Decreased depth distribution of Fucus vesiculosus (Phaeophyceae) in the Western Baltic: effects of light deficiency and epibionts on growth and photosynthesis

Sven Rohde [a] , Claas Hiebenthal [a] , Martin Wahl [a] , Rolf Karez [c] & Kai Bischof [b]

[a] Leibniz-Institute of Marine Sciences , Duesternbrooker Weg 20, 24105 Kiel, Germany

[b] University of Bremen , Leobener Str. NW2, 28359 Bremen, Germany

[c] State Agency for Nature and Environment of Schleswig-Holstein , Hamburger Chaussee 25, 24220 Flintbek, Germany
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Decreased depth distribution of *Fucus vesiculosus* (Phaeophyceae) in the Western Baltic: effects of light deficiency and epibionts on growth and photosynthesis

SVEN ROHDE[1], CLAAS HIEBENTHAL[1], MARTIN WAHL[1], ROLF KAREZ[3] AND KAI BISCHOF[2]

[1]*Leibniz-Institute of Marine Sciences, Duesternbrooker Weg 20, 24105 Kiel, Germany*
[2]*University of Bremen, Leobener Str. NW2, 28359 Bremen, Germany*
[3]*State Agency for Nature and Environment of Schleswig-Holstein, Hamburger Chaussee 25, 24220 Flintbek, Germany*

For many coastal areas of the world, a decrease in abundance and depth penetration of perennial macroalgae and seagrasses has been documented and attributed to eutrophication. A surplus of nutrients impairs perennial seaweeds in at least two ways: increased phytoplankton densities reduce the depth penetration of light and in addition filamentous seaweeds and microalgae growing epiphytically shade their perennial hosts. A reduction of depth limit and total abundance has also been observed for the brown seaweed *Fucus vesiculosus* at many sites in the Baltic Sea. However, in most cases the mechanistic reason for the loss of *Fucus* has been deduced from observations rather than from experimental evidence. Here, we present results of a two-factorial (water depth/light supply and epibionts) experiment that was run in the Kiel Fjord, western Baltic, from August to October 2005. Performance of *F. vesiculosus* was recorded by growth and chlorophyll measurements, PI-curves and *in situ* measurements of the photosynthetic activity as the relative rate of electron transport (rETR). rETR and growth decreased with water depth. Chlorophyll *a* concentrations increased with reduced light intensities, but this apparently could not compensate for the light deficiency. Epibionts enhanced the negative effect of reduced light conditions on growth. According to these findings we estimated the physiological depth limit of *F. vesiculosus* in the Kiel Fjord to lie between 4 and 6 m water depth.

Key words: Baltic Sea, depth limit, epibiosis, *Fucus vesiculosus*, PAM

Introduction

In many coastal areas of the world a shift from perennial benthic vegetation towards ephemeral macroalgae has been observed (e.g. Munda, 1993; Duarte, 1995; Schories *et al.*, 1997). In the Baltic Sea this led to a decrease in abundance of the formerly predominant *Fucus* species during the second half of the last century (e.g. Vogt & Schramm, 1991; Torn *et al.*, 2006). Among other reasons such as increased sedimentation, loss of appropriate habitats due to commercial harvesting of stones or increased grazing due to over-fishing of the mesograzers' predators (Kangas *et al.*, 1982; Salemaa, 1987; Lehtinen *et al.*, 1988; Vogt & Schramm, 1991; Schaffelke *et al.*, 1995; Pedersen & Snoeijs, 2001; Eriksson & Johansson, 2003; Nilsson *et al.*, 2004; Eriksson & Johansson, 2005), nutrient enrichment seems to be the major reason for this shift (Torn *et al.*, 2006). Enhanced nutrient supply favours filamentous and thin growth forms with a high surface to volume (SA:V) ratio at the expense of perennial forms with an often thicker and more complicated morphology (Pedersen & Borum, 1996; Karez *et al.*, 2004). Microalgae feature a particularly high SA:V, and thus epiphytic and, more importantly, phytoplanktonic microalgae are especially favoured by high nutrient supply. Measures of chlorophyll *a* and phyto-proteins in the water column indicate that phytoplankton densities almost doubled between 1958 and 1975 in the Kiel fjord, southern Baltic Sea (Babenerd & Zeitzschel, 1985; Babenerd, 1986), while water transparency measured as Secchi depth decreased (Sandén & Håkansson, 1996). Higher light attenuation is assumed to be the main reason for the observed upward shift of the lower depth distribution limit for *Fucus* spp. (Kautsky *et al.*, 1986; Vogt & Schramm, 1991; Schramm & Nienhuis, 1996). As a consequence, the total area available for *Fucus* populations is reduced, which probably explains most of the considerable loss.

