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# Influence of salinity, temperature, dissolved inorganic carbon and nutrient concentration on the photosynthesis and growth of *Fucus vesiculosus* from the Baltic and Irish Seas

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*Fucus vesiculosus* from the northern Baltic Sea (5 psu) and from the Irish Sea (35 psu) were cultivated at different temperatures, salinities and dissolved inorganic carbon (DIC) concentrations with the addition of different nutrient concentrations. The influence of these abiotic factors was assessed by measuring photosynthesis as electron transport rate (ETR) and growth as relative growth rate (RGR). The maximal ETR and the RGR of the Irish Sea plants in their natural seawater (50.8  $\mu\text{mol electrons m}^{-2} \text{s}^{-1}$ ; 0.024  $\text{g g}^{-1} \text{day}^{-1}$ ) were significantly higher than those of the Baltic plants in their natural seawater (21.9  $\mu\text{mol electrons m}^{-2} \text{s}^{-1}$ ; 0.007  $\text{g g}^{-1} \text{day}^{-1}$ ). When Baltic *F. vesiculosus* was cultivated at a DIC concentration similar to that of the Irish Sea, the ETR as well as RGR increased, but never equalled the rates of the marine *F. vesiculosus* from the Irish Sea. Cultivation at different salinities showed that *F. vesiculosus* from the Baltic has a higher ETR<sub>max</sub> and RGR at low salinities (5–10 psu) than *F. vesiculosus* from the Irish Sea, whose ETR and RGR decreased sharply in salinities below 20 psu. Plants from both sites grown at high nutrient concentrations, however, performed better at low salinities than those grown under low nutrient conditions. Salinity had the greatest impact on differences in ETR and RGR between the two populations, followed by differences in DIC and nutrient concentrations. There was a highly significant correlation between ETR<sub>max</sub> and RGR in plants from both sites and across the full range of culture conditions, indicating that the same amount of energy from photosynthesis is used for growth in both varieties of the species at different salinities. The photosynthesis of *F. vesiculosus* in the northern Baltic is close to the minimum demand for growth, which may account for their small size. The temperature optimum for *F. vesiculosus* from the Baltic was 4–10°C, while that for *F. vesiculosus* from the Irish Sea was 15–20°C. The photosynthesis of Irish Sea plants was less strongly affected by exposure to high irradiances than that of plants from the Baltic.

**Key words:** Baltic Sea, dissolved inorganic carbon, electron transport rate, *Fucus vesiculosus*, growth, high irradiance, Irish Sea, nutrients, photosynthesis, salinity, temperature

## Introduction

*Fucus vesiculosus* is a common intertidal brown seaweed on the rocky shores of the North Atlantic (van den Hoek *et al.*, 1995). On the European shores *F. vesiculosus* occurs from Northern Russia to Morocco (Powell, 1963), but it is also one of the few perennial marine macroalgae that have colonized the Baltic Sea (Ignatius, 1981). Bergström *et al.* (2005) have recently suggested that a dwarf morphotype of *F. vesiculosus*, with a shorter thallus, thinner and more richly branched fronds, which grows in mixed populations with *F. vesiculosus* in the northern Baltic, should be recognized as a new species, *Fucus radicans*. The Baltic is a

young sea, and most organisms are believed to have entered the area within the last 8,000 years (Snøeijls, 1999). The species diversity in the area is low, mainly due to the young age of the Baltic Sea and the low salinity of the water, which decreases from approximately 20 psu in the southwest, at its entrance from the Skagerrak, to 1 psu in the north (Rönnerberg & Bonsdorff, 2004). The lowered salinity is caused by the high inflow of fresh water from many rivers, especially in the north, and the weak exchange of saltwater with the Atlantic (Omstedt & Axell, 2003). The geographical distribution of *F. vesiculosus* in the Baltic appears to be limited by salinity (Russell, 1988), and plants can be found from the southern Baltic Sea to the Quark (63°50'N) in the Gulf of Bothnia at salinities down to 4 psu (Kautsky, 1992;

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Raven & Samuelsson, 1988) and in the Gulf of Finland down to 3–6 psu (Bäck & Ruuskanen, 2000). Whilst the most obvious difference between the Baltic and the Atlantic is salinity, this is correlated with other major environmental variables. For example, the concentration of dissolved inorganic carbon (DIC, i.e.  $\text{CO}_2 + \text{HCO}_3^- + \text{CO}_3^{2-}$ ) in fully marine waters (approximately  $2.0 \text{ mol m}^{-3}$ ; Surif & Raven, 1989) is substantially higher than in brackish waters like the Baltic Sea (approximately  $1.0 \text{ mol m}^{-3}$ ; Raven & Samuelsson, 1988). In contrast, the nutrient concentration in the Baltic Sea has increased several-fold during the last century, which has resulted in an increase in pelagic primary production by 30–70% (Elmgren, 1989) but also other significant ecological effects, such as the decrease in the depth limit of *F. vesiculosus* (e.g. Kangas *et al.*, 1985; Eriksson *et al.*, 1998). The nutrient concentrations in the Irish Sea are generally not elevated and the present anthropogenic nutrient input is not thought to have caused eutrophication in the coastal and offshore waters of the Irish Sea (McGovern *et al.*, 2002). Eutrophication in the Gulf of Bothnia is not as severe as in the central Baltic Sea (Swedish Environmental Protection Agency, 2001). The sea water temperature in the Baltic shows large variations between summer and winter, while the temperature range in Atlantic water is less pronounced. During the summer the surface water temperatures are similar in the Irish Sea and the Baltic Sea (approximately  $20^\circ\text{C}$ ), but during the winter the temperature in the northern Baltic might drop below zero due to ice (Andersson *et al.*, 1992; Swedish Environmental Protection Agency, 2001).

