

SUNLIGHT, SHADE AND TIDAL NIGHT: PHOTOADAPTATION IN *FUCUS VESICULOSUS* L.

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SARSIA



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This investigation compares two populations of *Fucus vesiculosus* L. in which the lower bathymetric limits are determined by insufficient light rather than by the presence of a superior algal competitor. In the tidal reaches of the R. Mersey (NW England), water turbidity is so severe that *Fucus* experiences darkness when covered by an incoming tide. These plants must therefore photosynthesise only when emergent and are hence exposed to full sunlight. Baltic Sea (SW Finland) *Fucus*, in contrast, is permanently submerged in an atidal environment and subject to shade conditions that increase with depth. Chlorophyll concentrations and ratios in these populations differ significantly. Significant morphological differences are also present, with Baltic thalli showing distal blade expansion and Mersey thalli proximal expansion. A transplant experiment involving Baltic thalli from different sites and depths suggested that morphological plasticity had a minor role in the observed differences. The adaptive implications are discussed.

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INTRODUCTION

There is a widely held belief that the upper limits of intertidal seaweeds are determined by their respective tolerances to emersion (physico-chemical) factors, while their lower limits are products of competition with other organisms (SOUTH & WHITTICK 1987; KIRK 1994). The supporting evidence has been examined by UNDERWOOD & DENLEY (1984) and found to be questionable; and exceptions to the rule have been reported (HAWKINS & HARTNOLL 1985). *Fucus vesiculosus* L., the subject of this investigation, is a common macrophyte of N. Atlantic shores, on which it forms a belt flanked above and below by other fucoid species. So, according to ecological theory, it is the presence of a competitively superior neighbour at its lower boundary that prevents this species realising its full zonal potential.

In the coastal waters of SW Finland no such constraint exists because *F. vesiculosus* is the only large perennial alga and, providing that suitable substrate is present, this plant will reach its maximum tolerable depth. Its limit is determined by light transmission and is hence a function of water clarity (KAUTSKY & al. 1996; KIIRIKKI 1996). The Baltic Sea is virtually atidal and the *Fucus* vegetation is therefore unusual in being restricted to the sublittoral zone. However, it is possible also to find tidal shores on which *F. vesiculosus* has no serious competitors and on which it grows to its physiological (light) limit. One such habitat is located in the estuary

of the R. Mersey, NW England, whose waters are very turbid because of suspended clay minerals and particulate organic matter (RUSSELL & al. 1998).

The purpose of this investigation was to compare the ways in which these two *Fucus* populations have adapted to their light deficient, but in other respects very different, environments.

MATERIAL AND METHODS

Populations

The main Baltic population was located on the exposed seaward side of Brännskär, a skerry in the outer archipelago zone of SW Finland (HÄLLFORS 1984). At this site, the *F. vesiculosus* forest reaches optimum development at a depth of 1.5 m; the maximum depth of continuous *Fucus* cover is at 4.0 m while 5.0 m is the lowest limit of the species. Ten-twenty whole thalli were collected by hand from each of these depths on two occasions (2 May 1997 and 12 May 1997) and returned to the laboratory in buckets of seawater. Baltic *Fucus* was collected also from the boathouse at Tvärminne Zoological Station, located about 1.4 km W. of Brännskär. These plants were all growing at a depth of 1.5 m. Water circulation at the boathouse is ensured by the action of boat propellers but otherwise this is a very sheltered habitat.

U.K. *Fucus* was sampled from a gently sloping intertidal reef at Grassendale on the N. bank of the R. Mersey (inner estuary zone). Here, the vertical distribution of *F. vesiculosus* lies entirely within the Neap Tide range, with its lower limit just above MLWNT. The estuary is about

