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Photosynthesis, carbon uptake and antioxidant defence in two coexisting filamentous green algae under different stress conditions

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ABSTRACT: The physiological basis for ecological processes is in many cases little understood. The purpose of this work was to link 3 important physiological processes in algae — photosynthesis, carbon uptake and antioxidant defence — to life form. The organisms used were the morphologically similar filamentous green algal species *Cladophora glomerata* and *Ulva procera*, which seemingly occupy the same niche when they co-occur in dense belts in the upper littoral zone of the brackish Baltic Sea in summer. Their life strategies are different: the annual *C. glomerata* usually stays attached throughout summer, while the ephemeral *U. procera* can appear and disappear from the same site from week to week. The algae were growing in the field under exactly the same conditions (mixed stands) and were immediately used in experiments at a field station. Fundamental ecophysiological differences were found between the 2 species. (1) Higher photosynthetic activity was detected in *U. procera*. (2) More shade-adaptations were found in *U. procera*, and more sun-adaptations in *C. glomerata*. (3) *C. glomerata* uses a proton pump for HCO_3^- transport, and carbon uptake does not depend on periplasmic carbonic anhydrase. This is an advantage in dense algal belts with longer periods of carbon limitation. (4) *C. glomerata* invests more in carotenoid protection against oxidative stress, including high carotenoid/chlorophyll ratios and a functional violaxanthin xanthophyll cycle. (5) *U. procera* was more sensitive to oxidative stress created by UV-B radiation than *C. glomerata*, which correlates with a more effective intracellular (carotenoid and enzymatic) defence against oxidative stress in *C. glomerata*. (6) H_2O_2 in the seawater medium had a negative effect on photosynthesis in *C. glomerata*, but not in *U. procera*. This suggests that a high release of H_2O_2 by *U. procera* under oxidative stress may damage *C. glomerata*. While the ecophysiological traits of *C. glomerata* seem to be directed toward persistence, those of *U. procera* seem to be more engaged with large but short-term gains. This is in accordance with their different life strategies.

KEY WORDS: Macroalgae · Ecophysiology · Photosynthesis · Carbon uptake · Oxidative stress · Xanthophyll cycle · Pigments · Baltic Sea

INTRODUCTION

Strong correlations occur between macroalgal morphologies, life strategies, ecophysiological traits and the environment in which they live. Macroalgal thallus morphology and photosynthetic rates are closely linked, with thin filamentous r-strategists having the highest rates per unit weight (Littler & Littler 1980, Weykam et al. 1996, Johansson & Snoeijs 2002). Patterns of disparate spatial occurrence are often related to ecophysiological traits. For example, algal depth zonations show gradients in compensation irradiances of species, with deeper growing algae being more sensitive to light, while UV-tolerant algae grow closer to the surface (Bischof et al. 1998, Johansson & Snoeijs 2002, Figueroa et al. 2003). Similarly, depth distribution and the possession of certain carbon-uptake mechanisms seem to be related to deeper growing red algae being unable to take up HCO_3^- (Maberly 1990), whereas algae in the upper littoral

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have flexible HCO_3^- utilisation systems (Axelsson et al. 1995). The hypothesis of the competitive exclusion principle postulates that species with the same requirements cannot live together in the same place (Stiling 2002). However, nature is full of coexisting and competing species with strongly overlapping requirements. In algal belts complicated ecological interactions involving dispersal mechanisms, herbivory and seasonality can partly explain patterns of coexistence (Lotze et al. 2000). However, it may also be possible that ecophysiological traits are coupled to patterns of spatial co-occurrence. We hypothesised that co-occurring species with very similar morphologies differ in life strategies as well as in ecophysiological traits and that these strategies and traits are correlated.