Tides are almost absent in the Baltic Sea with only small and irregular water level changes of up to 0.5 m from the mean water level, which are related to meteorological conditions (Ignatius *et al.*, 1981). Consequently, *F. vesiculosus* grows permanently submerged in the Baltic and experiences relatively stable abiotic conditions. In the Atlantic, *F. vesiculosus* grows in the intertidal zone and is exposed to regular variations in abiotic factors (e.g. salinity, temperature, nutrient concentration, carbon concentration and light exposure) during the tidal cycle (Dring & Brown, 1982).

These differences between the Baltic and the Irish Sea are likely to affect the physiology of *F. vesiculosus* in several ways. The aim of the present study was to examine the ability of *F. vesiculosus* from the Baltic and the Irish Seas to grow and photosynthesize in different conditions. The environmental conditions used in the experiments covered the range of temperatures, salinities, nutrient and DIC concentrations

experienced by plants in the two seas. In addition, the tolerance to high irradiance (photosynthetically active radiation, 400–700 nm, PAR) was studied for both populations. The main questions to be answered were: (i) Are photosynthesis and growth rates different for Baltic and marine *F. vesiculosus*? (ii) If so, which of the abiotic factors contribute most to the difference in photosynthesis and growth rate? (iii) Is the optimal temperature for photosynthesis different for the Baltic and the Irish Sea plants? (iv) Are the tolerances to high irradiance of PAR different for Baltic and Irish Sea plants?

## Material and methods

Experiments were carried out in February 2004. *Fucus vesiculosus* was collected in the middle of the intertidal zone in the Irish Sea (Portaferry, Northern Ireland;  $54^\circ 26' \text{N}$ ,  $05^\circ 26' \text{W}$ ) at a salinity of 35 psu, and from a depth of 1 m in the non-tidal Gulf of Bothnia, northern Baltic (Åstön, Sweden;  $62^\circ 24' \text{N}$ ,  $17^\circ 45' \text{E}$ ) at a salinity of 5 psu. The water temperatures measured at collection of the algae were  $5^\circ\text{C}$  in the Baltic and  $8^\circ\text{C}$  in the Irish Sea. The Baltic plants were transported moist in polythene bags inside an insulated container to the laboratory in Northern Ireland, where they were kept for recovery for 3 days at  $8^\circ\text{C}$  and  $50 \mu\text{mol m}^{-2} \text{s}^{-1}$  (10:14-h light–dark cycle), with daily measurements of the maximal quantum yield of electron transport through photosystem II ( $F_v/F_m$ ). Only plants that regained their initial  $F_v/F_m$  were used in the following experiments.

### Photosynthesis:irradiance (P:E) curves

Photosynthesis was estimated from chlorophyll fluorescence measurements using a pulse amplitude modulated fluorometer (Diving PAM, Walz, Effeltrich, Germany). The absolute electron transport rate (Abs ETR) was calculated as:

$$\text{Abs ETR} = \text{PAR} * \text{AF} * 0.5 * \Delta F/F'_m$$

AF (the absorption factor) was measured as the fraction of incident PAR absorbed by the thalli (plant tips,  $n=10$ ). Irradiance from the halogen light source of the diving-PAM was measured using the PAM's quantum sensor under water and compared to values obtained after the light sensor had been covered with an algal thallus. The reflection and absorption by non-photosynthetic pigments have earlier been found to be negligible while measuring under water (Beer *et al.*, 2000; Beer & Axelsson, 2004). The initial AF obtained was 0.74 for *F. vesiculosus* from the Baltic and 0.85 for *F. vesiculosus* from the Irish Sea. Following Beer *et al.* (2000), PAR was multiplied by 0.5 to allow for equal involvement of the two photosystems.  $\Delta F/F'_m$  is the effective quantum yield measured in light. After an initial dark adaptation of 10 min, the irradiance was increased stepwise from 20 to  $600 \mu\text{mol m}^{-2} \text{s}^{-1}$  with 5 min at each irradiance and 5 min darkness between

irradiance steps. The temperature was kept at 10°C during the measurements with a temperature-controlled water jacket around the sample (volume 10 ml). P:E-curves were measured on thallus tips ( $n=10$ ) to determine the saturating irradiance for plants from both populations. This irradiance was later used for the photosynthetic measurements in the salinity/nutrients/carbon experiment (described below).

### Optimal temperature

The effects of different temperatures on the photosynthesis of *F. vesiculosus* from the Baltic and the Irish Sea were examined by cultivating 10 thallus tips, each with a fresh weight (FW) of about 10 g, in their natural seawater at different temperatures (0, 4, 10, 15, 20 or 25°C) for a period of 1 week at  $100 \mu\text{mol m}^{-2} \text{s}^{-1}$  under a 10:14-h light–dark cycle. The water was changed every second day. Photosynthesis: irradiance curves were measured as described above. Measurements were performed initially and after 1 week of cultivation at the different temperatures.

### Salinity, carbon and nutrients

Artificial seawater (Instant Ocean Sea salt, Eco-systems Inc.) was used to obtain different salinities. The controls were kept in their natural seawaters. The artificial water did not contain any nutrients, which were added separately. Samples of the artificial seawater as well as the natural seawaters were deep frozen and sent for analysis of ion and nutrient contents, which was performed by LMI AB, Helsingborg, Sweden. The composition of the media is shown in Table 1.

In comparable studies of different salinity levels, it is quite common to dilute natural seawater with distilled water to obtain lower salinities and to evaporate seawater to obtain higher salinities. The problem with this approach is that the content of DIC and nutrients changes with dilution or evaporation, and that is why artificial water was used in this study. Vegetative tips (5 g fresh weight, FW,  $n=10$ ) from healthy looking plants of *F. vesiculosus* from the Baltic and the Irish Sea

were tied with strings to the bottom of aquaria, so that the plants floated at a water depth of approximately 30 cm. They were kept initially in seawater from their natural site under outdoor conditions with aeration for 24 h before onset of the experiment. Natural conditions of light (maximum irradiance  $500 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) and temperature (8–10°C) were used during cultivation and experiments. After 24 h the tips were blotted, weighed (to obtain initial FW) and transferred to culture media of different salinities (5, 10, 20, 35 or 45 psu), with two different nutrient levels (high or low concentration) and two different carbon concentrations (high or low concentration).