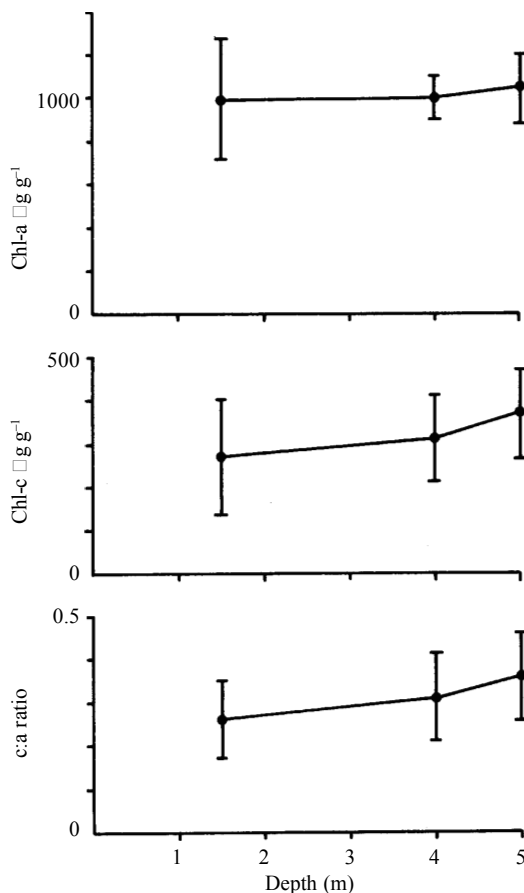


Fig. 1. Mean chlorophyll-a, mean chlorophyll-c and mean c:a ratios in *Fucus vesiculosus* at depths of 1.5 m, 4.0 m and 5.0 m in the Baltic Sea at Brännskär, SW Finland. Chlorophyll content is expressed in terms of blade tissue fresh weight. Error bars denote 2 standard errors on each side of the mean.

3.5 km wide at this point and sea conditions, though usually smooth, can be rough when wind speeds approach gale force. *Fucus* was collected at low tide and at monthly intervals from December 1996 until August 1997. Twenty equidistant plants, approximately 4 m apart, were collected in a line from the lower to the upper limits of *F. vesiculosus* and returned to the laboratory in plastic bags, where they were mixed.

Plants required for analysis were selected from every sample on the basis of least damaged blades (i.e. those flattened parts of the thallus, excluding stipe and holdfast) and fewest epiphytes.

Chlorophyll analyses

Chlorophyll analyses were carried out on discs of tissue cut with a sharpened cork borer from 4 *Fucus* blades that had been wiped clean with sterile tissues. The discs were cut from the position of maximum blade expansion, i.e. proximal to the tip and on tissues at least one year old. The discs had a mean radius of 2.16 mm and an area of

14.59 mm². Two discs were removed from the blade of each plant, usually on opposite sides of the midrib. The discs were macerated with a pestle and mortar in 1–2 cm³ cold 90 % acetone with a little sand and hydrated magnesium carbonate. The macerate was washed into a tube with more acetone – total volume 5 cm³. It was then stored in a refrigerator for approximately 20 h before centrifugation followed by spectrophotometric analysis. The method adopted was in essence that of RAMUS & al. (1997). The chlorophyll content was calculated from the equations of JEFFREY & HUMPHREY (1975).

The mean fresh weights of the discs from the three sites were as follows: Brännskär (0.0063 g); Grassendale (0.0051 g); Tvärminne boathouse (0.0041 g). These values, which express differences in blade thickness, differed significantly from one another ($p < 0.001$).

Blade morphology

Blade width was measured at intervals, usually midway between successive dichotomies, from just behind growing tips to the position at which the blade starts to narrow and merge with the stipe. Blade lengths (5) were measured at the same time.

Water clarity

Secchi disc extinction depths are measured routinely at one site (Storfjärd) close to Tvärminne Zoological Station. The clarity of R. Mersey water was also determined by this means at irregular intervals from November 1996 until October 1997. The Mersey readings were normally taken within 1 h of high tide.

Transplants

Eight stones bearing *Fucus* fronds were transferred from the boathouse at Tvärminne (depth 1.5 m) to the Brännskär site on 2 May 1997. The stones were placed at a depth of 4.0 m where water movement from wave action is minimal, as at the boathouse, but at which light is beginning to be limiting for *Fucus* growth. The stones were inspected monthly until 11 Sept. 1997 when the experiment was terminated and the plants harvested.

Growth of transplants and control *Fucus* was measured by removing from the thallus tips the amounts of new tissue produced during the course of the experiment. This rather subjective estimate was judged by eye and was based mainly upon the boundary of old (1996) *Electra* colonies on the blades. The thallus pieces were oven dried at 70 °C for 24 h and weighed.

RESULTS

Chlorophyll analyses

The chlorophyll content of the Brännskär *Fucus* from different depths is shown in Fig. 1. The results indicate small increases in chlorophyll-a and in chlorophyll-c as well as in the c:a ratios. None of these changes was statistically significant, however.