Correspondence to: Sven Rohde. e-mail: srohde@ifm-geomar.de

The historical and the current depth limits of *Fucus* are not uniform along the salinity gradient of the Baltic Sea (Torn *et al.* 2006). In the Kiel Fjord the depth limit of *Fucus* decreased from 10 to 2 m, while the total biomass decreased by 95% when data from 1988 and 1950 were compared (Vogt & Schramm, 1991). Recent monitoring found 3.5 m to be the limit for single thalli in the same area (Fürhaupter *et al.*, 2003). A substantial decrease in *Fucus* should affect large portions of the ecosystem since it provides food for numerous herbivores, substratum for epibionts and shelter for many associated species, plays an important role in biogeochemical cycles (e.g. Rangeley & Kramer, 1995) and provides other valuable ecosystem services (Rönnbäck *et al.*, 2007).

In addition to attenuation by phytoplankton, epibiosis may have a considerable effect on light availability to the basiphyte. All immersed surfaces inevitably become covered by inorganic, organic and organism components settling from the water body. The general phenomenon is called 'biofouling', with 'biofilm' designating the slime composed of macromolecules and microorganisms, and 'epibionts' comprising the multicellular components of the biofouling. The consequences for the fouled organism may be manifold (Wahl, 1989) and may be beneficial (e.g. associational defence, camouflage) or detrimental (e.g. weight increase, shading, competition for nutrients, co-consumption *sensu* Karez *et al.*, 2000). Additionally, since most interactions between a benthic aquatic organism and its environment pass through its outer body surface, an epibiotic layer will invariably modulate these interactions.

Both micro- and macroepiphytes may compete with their algal host for sunlight (Oswald *et al.*, 1984; Booth, 1987). At depths where light becomes limiting for a host alga, any kind of fouling may enhance energy limitation, potentially reduce the host alga's fitness and ultimately push the species distributional limit upwards. In nutrient-enriched coastal waters such as those of the Baltic Sea, filamentous macroalgae or periphytic microalgae as epiphytes on *Fucus* will be favoured (Rönnberg *et al.*, 1992). In addition, many animals (epizoans) may use *Fucus* as substratum. These may be favoured by eutrophication or not; e.g. filter feeders may benefit from enhanced plankton supply (Clausen & Riisgard, 1996).

Although the causal chain of eutrophication leading to reduced light penetration, which reduces overall photosynthetic carbon gains and ultimately results in a shallower depth distribution of *Fucus* is intuitive and generally accepted, it has rarely been confirmed experimentally. Recently, the depth distribution of *Fucus* (especially of *F. vesiculosus*) in the Baltic Sea received new attention in conjunction with the implementation of the EU Water Framework Directive (WFD, Directive 2000/60/EC of the European Parliament). The WFD requests a 'good' ecological status to be obtained by 2015 and macroalgae are a mandatory element in assessing the ecological quality of coastal waters. Thus, in the future, member states around the Baltic Sea will strive to increase the depth distribution of *F. vesiculosus* as a key macroalga with regard to numerous ecosystem services (Rönnbäck *et al.*, 2007, and references therein). The lower depth limit of *F. vesiculosus* will certainly be one of the main measures of ecological quality.