Nutrients were added from stock solutions of  $\text{NaH}_2\text{PO}_4$ ,  $\text{NH}_4\text{Cl}$  and  $\text{NaNO}_3$  to obtain final concentrations of  $12 \mu\text{mol NO}_3^- \text{l}^{-1}$ ,  $0.75 \mu\text{mol PO}_4^{3-} \text{l}^{-1}$  and  $0.2 \mu\text{mol NH}_4^+ \text{l}^{-1}$  ('high') or  $3 \mu\text{mol NO}_3^- \text{l}^{-1}$ ,  $0.185 \mu\text{mol PO}_4^{3-} \text{l}^{-1}$  and  $0.05 \mu\text{mol NH}_4^+ \text{l}^{-1}$  ('low'). At the 'high' concentrations used, both  $\text{NO}_3$  and  $\text{PO}_4$  were present in higher concentrations than normally found in the Gulf of Bothnia and the Irish Sea (SMHI, 2005; DEFRA, 2005). These concentrations of  $\text{NO}_3$  were higher than those found in the Baltic Sea proper (where eutrophication is a problem), but the  $\text{PO}_4$  concentration was equal to that in the Baltic Sea proper (SMHI, 2005). At the 'low' concentrations used, all three nutrients were lower than the concentrations in the Gulf of Bothnia and the Irish Sea.

Bicarbonate ( $\text{NaHCO}_3$ ) was added to obtain a low DIC concentration of  $1.0 \text{ mol m}^{-3}$  (similar to that found in the Baltic) or a high DIC concentration of  $2.0 \text{ mol m}^{-3}$  (similar to that found in oceanic seawater with a salinity of 35 psu). The pH was kept constant at 8.2 with Tris Biological buffer (Sigma-Aldrich Química SA, Madrid, Spain). At a natural pH of about 8, the major part of the DIC in seawater is present as bicarbonate ( $\text{HCO}_3^-$ , Stumm & Morgan, 1996). Earlier work has shown that *F. vesiculosus* is able to use  $\text{HCO}_3^-$  as a source of inorganic carbon (Surif & Raven, 1989, 1990).

Cultivation time was 5 weeks. Every culture treatment consisted of two replicate aquaria, with five replicate plants in each. No significant differences were observed

**Table 1.** The content of the major elements (B, Ca, Cl, K, Mg, Na and S) and nutrients ( $\text{NH}_4$ ,  $\text{NO}_3$  and  $\text{PO}_4$ ) in artificial seawater (ASW) of different salinities, and for natural seawater (NSW) from the Irish Sea (37.4 psu) and the Bothnian Sea (4.6 psu). The concentrations of B, Ca, Cl, K, Mg, Na and S, are expressed in  $\text{mmol l}^{-1}$ , whereas the concentrations of the  $\text{NH}_4$ ,  $\text{NO}_3$  and  $\text{PO}_4$  are expressed in  $\mu\text{mol l}^{-1}$ . The analysis was performed by LMI AB, Helsingborg, Sweden.

( $\text{mmol l}^{-1}$ )	ASW 5 psu	NSW Baltic	ASW 10 psu	ASW 20 psu	ASW 35 psu	NSW Irish Sea	ASW 45 psu
<b>B</b>	0.05	0.05	0.09	0.18	0.34	0.42	0.47
<b>Ca</b>	1.25	1.82	2.35	3.74	7.73	10.23	10.23
<b>Cl</b>	64.59	45.98	160.50	341.30	603.62	586.70	772.86
<b>K</b>	1.02	1.36	1.79	3.58	9.97	12.53	14.83
<b>Mg</b>	6.99	7.82	13.58	22.63	49.37	57.60	65.83
<b>Na</b>	73.95	65.25	147.89	317.53	478.48	478.48	652.47
<b>S</b>	2.56	4.05	4.37	9.67	22.45	27.76	34.30
 ( $\mu\text{mol l}^{-1}$ )							
<b>NH<sub>4</sub></b>	<0.005	0.12	<0.005	<0.005	<0.005	0.10	<0.05
<b>NO<sub>3</sub></b>	<0.48	4.52	<0.05	<0.05	<0.05	4.19	<0.16
<b>PO<sub>4</sub></b>	<0.02	0.32	<0.02	<0.02	<0.02	0.42	<0.02



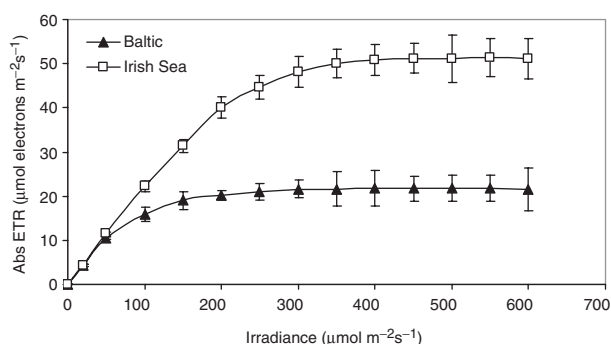
between the replicate aquaria, and the results were therefore pooled in the analysis and presentation. The water was changed every second day. Controls, with untreated natural seawater from the respective collection sites, were used. To make sure that the process of separating the tips from the rest of the plant did not affect photosynthetic performance, whole plants ( $n=5$ ) as well as tips ( $n=5$ ) were used as controls for photosynthetic measurements.