The results from the R. Mersey population are given in Fig. 2. These show no seasonal trend in either chlorophyll-a content or in that of chlorophyll-c, while the c:a

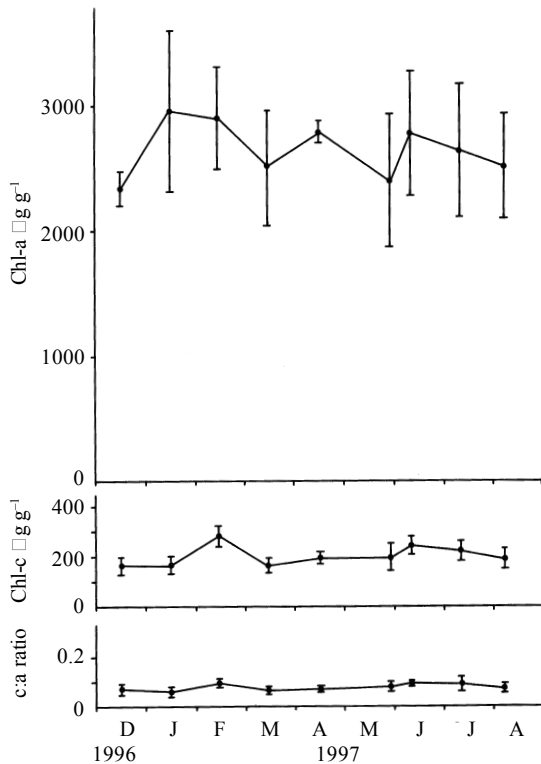


Fig. 2. Mean chlorophyll-a, mean chlorophyll-c and mean c:a ratios in *Fucus vesiculosus* from Grassendale, R. Mersey, NW England, sampled at monthly intervals from December 1996 until August 1997. Chlorophyll content is expressed in terms of blade tissue fresh weight. Error bars denote 2 standard errors on each side of the mean.

ratio remained almost constant throughout the sampling programme. A further chlorophyll analysis of Mersey *Fucus* was carried out in October 1997 (E. Butler, pers. commn). This analysis, of 7 plants, resulted in a mean chlorophyll-a value of $2313 \mu\text{g g}^{-1}$. This measurement, obtained from the proximal parts of the blades, is very similar to those shown in Fig. 2. However, the mean chlorophyll-a content of the growing tips of the same plants was only $845 \mu\text{g g}^{-1}$, significantly lower than that of the older discs ($p < 0.001$). The lower chlorophyll concentrations in the tips is evident to the naked eye from their pale olive colour.

Blade morphology

Blade widths in all *Fucus* samples are shown in Fig. 3. The widths are given at 10 % length intervals from the tip (0 %) to the point at which the blade begins to narrow as it merges with the stipe (100 %). The 1.5 m Brännskär sample (Fig. 3A) had a mean blade length of 10.9 cm; the mean length at 4.0 m (Fig. 3B) was 8.9 cm; and at 5.0 m (Fig. 3C) it was 6.2 cm. The boathouse blades (Fig. 3D) had a mean length of 22.9 cm. In spite of the obvious

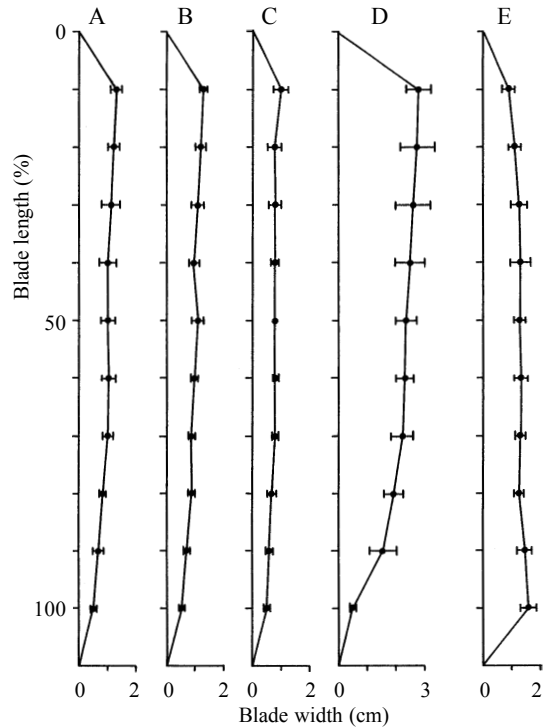


Fig. 3. Blade morphology of *Fucus vesiculosus* samples from SW Finland the Mersey estuary. Mean blade widths are shown at 10 % length intervals from the tip (0 %) to the position at which the blade begins to narrow before merging with the stipe (100 %). A. Brännskär 1.5 m. B. Brännskär 4.0 m. C. Brännskär 5.0 m. D. Tvärminne boathouse 1.5 m. E. intertidal Mersey. Error bars denote 2 standard errors on each side of the mean.