The present study aims to investigate, experimentally and *in situ*, the depth distribution limit for *F. vesiculosus* and to estimate how epibionts may further reduce its physiological and ecological potential. We tested the following hypotheses. (i) In the Kiel Fjord *F. vesiculosus* is light limited and therefore growth and photosynthesis will decrease with increasing depth. (ii) If light conditions alone are responsible for the depth distribution of *F. vesiculosus*, the physiological growth limit should be at approximately 3 to 4 m depth, the maximum depth at which the alga is currently found in the Kiel fjord. (iii) The presence of epibionts should further decrease the growth of *F. vesiculosus*. (iv) To compensate for decreasing light, *Fucus* should increase its chlorophyll *a* content with depth.

Materials and methods

Study site and experimental design

All specimens of *Fucus vesiculosus* were collected in the Kiel Fjord, western Baltic (54°22′N; 10°09′E), where *Fucus* forms dense, macroscopically almost monospecific stands on stones. We chose *Fucus* individuals of 7–10 cm length, growing on pebbles (3–5 cm in diameter) at depths of 0.2–1 m. Additional organisms on these stones and macroscopic epibionts were removed by hand leaving only one *Fucus*-individual per stone.

The experimental set-up was located at a pier in the inner Kiel Fjord (54°19.5′N; 10°09′E). Ten ropes with ground weights were lowered from the pier to a water depth of 7 m. The horizontal distance between the ropes was approx. 2 m. At depths of 1, 2, 3, 4 and 6 m PVC-gutters were fixed at the centre of the ropes. This experimental setup and the location prevented consumption by the most dominant local herbivores, the snail *Littorina littorea* and the isopod *Idotea baltica*. At each end of the gutters one pebble with an attached *Fucus* individual was fixed with cable ties, resulting in two *Fucus* individuals per gutter that represented one replicate (*n* = 10; see below). One end of each gutter was marked with an additional cable tie to allow the identification of each *Fucus* individual during

the experiment. To investigate the effect of epibionts on growth and photosynthesis of *Fucus*, one individual per pair was cleaned manually every second week, while the other was left uncleaned. The height and the structure of the pier prevented shading effects on the algae. The study was run from 14 August–13 October 2005. During that time surface water temperature is highest, varying from 15 to 18°C. Thus, respiration costs in *Fucus* are highest and may limit depth distribution.

Light conditions

To obtain information about the ambient light conditions at the different water depths, we measured the daily solar irradiation (photosynthetically active radiation, PAR) at the water surface during the course of the experiment, using a solarimeter CM 11 (Kipp & Zonen B.V., The Netherlands). Additionally, around noon of five different days we measured light intensities in water depths from 0–6 m using a Licor Li-192 underwater quantum sensor (LI-COR Bioscience, Bad Homburg, Germany) and calculated the local attenuation coefficient (k_d) as $k_d = -\ln(I_2/I_1)/d$, where I_1 and I_2 are the irradiance intensity in depths 1 and 2, respectively, and d is the layer depth. The coefficient of all days was averaged. Irradiance decrease from air into the water column due to reflections from the water surface was taken into account by subtracting 6.6% of the irradiance values (Kirk, 1994). Thus, we could estimate the total fluence of PAR and the average irradiance over the depth range from 0 to 6 m.

Algal growth, chlorophyll a concentrations and epibiont load

At the beginning and end of the experiment the length of the longest fronds of all *Fucus* individuals were measured with a ruler to the nearest mm in order to quantify growth.

To estimate chlorophyll *a* concentrations, a piece from every individual (0.4–1.5 g WW) was stored for one week in 10 ml N,N-dimethylformamide (DMF) in the dark at 7°C after the experiment (i.e. after 8 weeks of exposure to the different depths). Then, chlorophyll *a* concentrations were estimated as:

Chl *a* [g/l] = 12.7 A_{664} − 0.08 A_{630} (modified from Moran, 1982)

At the end of the experiment all epibionts were removed from a middle piece (ca. 0.1 gDW) of the fouled *Fucus*, dried in an oven (60°C) to constant weight and weighed. The *Fucus*-piece was treated in the same way and the epibiont load was estimated as Epibionts [gDW]/Alga [gDW].

The effect of epibionts on growth were analysed by an analysis of covariance (ANCOVA) with epibionts as independent factor and depth as covariate. Differences in chlorophyll *a* concentrations between different depths and epibiont load between different depths were analysed by separate one-way ANOVAs.