The results from the P:E-curves revealed that the photosynthesis of both populations was saturated at  $400 \mu\text{mol m}^{-2} \text{s}^{-1}$  (see Fig. 1), so that Abs ETR was measured with dark adapted algae (10 min dark adaptation) after 5 min exposure to this irradiance. These measurements were performed initially and after 5 week's cultivation in the different seawater treatments, using the initial AF and the AF measured after 5 week's exposure to the different treatments. All measurements were performed around midday (12:00–14:00 h) to avoid possible diurnal variations in photosynthesis. At the end of the experiment, new P:E-curves were measured (as described above) for the control algae. No significant differences from initial values were observed (Fig. 1).

The growth was calculated as relative growth rate (RGR), based on changes in dry weight (DW):

$$\text{RGR} = (\ln W_f - \ln W_i) / t$$

where  $W_f$  and  $W_i$  are final and initial algal DW (g), respectively, and  $t$  is time (days). Initial DW was obtained for tips that were not included in the experiment but originated from the same thalli as used in the experiments (about 5 g;  $n=5$ –10 per individual thallus) by drying to constant weight at  $80^\circ\text{C}$ . The final DW was obtained by drying the tips used in the experiment to constant weight at  $80^\circ\text{C}$ . Dry weight was measured and not FW, since the latter was unreliable because of significant water uptake by the Irish Sea plants at low salinities (see Fig. 2).



**Fig. 1.** Photosynthesis, expressed as absolute electron transport rate (Abs ETR), as a function of irradiance for *Fucus vesiculosus* from the Gulf of Bothnia (northern Baltic, 5 psu) and from the Irish Sea (35 psu). Measurements were performed with thallus tips ( $n=10$ ). Irradiance was increased stepwise from 20 to  $600 \mu\text{mol m}^{-2} \text{s}^{-1}$ , with 5 min at each irradiance and 5 min darkness in between. Temperature =  $10^\circ\text{C}$ . Error bars are 95% confidence intervals.

### Tolerance to high PAR

The tolerance of plants to high irradiance ( $1,500 \mu\text{mol m}^{-2} \text{s}^{-1}$  PAR) was measured after the 5-week culture treatment (described above). Samples were fastened in the leaf clip (used for all fluorescence measurements), placed in a beaker filled with seawater (with the same composition as used in the 5-week treatment) in a constant temperature water bath at  $10^\circ\text{C}$ . Initial values of  $F_v/F_m$  were measured after 10 min dark adaptation. The plants were exposed to high PAR for 1 h and allowed to recover in dim light ( $30 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) for 1 h.  $F_v/F_m$  was measured again after 10 min dark adaptation after the recovery period.

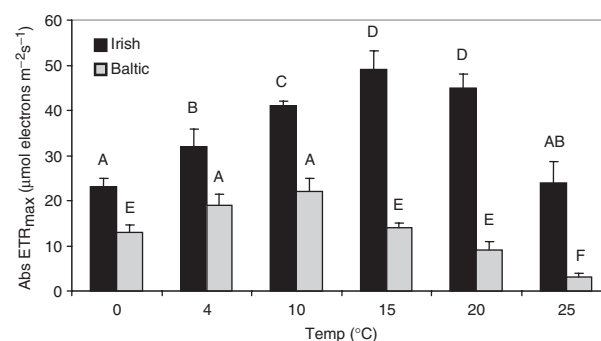
### Statistics

Paired  $t$ -test (comparison of values before and after treatment) and two-way ANOVA (between treatments) were used for statistical analysis with a 95% significance level. The data were analysed by multivariate linear regression with photosynthesis, RGR or recovery in  $F_v/F_m$  after exposure to high PAR, as dependent variables and salinity, nutrients and carbon as covariates. The data was classified into Baltic or Atlantic origin of the alga. The data on  $F_v/F_m$  recovery were subjected to angular transformation before analysis.

## Results

### P:E-curves

$\text{ETR}_{\text{max}}$  of *F. vesiculosus* from the Irish Sea was significantly higher (ANOVA,  $p < 0.001$ ) than that of *F. vesiculosus* from the Baltic ( $50.8$  vs  $21.9 \mu\text{mol electrons m}^{-2} \text{s}^{-1}$ ; Fig. 1). Plants from the Baltic reached light saturation at lower irradiances than plants from the Irish Sea, but plants from both populations had reached the  $\text{ETR}_{\text{max}}$  value at  $400 \mu\text{mol m}^{-2} \text{s}^{-1}$ , the irradiance that was used to measure ETR in the 5-week experiment. There was



**Fig. 2.** Saturated photosynthetic rate (Abs  $\text{ETR}_{\text{max}}$ ) of *Fucus vesiculosus* from the Gulf of Bothnia (northern Baltic, 5 psu; grey) and the Irish Sea (35 psu; black) at different temperatures. Plant tips (10 g FW each,  $n=10$ ) were cultivated in their natural seawater for 1 week at  $100 \mu\text{mol m}^{-2} \text{s}^{-1}$  under a 10:14-h light–dark cycle. Means with the same letter are not significantly different at  $p=0.05$  (Tukey tests).

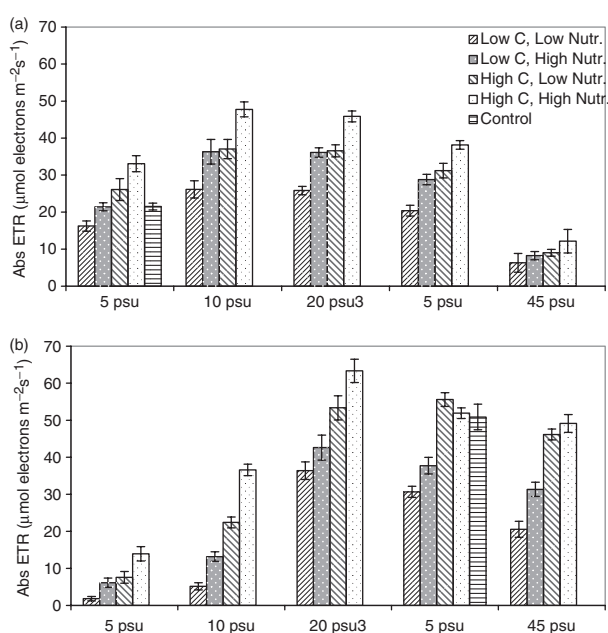
no difference between the populations in the ETRs recorded at the two lowest irradiances tested (Fig. 1).

