width and length increased in a northerly direction. However, this may be an overgeneralization since their study concentrated on *F. distichus* in the North Atlantic; this trend has not been shown for *F. gardneri* in the Pacific.

We tested only one cartographic method in this study. The Baardseth method is a simple one, which is advantageous under the present field conditions and which has been used in some earlier studies as well (e.g. Kalvas & Kautsky 1998, Ruuskanen *et al*. 1999, Ruuskanen & Bäck 1999b). One fetch sector extends 7.5 km, whereas in some other methods, e.g. Håkansson's (1981) effective fetch method, a fetch must be drawn to the opposite shore, here located on the Asian continent. Some cartographic methods with adjustable fetch lines incorporating wind data, such as that described by Ekebom *et al*. (2003), may give different results, however, this type of data may not always be available from all locations in certain field conditions.

Our results demonstrate that differences in morphology between Bodega Bay and Scott Creek *F. gardneri* are probably not caused solely by wave action; other factors may be involved. Schonbeck and Norton (1981), in studying the same species and the same problem, speculated that exposed and sheltered forms might not be genetically identical. Recent molecular genetic studies have suggested that different morphs are distinct genotypes representing adaptation to the local environment rather than opposite ends of a continuum of morphological variation along such environmental gradients as the wave exposure gradient (Anderson & Scott 1998, Scott *et al*. 2001). Thus, as Kalvas and Kautsky (1998) discussed, the similarities or differences in *Fucus vesiculosus* morphology between studied sites can be caused by a combined effect of environmental and genetic factors. The low number of sites in our study makes it difficult to generalize about a possible cline in morphological variation or a mosaic system, as described by Rice *et al*. (1985). The difference between shores and sites may be random or due to variation in other factors that vary on a small to intermediate geographical scale.

If exact measurement of wave force of a shore is needed, using only cartographic methods to describe wave force is insufficient. These methods provide values based on the geographical distance that wind or wave can travel and develop before it reaches the shore. Wind speed could also be a relevant factor in describing formation of wave force under optimal conditions. However, in the present case, because waves are generated hundreds or thousands of kilometres from the Pacific coast, measuring only local wind speed will not properly describe these conditions. Thus, wave height is a more accurate parameter to describe energy of waves produced by wind elsewhere. We studied completely exposed shores and found it problematic to evaluate actual wave force affecting *F. gardneri* morphology using only the Baardseth cartographic method. However, cartographic methods with a shorter fetch, can be more appropriately applied to estimate shore exposure in areas with relatively short wave travelling distances such as the Baltic Sea.

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