Photosynthesis

Photosynthetic activities of the algae during the experiment were measured *in situ* with a Diving-PAM-fluorometer (Walz GmbH, Effeltrich, Germany) by SCUBA divers. As photosynthetic characteristics, we measured the effective fluorescence yield ($\Delta F/Fm'$) and calculated the relative rate of electron transport (rETR) on day 56 of the experiment. To calculate rETR, *in situ* irradiance was measured by the quantum sensor provided with the Diving PAM, previously intercalibrated with a Licor Li-192 underwater quantum sensor (LI-COR Bioscience, Bad Homburg, Germany). The fluorescence was estimated as the average of five consecutive measurements for each individual. To reduce the variability of the integrated light sensor, we used the mean of all measured light intensities at one depth to calculate the rETRs. Differences in photosynthesis were analysed via an analysis of covariance (ANCOVA) with epibionts as independent factor and depth as covariate.

To estimate the physiological condition of the algae at the start of the experiment, 20 individuals of the collected *Fucus* were used to determine the optimum quantum yield of photosynthesis (Fv/Fm) by PAM-fluorescence measurements according to Hanelt (1998). Subsequently, we recorded a photosynthesis (rETR) vs irradiance curve (PI-curve) for each individual with eight consecutive measurements of the effective quantum yield ($\Delta F/Fm'$) at increasing irradiances (rETR = $\Delta F/Fm'$ x PPFD). The illumination series ranged from 8 to 470 µmol m^{-2}s^{-1}. To estimate acclimation of photosynthesis to the light regime at different depths, light curves were measured again at the end of the study with all remaining algae. Prior to the measurements, all *Fucus* were cleaned of macroscopic epibionts. Differences in photosynthetic performance (rETR) in PI-curves of *Fucus* individuals exposed to different depths were analysed by a two-way ANOVA (factors: illumination and depth). To assess acclimation over time we compared PI-curves recorded prior and after the experiment as interpolated with the model of Eilers & Peeters (1988). Differences between the two groups of PI-curves (before, after) were checked by comparing the following parameters and their confidence intervals: initial slope *alpha*, light saturation point (I_k) and maximum electron transport rate (rETR$_{max}$). Because one independent curve was obtained for each *Fucus* individual, each parameter was replicated 20-fold (before the experiment), or 62-fold (after the experiment).

Results

Light conditions during the experiment

Incoming radiation (PAR) was measured above the water surface and the irradiance reaching the different depths was calculated using an attenuation coefficient of $k_d = 0.43$ m^{-1}. Given this k_d-value, the 1%-depth of surface PAR was at 10.71 m for the measured period. Figure 1 shows the calculated mean irradiance and the total
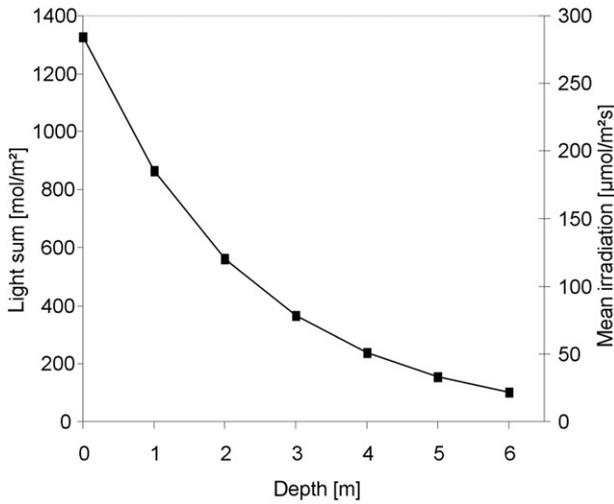
Fig. 1. Light conditions during the experiment are presented as accumulated light sum measured continuously throughout the 8 weeks of the experiment and the mean irradiance per second calculated on 24 h basis.

Fig. 2. Growth rates ($\pm$ SE) of *Fucus vesiculosus* during the experiment (black circles: fouled *Fucus*; white squares: cleaned *Fucus*; ($n = 7$–10). The lengths of the longest fronds were recorded before and after 8 weeks and the absolute increase was calculated.

fluence of PAR that reached the different depths in the course of the experiment.