### Optimal temperature

*Fucus vesiculosus* from the Irish Sea had the highest  $ETR_{max}$  at 15–20°C, while plants from the Baltic showed the highest  $ETR_{max}$  at 4–10°C (Fig. 2).  $ETR_{max}$  decreased at 25°C for plants from both populations, with a more pronounced drop for Baltic plants. At all temperatures,  $ETR_{max}$  for Irish Sea plants was higher than for Baltic plants. The temperature during the 5-week culture experiment was 8–10°C, which is slightly below the optimal temperature for *F. vesiculosus* from the Irish Sea, but falls within the optimal temperature range for *F. vesiculosus* from the Baltic.

### Salinity, carbon and nutrients

After cultivation for 5 weeks in high nutrients and DIC concentrations, *F. vesiculosus* from the Irish Sea exhibited higher  $ETR_{max}$  than the Baltic plants at salinities from 20 to 45 psu (Fig. 3b), whereas the  $ETR_{max}$  of Baltic plants was higher at salinities of

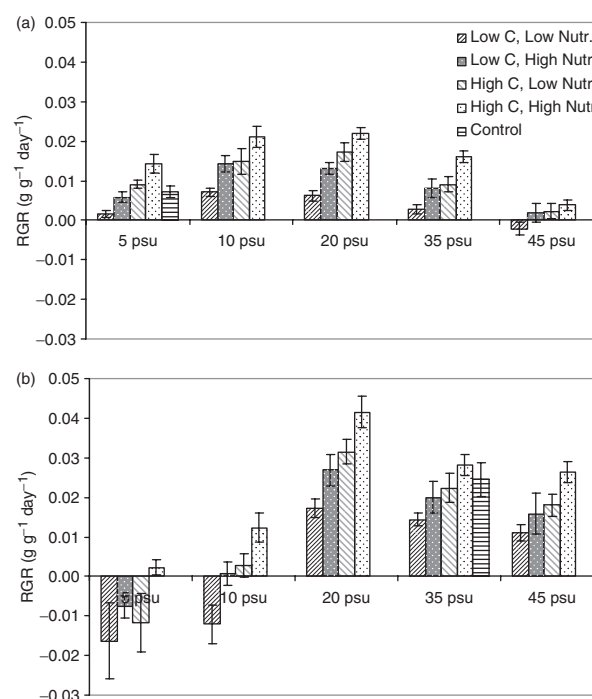


**Fig. 3.** Saturated photosynthetic rate (Abs ETR) of *Fucus vesiculosus* from (a) the Gulf of Bothnia (northern Baltic, 5 psu) and (b) the Irish Sea (35 psu), cultivated at different salinities for 5 weeks. Two concentrations of dissolved inorganic carbon (DIC) were used (Low C = 1.0 mol DIC m<sup>-3</sup>; High C = 2.0 mol DIC m<sup>-3</sup>) as well as two concentrations of nutrients (Low = 3 μmol NO<sub>3</sub> l<sup>-1</sup>, 0.185 μmol PO<sub>4</sub> l<sup>-1</sup>, 0.05 μmol NH<sub>4</sub> l<sup>-1</sup>; High = 12 μmol NO<sub>3</sub> l<sup>-1</sup>, 0.75 μmol PO<sub>4</sub> l<sup>-1</sup>, 0.2 μmol NH<sub>4</sub> l<sup>-1</sup>). Abs ETR measured after 5-min exposure to 400 μmol m<sup>-2</sup> s<sup>-1</sup>, after a 10 min dark adaptation. Histograms show means of 10 replicates and error bars are 95% confidence limits.

5 to 10 psu (Fig. 3a). The optimal salinity for *F. vesiculosus* from the Baltic was 10 to 20 psu, while that for plants from the Irish Sea was 20 to 35 psu (Fig. 3a,b). The salinities at which the ETR-values were lowest were 45 psu for *F. vesiculosus* from the Baltic and 5 psu for the Irish Sea plants (Fig. 3a,b).

Cultivation at the higher nutrient concentration resulted in higher  $ETR_{max}$  than in the lower nutrient concentration over almost all salinities for *F. vesiculosus* from both sites (Fig. 3a,b).  $ETR_{max}$  was also higher following cultivation in the higher concentration of DIC at most salinities, and the effects of high nutrients and high DIC were additive, so that the highest ETR-values were obtained when both nutrients and DIC were high, and the lowest when both nutrients and DIC were low (Fig. 3a,b).

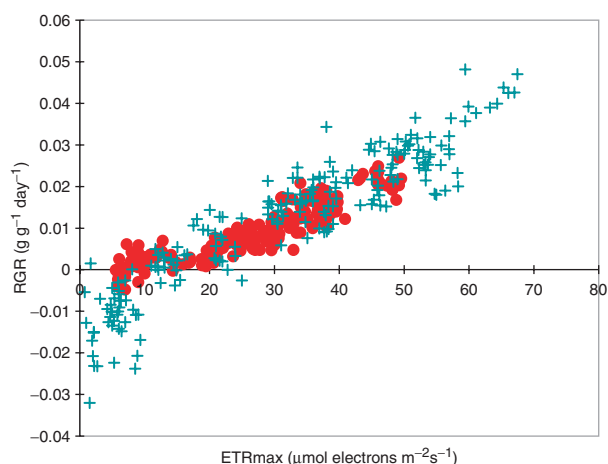
The pattern of variation of RGR for *F. vesiculosus* from both sites across the full range of salinities, nutrients and DIC was similar to that of  $ETR_{max}$  (Fig. 4). Consequently, there was a highly significant correlation between RGR and  $ETR_{max}$  over the full range of treatments (ANOVA,  $F_{1,398} = 1975.48$ ,  $r^2 = 0.832$ ; Fig. 5). One difference between RGR and  $ETR_{max}$  was the absence of significant differences in RGR for the Irish Sea plants at the salinities 20–45 psu with a