An excellent example of the co-occurrence of algae with similar morphologies is that of *Cladophora glomerata* (L.) Kütz. and *Ulva procera* (Ahlner) Hayden et al. (= *Enteromorpha procera* Ahlner = *Enteromorpha ahlneriana* Bliding, see Hayden et al. 2003). *C. glomerata* is of freshwater origin and *U. procera* is of marine origin, but in the brackish Baltic Sea they co-exist (Snoeijs 1999). Together these 2 filamentous green algae dominate the upper metre of the littoral zone of the northern Baltic Sea during summer. This zone is known as the '*Cladophora*-belt', but, in fact, it consists of the 2 species mentioned and low abundances of some other filamentous algae. This belt is an important habitat for many invertebrates. Macroscopically, *C. glomerata* and *U. procera* are difficult to distinguish from each other because they have the same finely branched filamentous morphology, the same colour and the same size (10 to 30 cm high). Microscopically, they differ in that *C. glomerata* has larger uniseriate cells, while the cells of *U. procera* are smaller and arranged in 1-cell-layer thick tubes. *C. glomerata* and *U. procera* are found in single-species belts, but very often also in patches in mixed stands (Snoeijs 1992, 1999). *C. glomerata* is slightly more abundant than *U. procera*; at 20 sampling sites visited monthly from March to November, *C. glomerata* occurred on 86% and *U. procera* on 71% of 180 sampling occasions (Snoeijs 1992). The upper littoral of the Baltic Sea is a highly dynamic environment; lunar tides are virtually absent, but daily changes in the water level of up to ca. 0.5 m may occur, together with changes in temperature and irradiance. In this habitat, the annual *C. glomerata* usually stays attached throughout summer, while the ephemeral *U. procera* can appear and disappear at the same site from week to week.

Previous studies on cellular defence strategies against oxidative stress by Choo et al. (2004) showed that *Cladophora glomerata* can be classified as a more stress-tolerant species and *Ulva procera* as a more stress-susceptible species. Low temperature in combination with high irradiance created less lipid oxidative damage in *C. glomerata* than in *U. procera*, which was correlated to higher regular activities of the H_2O_2 scavenging enzymes catalase and ascorbate peroxidase in *C. glomerata* cells. Higher activities of these enzymes in *U. procera* were only mobilised after the introduction of oxidative stress. Superoxide dismutase activities were similar in both species, but the mechanisms to remove the H_2O_2 produced by the action of this enzyme were different: more through scavenging enzymes inside *C. glomerata* cells and more through diffusion into the seawater medium for *U. procera*. In the present paper, we make further comparisons on antioxidant defence by carotenoids against high photosynthetically active radiation (PAR) and sensitivity to ultraviolet-B (UV-B) radiation (creating oxidative stress) of the 2 species. As both species occur in the upper littoral zone, it would be expected that they are well protected against supersaturating PAR and UV-B radiation, which can damage components of metabolic processes in algal cells and lower the photosynthetic capacity (Lorenz et al. 1997, Bischof et al. 2002, Figueroa et al. 2003).

In 2 previous papers (Abrahamsson et al. 2003, Choo et al. 2004) we compared the releases of H_2O_2 into the seawater medium by *Cladophora glomerata* and *Ulva procera* sampled from the same sites in the Baltic Sea and incubated under the same stress conditions in the laboratory (high irradiance and carbon deficiency). *C. glomerata* and *U. procera* from Forsmark, in the southern Bothnian Sea, released up to 2.2 and 49 µmol H_2O_2 (g DW)$^{-1}$ h^{-1}, respectively. *C. glomerata* and *U. procera* from Askö, in the northern Baltic Sea proper, released up to 1.3 and 6.0 µmol H_2O_2 (g DW)$^{-1}$ h^{-1}, respectively. We speculated that the release of H_2O_2 may function as a chemical defence against herbivores and epiphytes or as an allelochemical in direct competition with other algal species. For *Ulva rigida* C. Ag., Collén & Pedersén (1996) found that photosynthesis and carbon uptake were inhibited at a concentration of 1000 µM H_2O_2 in seawater, but not at concentrations as high as 100 µM. They concluded that the release of H_2O_2 by *U. rigida* of up to 1.2 µmol H_2O_2 (g fresh weight)$^{-1}$ h^{-1} (Collén et al. 1995), which is about 12 µmol H_2O_2 (g DW)$^{-1}$ h^{-1}, had no direct autotoxic effect. In the present study, we test whether there are differences in sensitivity to extracellular H_2O_2 between *C. glomerata* and *U. procera*, in support of a possible role of H_2O_2 in interspecific competition between these 2 species.