Growth of Fucus vesiculosus

Growth rates were measured as increase in maximum length (Fig. 2). They decreased significantly following the depth gradient, from 3.7 cm at 1 m depth to 1.7 cm at 4 m, while at 6 m depth the least growth (0.5 cm) was measurable (ANCOVA, $F = 51.89$, $p < 0.001$). Individuals covered with epibionts grew on average 2.0 cm, compared with the growth of clean *Fucus* of 2.7 cm. Epibiont load significantly decreased the growth of *Fucus* (ANCOVA, $F = 9.07$, $p = 0.004$) by an average of 26%. At 6 m depths, epibiont load was lowest (see below). Here, *Fucus* individuals with epibionts grew better than cleaned individuals. However, this may have been an artefact. These severely light-limited individuals started to disintegrate and may have lost tissue when epibionts were removed leading to an observed weight loss in almost half of the replicates.

Chlorophyll a concentrations

Epibionts had no effect on the chlorophyll concentrations (ANOVA, $F = 0.19$, $p = 0.66$). Therefore, the data of both epibiont treatment levels were pooled for further analysis. With increasing depth from 1 to 4 m, the chlorophyll *a* concentrations in *Fucus* increased from 500 to 750 µg/g FW. At and below 4 m, chlorophyll *a* concentrations were significantly higher than at and above 2 m depth (ANOVA, $p < 0.001$, Tukey HSD posthoc, $p < 0.05$, Fig. 3).
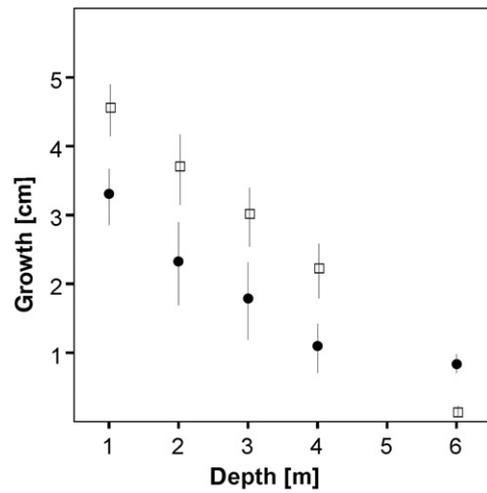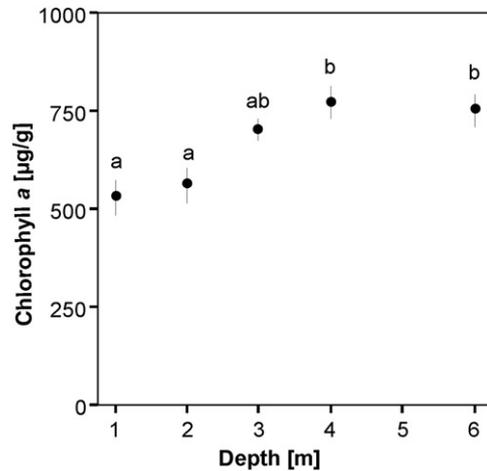

Fig. 3. Chlorophyll *a* concentrations ($\pm$SE) in *Fucus vesiculosus* after 8 weeks. Letters indicate significant differences (ANOVA, $p < 0.05$). Data from fouled and cleaned *Fucus* did not differ and were therefore combined.