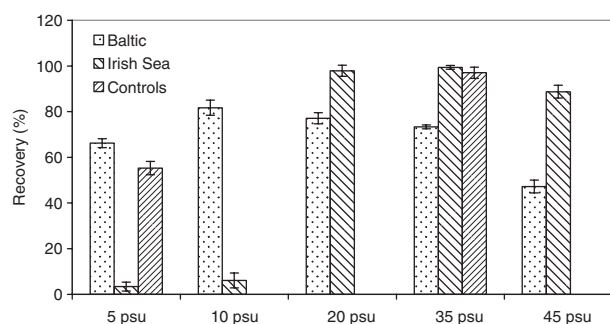
**Fig. 4.** Relative growth rate (RGR) of *Fucus vesiculosus* from (a) the Gulf of Bothnia (northern Baltic, 5 psu) and (b) the Irish Sea (35 psu), cultivated at different salinities for 5 weeks (nutrient and DIC concentrations as in Fig. 3). RGR estimated from changes in dry weight (DW) and expressed as g (DW) per g (DW) and day. Histograms show means of 10 replicates and error bars are 95% confidence limits.

low DIC concentration (Fig. 4b). At the two lowest salinities (5 and 10 psu), *F. vesiculosus* from the Irish Sea lost tissue, resulting in negative values of RGR (Fig. 4b). This was probably caused by destruction of the tissue due to a high water uptake.

A multivariate linear regression model with  $ETR_{max}$  or RGR as dependent variable was significant (for  $ETR$ :  $F_{8,391}=75.175$ ; for RGR:  $F_{8,391}=6.612$ ), and explained 61% and 58% of the variations in photosynthesis and growth, respectively. Salinity had the greatest impact on the model for  $ETR$  ( $F_{4,391}=90.432$ ), followed by nutrients together with DIC ( $F_{3,391}=74.257$ ), but



**Fig. 5.** Correlation between photosynthetic rate ( $ETR_{max}$ ) and growth rate (RGR) for *Fucus vesiculosus* from the Gulf of Bothnia (●) and the Irish Sea (+). Both variables measured after 5 weeks' cultivation at different salinities (5, 10, 20, 35 and 45 psu) with different nutrient concentrations (see Fig. 3) and inorganic carbon concentrations ( $1.0$  or  $2.0 \text{ mol m}^{-3}$ ).



**Fig. 6.** Recovery of photosynthesis following exposure to high irradiance ( $1500 \mu\text{mol m}^{-2} \text{ s}^{-1}$  PAR) for *Fucus vesiculosus* from the Gulf of Bothnia (northern Baltic, 5 psu) and the Irish Sea (35 psu), cultivated for 5 weeks at different salinities with high concentrations of nutrients and DIC (details as Fig. 3).  $F_v:F_m$  after 1 h recovery at  $30 \mu\text{mol m}^{-2} \text{ s}^{-1}$  and 10 min dark adaptation, following exposure to high PAR for 1 h, is expressed as a percentage of initial  $F_v:F_m$ . Histograms show means of 10 replicates and error bars are 95% confidence limits (calculated after angular transformation of percentage data).

the sites from which the plants were obtained contributed relatively little to the variation ( $F_{1,391}=16.899$ ).

#### Tolerance to high PAR

*Fucus vesiculosus* from the Irish Sea showed over 90% recovery of  $F_v/F_m$  following exposure to high irradiance in salinities from 20 to 45 psu, but almost no recovery was observed in salinities of 5 and 10 psu (Fig. 6). At these two lower salinities, the tolerance was higher for *F. vesiculosus* from the Baltic but, at all higher salinities, the tolerance of the Baltic plants was lower than those from the Irish Sea (Fig. 6). Variation in nutrient and DIC concentrations had little effect on degree of recovery of  $F_v/F_m$  following exposure to high irradiance (data not shown). A multivariate linear regression model with recovery in  $F_v/F_m$  as dependent variable was significant (ANOVA,  $F_{8,391}=49.503$ ) and explained 50% of the variation in recovery of  $F_v/F_m$  after exposure to high PAR. Salinity ( $F_{4,391}=92.277$ ) had the greatest impact on the model, whereas the nutrient and DIC contributed relatively little to the variation ( $F_{3,391}=7.214$ ).

#### Discussion

##### P:E-curves

*Fucus vesiculosus* from the Baltic possessed a lower  $ETR_{max}$  and photosynthesis became light saturated at a lower irradiance than in *F. vesiculosus* from the Irish Sea. Photoacclimation and/or photoadaptation to low light environments frequently results in reduced  $P_{max}$  (when expressed per unit chlorophyll) and reduced saturating photon irradiance ( $E_k$ ; see Dring, 1992, fig. 3.5), and is often accompanied by an increase in the initial slope of P:E curves ( $\alpha$ ) when photosynthesis is expressed per unit area or weight (e.g. Figueroa *et al.*, 2003) and an increased Chl *a* content (Ramus *et al.*, 1977; Ruokalahti & Rönnerberg, 1988). In the present study, no differences were found in  $\alpha$  between the two populations but this would not be expected because the calculation of  $ETR$  involves division by the absorption factor, so that  $ETR$  is more closely related to photosynthesis per unit chlorophyll than to photosynthesis per unit area. The feature of these plants that does not accord with the norm for high and low light populations is that the pigment content of *F. vesiculosus* from the Baltic has been shown previously to be lower than for *F. vesiculosus* from the Atlantic (Nygård & Ekelund, 2006). It seems, therefore, that, even though *F. vesiculosus* in the Baltic and the Irish Sea experience different light regimes because of the

absence of tides in the Baltic, the observed differences in photosynthesis cannot be completely explained by light acclimation, but are probably affected by other abiotic differences between the Baltic and the Atlantic waters, such as will be discussed below.