differences in length and width, all Baltic samples had a consistent morphology with blade widths in the distal half (i.e. from 10-50 %) exceeding those in the proximal half (60-100 %). The Mersey blades (mean length 24.7 cm) reversed this pattern with the distal half being narrower than the proximal half (Fig. 3E). The distribution of above-median widths in proximal and distal portions of these two populations differed significantly ($X^2 = 11.95$; $p < 0.001$).

Transplants

The need for a transplant experiment arose when the morphologies of the boathouse and Brännskär samples were compared (Fig. 3). Thus, boathouse *Fucus*, with its broad thin blades, might be expected to perform a little better at a depth of 4.0 m than the Brännskär plants, i.e. under light-limiting but equally calm conditions. However, the results proved to be negative.

At the end of the 19 week period of the experiment, the mean dry weight of new thallus tissue in the boat-

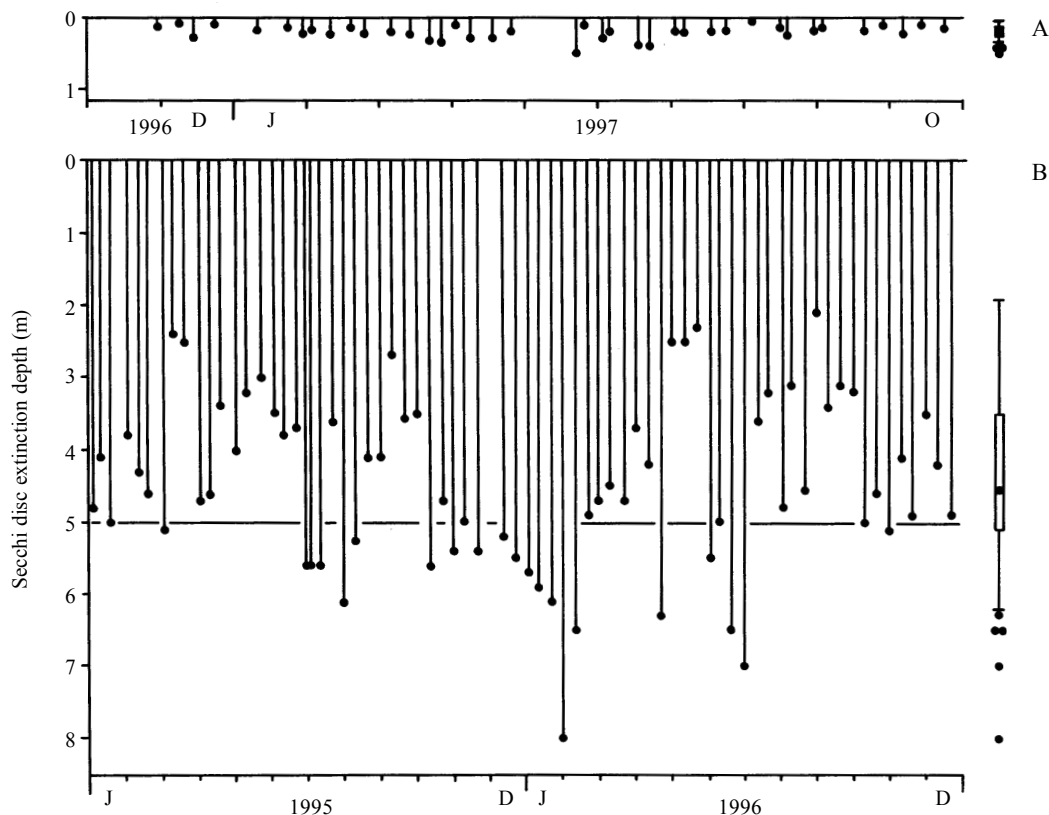


Fig. 4. Secchi disc extinction depth measurements. A. Mersey estuary water measured at high tide (± 1 h) from November 1996 until October 1997. B. Baltic Sea water measured at Storfjård, Tvärminne during 1995 and 1996. Median extinction depths plus upper and lower quartiles and interquartile distances are shown for both localities.