Epibiont load

The epibiont load did not differ between *Fucus* individuals exposed at depths of 1, 2, 3 and 4 m (13–23 gDW epibionts/gDW *Fucus*), but was significantly lower at 6 m depth (8 gDW epibionts/gDW *Fucus*) (ANOVA, $F = 5.33$, $p = 0.02$, Fig. 4). However, the composition of the epibiotic community changed with depth. While on *Fucus* individuals from 1 m depth filamentous algae (*Enteromorpha* sp., *Ceramium* sp.) and polychaetes (*Polydora* sp.) dominated, the proportion of barnacles (*Balanus improvisus*) increased continuously with depth. *Fucus* individuals at 4 m depth were almost completely covered with barnacles, resulting in the high epibiont to *Fucus* dry weight ratios. At 6 m depth epibiont cover was clearly less
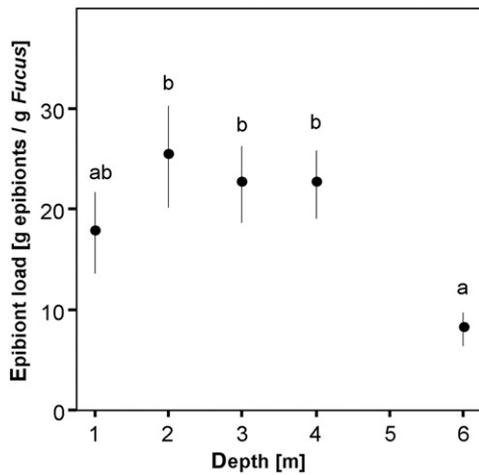
Fig. 4. Epibiont load (±SE) on *Fucus vesiculosus* after 8 weeks of exposure to experimental water depths ($n = 7$–10). Letters indicate significant differences (ANOVA, $p < 0.05$).

Fig. 5. Photosynthesis in terms of the electron transfer rate (rETR, ±SE) of *Fucus vesiculosus* (black circles: fouled *Fucus*; white squares: cleaned *Fucus*; $n = 7$–10) 8 weeks after transplantation to the different depths. Note that both treatments were placed at the same depth and are only shown juxtaposed to avoid overlap.

than at the depth from 2 to 4 m and consisted mainly of *Polydora* sp.

Photosynthesis

Measurements of the *in situ* rETR after 8 weeks did not reveal any effect of epibionts on the photosynthesis of *F. vesiculosus* (ANCOVA, $F = 0.107$, $p = 0.74$, Fig. 5). Along the gradient of decreasing *in situ* irradiance at increasing depths, photosynthetic electron transport decreased from 115 to 15 relative units.

PI-curves recorded before and after the experiment did not indicate any acclimation of photosynthetic performance to the progressively reduced light regime at increasing depths (ANOVA, $F = 2.05$, $p = 0.08$, Fig. 6a, b). Such an adaptation would have been indicated by an increase in the initial slope *alpha*, a reduction in the light saturation point (I_k) and maximum electron transport rate (rETR$_{max}$). Interpolation with the model of Eilers & Peeters (1988) revealed a rETR$_{max}$ of 85.9 ± 3.1 CI before and 81.8 ± 9.3 CI after the experiment. Mean *alpha* remained practically unchanged (0.65 ± 0.07 CI before and 0.64 ± 0.04 CI after the experiment) and I_k decreased only slightly from $135.0 \, \mu mol \, m^{-2} s^{-1} \pm 9.7$ CI to $128.0 \, \mu mol \, m^{-2} s^{-1} \pm 3.9$ CI. Thus, there were no significant differences in PI-parameters recorded before and after the experiment (Fig. 6a, b).

Discussion

Results presented here shed light on the physiological basis for upward-shifts in the lower distributional limit of *Fucus vesiculosus* in the Kiel Fjord. Photosynthesis and growth decreased with
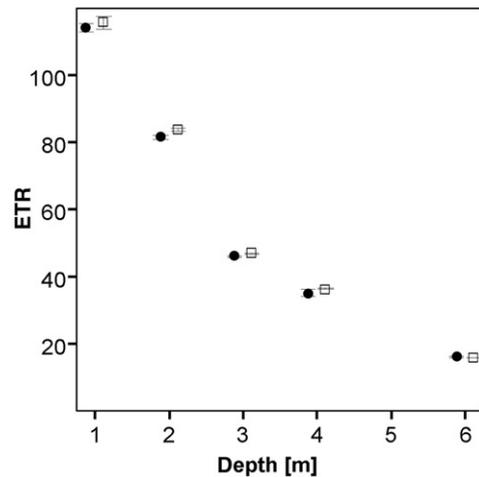

Fig. 6. PI-curves measured prior to (*a*) and after (*b*, ±SE) exposure to experimental different depths (1–6 m).