#### Optimal temperature

The results indicate that *F. vesiculosus* from the Baltic is better adapted to low water temperatures than *F. vesiculosus* from the Irish Sea. The plants in the northern Baltic are usually exposed to lower winter temperatures than those in the Irish Sea, and this may have generated a different temperature optimum for the two populations. Temperature is a major factor controlling the rate of photosynthesis in all plants (Davison, 1991). It has been found to affect the availability of inorganic carbon (Surif & Raven, 1989) and the rate of carbon fixation by RuBisCO (Sukénik *et al.*, 1987). For some algal species, the rate of nutrient uptake has been found to be correlated with temperature, but this has not been found so far in *Fucus* (Topinka, 1978). The upper thermal tolerance limit of photosynthesis appears to be set by the thermal stability of PSII, which in turn is controlled by the degree of saturation of fatty acids in the thylakoid membrane (Lynch & Thompson, 1984). Photorespiration has also been found to increase at high temperatures (Berry & Raison, 1981). The general trend is that algae from low-temperature environments show higher photosynthetic rates at low temperatures and have a lower optimal temperature for photosynthesis than algae from warmer environments (Kübler *et al.*, 1991). This is supported by the present study, since *F. vesiculosus* from the Gulf of Bothnia had a lower temperature optimum than *F. vesiculosus* from the Irish Sea. The relatively broad range of optimal temperatures for photosynthesis observed here is typical of other fucoid species (Madsen & Maberly, 1990).

#### Salinity

Both the photosynthesis and growth of *F. vesiculosus* from the Irish Sea decreased sharply between salinities of 20 and 10 psu (Figs 3b, 4b). This result is in line with the observations of Tropin *et al.* (2003) on *F. vesiculosus* in the Barents Sea. A salinity of 20 psu (with an exposure time of 14 days) had no effect on cell structure, whereas a lower salinity resulted in severe damage to cell structure. Earlier work on *F. vesiculosus* from the Irish Sea, however, has shown that growth rate was

not affected by a 50% reduction in salinity (approximately 16 psu; Gordillo *et al.*, 2002), so that the tolerance limit for *F. vesiculosus* from the Irish Sea seems to occur in the range of 10–16 psu.

Successful growth provides a good indication of the plant's ability to tolerate a changed salinity because it requires maintenance of cell turgor (Hellebust, 1976). It is also important to measure growth because it reflects the balance between photosynthesis and respiration (Kirst, 1989). The strong correlation between RGR and ETR in the present study (Fig. 5) indicates that growth was largely controlled by photosynthesis, and that nutrient supplies were limiting only in so far as they limited photosynthetic capacity (possibly by restricting the concentration of RuBisCO). The constant ratio of photosynthesis and growth indicates that the same amount of energy relative to photosynthesis is used for growth in plants from the two localities and at the different salinities. The smaller size of Baltic plants is probably caused, therefore, by lower photosynthesis. The ratio of photosynthesis to growth also shows that *F. vesiculosus* from the Baltic and the Irish Sea respond in a similar way to salinity, nutrients and DIC, but within a different range. The plot of RGR against ETR also indicates that a certain amount of energy from photosynthesis is required before the plant starts to grow. The limit seems to be an ETR of approximately  $20 \mu\text{mol electrons m}^{-2} \text{s}^{-1}$ , below which no growth occurs (Fig. 5). Since the  $\text{ETR}_{\text{max}}$  of plants from the Gulf of Bothnia in their natural seawater was about  $21\text{--}22 \mu\text{mol electrons m}^{-2} \text{s}^{-1}$  (Figs 1, 2, 3a), they were close to the minimum demand of photosynthesis for growth, and this may explain their small size. If their photosynthesis decreased any further, it is likely that the plants would stop growing.

Alternative explanations for the small size of Baltic plants may be that they do not live as long as on the Atlantic shores, or that they are more heavily grazed or abraded in the Baltic. The evidence, however, suggests the opposite. The average life span of *F. vesiculosus* on the North Sea coast of the British Isles is 3 years, with a maximum of 4–5 years in sheltered areas (Knight & Parke, 1950), whereas *F. vesiculosus* does not become reproductive in the Baltic Sea until 4–5 years and single fronds in sheltered areas may be up to 20 years old (Malm & Kautsky, 2004). In addition, marine limpets and littorinid grazers are absent from the less saline areas of the Baltic, and the only grazing gastropods that occur in substantial quantities on rocky shores are the freshwater snails *Theodoxus fluviatilis* and *Lymnaea peregra* (Malm *et al.*, 1999). Grazing by these two species was not found to affect the frond growth of



*F. vesiculosus* in the Baltic Sea (Malm *et al.*, 1999). One of the commonest herbivores in the northern Baltic is the isopod *Idotea baltica*, but this isopod has a preference for filamentous algae and mainly uses *F. vesiculosus* as shelter (Orav-Kotta & Kotta, 2001). Abrasion by wave action is also likely to be lower in the Baltic than in the Atlantic because storms are less severe and the plants are continually submerged.