house control (1.5 m) plants was 0.1031 g ($n = 29$). The mean increments in the 1.5 m and 4.0 m Brännskär controls were 0.0316 g ($n = 31$) and 0.0151 g ($n = 30$) respectively, and the difference between these two means was significant ($p < 0.001$). Growth in the transplanted boathouse *Fucus* was 0.0270 g ($n = 11$), i.e. higher than the figure for the 4.0 m Brännskär controls and lower than that for the 1.5 m controls, but not significantly different from either ($p > 0.05$). It was also observed that while growth in the 4.0 m controls was 52 % poorer than in the 1.5 m controls, growth of the transplants was 74 % less than in the boathouse controls. So, despite apparent morphological advantages (broad, thin, long blades) the boathouse plants performed no better at 4.0 m at Brännskär than the native population.

The transplants underwent no appreciable morphological change. The new blade tissue produced over the course of the experiment was no narrower than the older tissues and new gas bladders were initiated, although these are infrequent or absent in the Brännskär plants.

DISCUSSION AND CONCLUSIONS

When green algae and aquatic angiosperms are subject to an increase in water depth and/or a decrease in irradiance, the classic response is to raise concentrations of chlorophyll-a and/or to increase the proportion of chlorophyll-b, but in brown algae the proportion of chlorophyll-c decreases (KIRK 1994). In the case of *F. vesiculosus*, the c:a ratio has been reported to fall when under shade conditions (RAMUS & al. 1977). In this investigation, the results from the Baltic population showed only statistically insignificant changes with depth (Fig. 1). This implies rather weak adaptability and suggests that any decrease in the transparency of Baltic coastal water is likely to result in a retreat by *Fucus* from greater depths to shallower, and this is indeed what appears to be happening over much of the Baltic coastline (KAUTSKY & al. 1986).

The concentrations of chlorophylls reported here are somewhat higher than those measured by RAVEN & SAMUELSSON (1988) in Baltic *Fucus*, using the same methods, but this discrepancy may be due simply to differ-

ences in the tissues analysed. Growing tips of the fucoid *Ascophyllum* evidently possess smaller amounts of chlorophyll than older tissues (COUSENS 1982) and comparable differences plainly occur also in Mersey *Fucus* (this study). Ontogenetic patterns of this kind are probably widespread in fucoid algae and are an innate characteristic of the fucoid thallus. The chlorophyll concentrations measured here cannot be compared easily with those reported recently in Baltic *Fucus* by BIANCHI & al. (1997), because of differences in analytical technique, but the c:a ratio recorded by them is similar to ours.

The R. Mersey population provided no evidence of any seasonal trend in either chlorophyll-a or chlorophyll-c concentrations and the c:a ratios remained virtually constant throughout the period of study (Fig. 2). However, if there is an absence of significant differences within both populations, there is one strikingly significant difference between them. Mersey *Fucus* had a chlorophyll-a concentration much higher than that in the Baltic samples ($p < 0.001$), reaching levels that have been reported as indicative of shade adaptation in this species (RAMUS & al. 1977).

The water transparency data from the two sites are given in Fig. 4. At Tvärminne, the Secchi disc extinction depths varied from 2.0 m to 8.0 m, with a median value of 4.5 m (Fig. 4B). The maximum depth for *Fucus* at this locality is 5.0 m, coinciding almost exactly with the position of the higher quartile, i.e. with the depth reached by 75 % of the Secchi disc readings. By contrast, the median extinction depth of Mersey water was 0.2 m and the higher quartile value was 0.25 m (Fig. 4A). This bears no relationship to the width of the *Fucus* zone (2–3 m) but it does approximate to the length of the *Fucus* blades. Once an incoming tide has covered these plants, they will experience the darkness of night. The timing of the onset of tidal night will depend upon the chronology of the tidal cycle but, in the Mersey estuary, HWST normally occurs at about midday. It follows therefore that the daily irradiance experienced in winter during periods of spring tides must be rather short.