decreasing light intensity to the extent that at 6 m depth growth was reduced to less than 1 mm per week. Since such growth rates are presumably too low to compensate for physical damage or consumption, the lower physiologically determined distribution limit of *F. vesiculosus* in the western Baltic seems to be situated between 4 and 6 m depth. We found no effect of epibionts on the photosynthetic rate, but fouled *Fucus* individuals grew significantly slower than unfouled organisms. The PI-curves measured after the experiment with transplanted algae revealed no differences in

acclimation to different depths. Also comparisons of PI-curves measured before and after the experiment indicated only slightly lower rETRs at low-light intensities after the experiment compared with the initial values. However, in response to reduced light availability along the depth gradient, the algae increased cellular chlorophyll *a* concentrations. Epibiont mass was lower at 6 m depth compared with the intermediate depths of 2–4 m.

Differences in light availability only resulted in minor changes in average light use characteristics of the experimental individuals. Thus, I_k values at about 130 $\mu mol\,m^{-2}\,s^{-1}$ were remarkably stable over time and depth in our study. Middelboe *et al.* (2006) found that even in the course of one year I_k values in *F. vesiculosus* were only responding weakly to changes in light availability. In a year round field study conducted at the shoreline of Zealand (Denmark, Baltic Sea) at 1 m water depth, maximal variation in I_k values of *F. vesiculosus* was about approx. 40 $\mu mol\,m^{-2}\,s^{-1}$ (range between approx. 100 and 140 $\mu mol\,m^{-2}\,s^{-1}$), despite strong variation in irradiance and temperature in the course of the seasons. In contrast, large seasonal variation in light compensation points was observed by Middelboe *et al.* (2006), i.e. from maximal values of 35 $\mu mol\,m^{-2}\,s^{-1}$ in summer (June–August) down to 8 $\mu mol\,m^{-2}\,s^{-1}$ in February. The plasticity to adjust compensation points to seasonal variation in light availability (e.g. by reducing respiration rates) allows positive net carbon gains over a wide range of radiation conditions, either in the course of the year (Middelboe *et al.*, 2006) or presumably also along the depth gradient (our study).

In our study no data on respiration and, thus, light compensation could be collected. During winter, surface water temperature in the Kiel Fjord typically drops down to approx. 3°C and in the course of our study a maximum temperature of 18°C was recorded. As respiration is highly temperature dependent, at least a transient shortage in energy supply may be likely for deep-water algae in the summer months, when *Fucus* may exhibit high respiration rates, and thus, increased compensation levels for photosynthesis. As indicated in Fig. 1, specimens kept at 6 m water depth were exposed to a mean irradiance of about 20 $\mu mol\,m^{-2}\,s^{-1}$, and, thus, below summer values for light compensation of 35 $\mu mol\,m^{-2}\,s^{-1}$ reported for *Fucus* from Zealand (Middelboe *et al.*, 2006).

In *F. vesiculosus* from the Gulf of Finland, summer values of light compensation points were determined at 25 $\mu mol\,m^{-2}\,s^{-1}$ and light saturation of photosynthesis was recorded at 300 $\mu mol\,m^{-2}\,s^{-1}$ (Bäck & Ruuskanen, 2000). Based on data on photosynthetic performance and light attenuation the authors determined the depth for optimum growth of *F. vesiculosus* to be at <3 m. At depths greater than 5 m light quantity was found to be insufficient to support growth. Due to the limitation of the PAM fluorescence method no information on compensation points could be deduced from our experiment.

Irradiances just above the compensation point might be sufficient to maintain the integrity and functionality of the photosynthetic apparatus even during long periods of light limitation at the expense of growth. Even under exposure to irradiances below the compensation point, internal energy reserves (e.g. mannitol, Lehvo *et al.*, 2001) might be used to compensate temporarily for variation in light availability. However, this strategy only allows survival of algae for a limited period of time under reduced light conditions. This process enables *F. vesiculosus* to survive below ice cover in the Gulf of Finland for several months (Lehvo *et al.*, 2001). Thus, the duration of our experiment (8 weeks) might be too short to observe substantial changes in photosynthetic parameters by PAM fluorescence, as only information on photosystem II functionality and not on variation in light compensation can be provided by this technique. Future transplantation experiments should include measurements of changes in respiration rates and thus compensation points.