The optimum salinities for ETR and RGR, as measured here, were 10–20 psu for *F. vesiculosus* from the Baltic and 20–35 psu for *F. vesiculosus* from the Irish Sea (Figs 3, 4). Thus, *F. vesiculosus* from the Baltic has the ability to grow in lower salinities than *F. vesiculosus* from the Irish Sea. The optimum salinity for photosynthesis was found in previous studies to be 6 psu for *F. vesiculosus* from the Baltic and 11–35 psu for *F. vesiculosus* from the Atlantic (Russell, 1988; Bäck *et al.*, 1992a), but the acclimation times in these studies were considerably shorter (24–48 h) than in the present work. Russell (1988) found that *F. vesiculosus* from the Baltic was harmed by salinities above 6 psu. This result was not supported by the present work, since ETR and RGR both increased significantly from 5 to 10 psu. Again, a possible explanation is the longer cultivation times in the present study (5 weeks). Other work in which a longer cultivation time was used (7 weeks) did not include photosynthetic measurements but showed a maximum growth rate (measured as increase in length) of *F. vesiculosus* from the Baltic at 6–12 psu and from the Atlantic at 12 psu (Bäck *et al.*, 1992b). Although no salinities were tested between 12 and 35 psu, these data may indicate that the salinity tolerance limit for *F. vesiculosus* from the Irish Sea can be narrowed to 12–16 psu. Future work on the salinity tolerance limits for *F. vesiculosus* should use exposures of several weeks and salinities within this range. *Fucus vesiculosus* from the Baltic maintained ETR and RGR over a wider range of salinities, and appeared to be more tolerant of salinity variations, than plants from the Irish Sea, although they were less resistant to hyper-saline conditions (45 psu). These differences are similar to those observed between estuarine and fully marine strains of the filamentous brown alga *Pilayella littoralis* (Reed & Barron, 1983).

#### Effects of DIC concentration

Earlier studies have suggested that Fucaceae in marine waters are saturated with DIC at ambient levels (Surif & Raven, 1989; Mercado *et al.*, 1998). The present study shows, however, that the DIC concentration in the Baltic is not sufficient for

maximal photosynthesis and growth of *F. vesiculosus*. The results obtained emphasize the importance of maintaining the DIC level when diluting seawater to obtain lower salinities. Dilution also reduces DIC, which will inevitably reduce photosynthesis. The multivariate regression analysis showed that the concentration of DIC had a significant influence on the photosynthesis of *F. vesiculosus*, even when the dominant factor was salinity. Consequently, increasing DIC does not compensate for decreases in salinity, but it is a contributing factor.

#### Effects of nutrients

A high nutrient content in the water not only increased the photosynthesis and growth rates of *F. vesiculosus* from both localities, but also provided increased tolerance to low salinities (except for *F. vesiculosus* from the Irish Sea at 5 psu, which lost tissue probably because of osmotically damaged cells). The growth of *F. vesiculosus* has been found to be stimulated by high nutrient loads from sewage outlets in areas with low salinity (Waern, 1952; Pekkari, 1973). These authors found plants of *F. vesiculosus* just outside untreated sewage outlets in areas with salinity below the usual tolerance limit. If this applies to species other than *F. vesiculosus*, then high eutrophication in the Baltic Sea could make it possible for new marine species to enter the Baltic ecosystem. An increased nutrient concentration might also enable marine species already present in the northern Baltic to extend further north.

As in higher plants, N is important for all enzymatic reactions in algae and N-limitation has been found to decrease both growth and fluorescence yield in brown algae (Kuppers & Weidner, 1980). It is clear that N-limitation affects the photosynthetic rate, but the mechanisms are not completely known, although carbon fixation and nitrogen metabolism have been found to be coupled (Turpin, 1991). The content of RuBisCO (and hence photosynthetic rate) has been shown to be dependent on nitrogen availability and sensitive to nitrogen starvation (Wheeler & Weidner, 1983). Therefore, the low ETR<sub>max</sub> obtained at low nutrient concentration is probably caused by a limitation of RuBisCO. Few studies have been performed of the effects of phosphorus on the photosynthesis of macroalgae, but work with microalgae has shown that phosphorus affects the active uptake of NO<sub>3</sub> (Beardall *et al.*, 2005).

#### Tolerance to high PAR

A lowering of optimal fluorescence yield ( $F_v/F_m$ ) that persists for 40 min after exposure to high light

has been used as a measure of photoinhibition of photosynthesis in flowering plants (Schreiber, 1997). If that definition is applied in the present study, where a recovery time of 1 h was used, the Baltic *F. vesiculosus* show photoinhibition at all salinities used, suggesting a low tolerance to high PAR. The photoinhibition in these plants was least pronounced in salinities 10–20 psu, indicating that the low salinity in the Baltic generates a low tolerance to high PAR. The plants from the Irish Sea showed almost full recovery of  $F_v/F_m$  in salinities of 20–35 psu, but enhanced photoinhibition in low salinity (5–10 psu), where also a deterioration of tissue was observed. Low salinities appear, therefore, to make the photosynthetic apparatus more sensitive to photoinhibition. Even though the statistical analysis showed a strong correlation between tolerance to high PAR and salinity, the multivariate regression showed that DIC and nutrients also contributed to photoinhibition. Another possible factor affecting the tolerance to high PAR for the Baltic plants could be the different light regimes in the Baltic and the Irish Seas. In the Baltic the plants grow constantly submerged and are not exposed to the high levels of PAR that plants in the Irish Sea experience at low tides.

### Conclusions

*Fucus vesiculosus* from the Irish Sea had a higher  $ETR_{max}$  and RGR than *F. vesiculosus* from the Baltic. The main explanation for these differences was found to be salinity, followed by DIC and nutrient concentrations. Although the addition of DIC (to the levels found in the Irish Sea) increased photosynthesis and growth of *F. vesiculosus* from the Baltic, the values of  $ETR_{max}$  and RGR never equalled those of *F. vesiculosus* from the Irish Sea. The differences in tolerance to high PAR could also be partly explained by the salinity, followed by DIC and nutrient concentration, but the degree of acclimation to high PAR at the natural growth sites seems to be a significant contributor.

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