The term 'shade', though widely adopted by authors for a variety of light conditions, does not seem ever to be used as a synonym for darkness. The peculiar conditions in the R. Mersey ensure that its *Fucus* does not experience shade. So, it is of some interest that exposure to brief periods of sunlight can result in similar concentrations of chlorophyll-a to those found in shade-adapted plants (RAMUS & al. 1977). However, the light conditions that obtain in the R. Mersey, and to some extent also in the Baltic, are likely to be very different from those occurring over most of the geographical range of *F. vesiculosus*. It might be unwise, therefore, to draw

any inferences on the species as a whole from the observations on these two populations.

Blade morphology in *Fucus* is, in large part, the product of its rate of axial elongation acting together with its rate of lateral expansion. In the case of Mersey *Fucus*, it is evident that lateral expansion was a continuing process with the result that the widest part of the blade lay in the older proximal portion (Fig. 3E). These measurements were made on a single (April) sample but there was no obvious change in the morphology of the population over the period of the sampling programme. Baltic blades, in contrast, were expanded distally and, since *Fucus* tissues are not known to shrink with age, it seems reasonable to conclude that when blade length increases so too does its ability to expand laterally. The process of blade widening seems not to persist in older tissues, as it does in the Mersey plants. The Baltic (May) sample coincided with the resumption of active growth in the population and the observed morphology may therefore be open to interpretation as a spring artifact. However, the first width measurements, at the 10 % point, were located in older tissues laid down at an earlier date (Fig. 3A–D) so the pattern of development shown does appear to be a consistent one.

Nevertheless, if blade shrinkage does not occur, tissue loss through grazing or wave action is possible. Grazing of Baltic *Fucus* can be severe and it has been implicated in its decline (KANGAS & al. 1982) but, as explained earlier, thalli damaged for any reason were rejected and no evidence of grazing was seen on the blades measured. Selective loss of older tissue through wave action is also unlikely. There was no change in the morphology of the Brännskär *Fucus* as wave action decreased with depth, although the blades were undoubtedly shorter as depth increased. Whatever combination of extrinsic and intrinsic factors have determined blade shape, the single obvious consequence for Baltic *Fucus* is that the broadest parts are located relatively high in the water column and hence in a position to maximise light interception. For emergent Mersey *Fucus*, the location of the position of maximum blade width is assumed to be less important.

Two-three days after the start of the transplant experiment the wind strengthened and remained high for a period of 10 days during which, on numerous occasions, its speed measured at Tvärminne exceeded 15 ms^{-1} (J. Pokki, pers. commn). Offshore at Brännskär higher wind speeds were likely. When diving resumed on 12 May 1997 the transplants were inspected and no thallus damage or plant losses could be detected. At 4.0 m, therefore, conditions seem to have been calm and they were to remain so throughout the experimental period.

When the experiment was terminated and growth measured, it was clear that the boathouse control plants

had produced more new tissue than the Brännskär plants from the same depth (1.5 m). This is in agreement with the observation by BÄCK & al. (1992) that sheltered-shore Baltic *Fucus* has a higher intrinsic rate of growth than wave exposed populations. It is evident also that the transplants, in spite of some apparently advantageous morphological features, performed no better than the Brännskär plants living naturally at 4.0 m. There was likewise no evidence of morphological plasticity in the transplants and its absence echoes the rather weak ability of Brännskär plants to increase their chlorophyll content in the field. In the Mersey population too, there was no pattern of seasonal change in chlorophyll concentrations in the mature blade and the low chlorophyll content of the thallus tips indicates ontogenetic processes rather than plasticity.

The differences in the light environments of these two unusual populations are striking, as are their chlorophyll characteristics. Their blade shapes are also significantly different. The expanded distal portions of Baltic blades must experience more light in nature than proximal parts and may therefore be more active photosynthetically but the former are also more active

in growth. So, for ontogenetic reasons, they are likely to have relatively low chlorophyll levels. It is possible that this combination of functions may make Baltic *Fucus* vulnerable to the effects of reduced water transparency. There is need for a more rigorous experimental programme of reciprocal field transplants in the Baltic Sea together with analyses of a wider range of pigments, using standard techniques throughout. It is of some importance to establish the extent to which Baltic *Fucus* may adjust its pigment content with depth and season and hence to assess its ability to meet the extra demands of a deteriorating light climate.

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Dedicated to Professor Åke Niemi, University of Helsinki, on the occasion of his retirement.

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