Due to the large differences in light climate along the depth gradient and, thus, for *in situ* photosynthetic performance (Fig. 5), growth rates were strongly diminished. Epibiont load was shown to contribute to the reduction in growth rates. Several causes may be responsible for these effects, either singly or in combination (reviewed in Wahl 1997). Most organisms reflect or absorb light to some extent and, thus, reduce the amount of light reaching the substratum they grow on – *Fucus* in this case. Additionally, the access of *Fucus* to nutrients may be modified in three ways: (i) the thallus portion serving as attachment area is unavailable for nutrient uptake, (ii) epibionts tend to increase the boundary layer and, thus, hinder the exchange of water at the thallus surface, and (iii) epiphytes may compete with the algal basiphyte for nutrients while epizoans may excrete nutrients benefiting the host alga. Taken together, the nutrient-reducing effects seem to dominate. The effect of epibiosis depends on the species comprising the epibiotic community and on the degree of fouling. Epibiont mass was lowest at 6 m depth, relatively high at intermediate depths of 2–4 m and slightly lower again at 1 m depth. However, it is not always possible to extrapolate from epibiont mass to percent cover or the shading effect. Regular observations revealed that the fouling community changed along the depth gradient. While at 1 m depth ephemeral algal

species (*Ceramium* sp., *Enteromorpha* sp.) dominated, barnacles constituted an increasing part of the fouling community from 2 to 4 m depths. Increasing proportions of barnacles lead to increasing load ratios due to the heavy calcareous shells and percent cover (which was not measured) by epibionts may be more equally distributed between depths than suggested by dry weight. However, visual impression suggested that at 6 m depth, percent cover was lower than in all other depths. The fact that only at this greatest depth the effect of epibiosis on growth was null or even positive may have several reasons. Either shading no longer had an effect because even un-fouled algae were light-limited or at that depth nutrients were so plentiful that even the reduced water exchange at the thallus surface caused by epibionts did not entail nutrient starvation.

If growth is an adequate proxy for algal fitness, then the stress (e.g. by light limitation) exerted by epibionts at the density and composition found here is equivalent to a downward shift of 2 m depth. Indeed, at all depths between 1 and 4 m, the growth rates of fouled *Fucus* were equivalent to the growth rates of epibiont-free *Fucus* situated 2 m deeper (Fig. 2). The most probable effect of epibionts on growth was shading, because physiologically different epibiont species (e.g. autotrophic and heterotrophic epibionts) had similar impacts on growth. Consequently, if the alga does not control fouling at its surface, the stress of diminishing light with increasing depth is enhanced through shading by epibionts provoking a further upward shift in the distribution of *Fucus*.

The physiological depth limit of *F. vesiculosus* suggested by our study lies between 4 and 6 m. However, today in the Kiel Fjord the actual depth limit seems to be at approximately 3.5 m with only single plants are found at that depth the main *Fucus* belt normally not found below 2 m (Fürhaupter *et al.*, 2003 pers. obs.). The absence of *Fucus* between its physiological depth limit and the observed depth limit may partly be explained by the additive light reduction effect caused by epibionts. Occasionally, single plants can be found considerably deeper (Dirk Schories, pers. comm. and monitoring programmes in northern Germany), but it is unclear if these are local effects of enhanced light penetration.

Fucus depth limit thus seems to be a suitable metric for the assessment of ecological quality for the WFD, since its reduction seems to indicate the current high levels of eutrophication. However, our study emphasizes that growth at a certain depth may be further reduced by epibionts and that it is not only epiphytes, which may also be directly connected to high nutrient levels (e.g.

Karez *et al.*, 2004), but also or mainly animals whose indicative value for water quality is unclear. An additional important factor, not surveyed in our study, is salinity, which shows a strong gradient along the shores of the Baltic Sea and to which the deeper depth limits in the inner Baltic Sea (the 'downward process' after Waern 1952) is related. If depth limit is used to assess water quality, it is crucial to understand better the influence of these (and more) factors on local *Fucus* depth limits in the Baltic Sea, and thus more experimental rather than observational evidence along gradients of light and salinity is needed.

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