In the light of their coexistence and similar morphologies, but different life strategies and different defences against oxidative stress, we investigate here the hypothesis that the annual *Cladophora glomerata* and the ephemeral *Ulva procera* exhibit differences in the fundamental cellular processes of photosynthesis

and carbon uptake. We also study carotenoid responses to high irradiance and photosynthetic responses to H_2O_2 and UV-B radiation for a further comparison of the 2 species' ecophysiological traits with respect to their life strategies. To be able to relate the results to field conditions, the algae were not transported or cultivated, but were taken directly in the field, 20 m from the field station where all experiments were carried out. Our study does not include seasonal variation and only reflects summer conditions, when the *Cladophora*-belt in the Baltic Sea has already been established and is at its highest state of development.

MATERIALS AND METHODS

Cladophora glomerata and *Ulva procera* were collected from a mixed stand at a water depth of 0.2 to 0.3 m on the island of Askö, in the northern Baltic Sea proper (58° 50' N, 17° 39' E). All algae were growing on a concrete ridge at a 45° angle to the water surface, so that the microhabitat was as uniform as possible. Fresh algal samples were collected, rinsed several times with filtered seawater to remove epiphytes and pre-incubated in the darkness at 25°C for at least 2 h, to avoid acclimation to different irradiances in the field before use in the experiments. Algae sampled from 24 July to 2 August 2002 were used for measurements of photosynthesis, carbon uptake and pigment dynamics. Sensitivity to UV-B radiation and sensitivity to the carbon-uptake inhibitor acetazolamide were studied on 30 and 31 August 2000 in algae taken at the same site and sampled in the same way as in 2002. In both years, salinity was 6.5 practical salinity units (psu) and water temperature in the upper littoral was 20 to 25°C during sampling.

Measurements of photosynthetic rates (O_2 evolution) were carried out with 2 intercalibrated computer-steered Illuminova Light Dispenser Systems ('Light Pipette'); each was equipped with a halogen lamp, a patented IR deflector and a waveband definer delimiting radiation between 400 and 700 nm. One of the advantages of the Light Pipette is its great illumination precision. Illumination was calibrated with a Li-Cor radiometer, with a cosine-corrected sensor inserted in the Light Pipette exactly at the site of incubation of the algae. During the experiments, irradiance was measured by a light sensor positioned immediately next to the incubation chamber of the Light Pipette at the same distance from the PAR and UV light sources as the incubated algae. The percent O_2 saturation and change in the percent O_2 saturation (photosynthetic rate) were recorded every 2 s. In all experiments pieces of *Cladophora glomerata* or *Ulva procera* of 0.03 to 0.04 g fresh weight were incubated in nutrient-enriched, filtered (0.2 µm) natural seawater (NSW) with an air-calibrated O_2 concentration in a 2.6 ml incubation chamber with an O_2 electrode (Microelectrodes) inserted. Since the NSW at the sampling site is low in nutrients in July (mean ± SD for 8, 14 and 19 July 2000: 0.29 ± 0.26 µM dissolved inorganic N and 0.14 ± 0.06 µM dissolved inorganic P; I. Wänstrand & P. Snoeijs unpubl. data), 6.4 µM of $NaNO_3$ and 0.4 µM of NaH_2PO_4 (approximate winter concentrations in the area) were added to the filtered NSW to avoid nutrient limitation during the experiments. All experiments were carried out at 25°C. For each treatment, 3 to 5 replicate measurements were carried out, each on a different algal specimen. Replicate experiments were performed at different times of the day to minimise possible diel effects. Photosynthetic rates were normalised to algal dry weight (DW) measured after 24 h of oven-drying at 80°C and to chlorophyll *a* (chl *a*). Separate samples were taken for the analyses of total C, N and P in the algal thalli with a LECO CHNS-932 elemental analyser.

Photosynthetic properties were studied by constructing photosynthesis versus irradiance curves (*P-E* curves). A 1200 s programme was run, starting with 120 s in the darkness followed by 18 alternating light and dark periods of 60 s each. The photon flux density was increased for each of the 9 light periods and measured 10, 20, 50, 100, 300, 600, 900, 1500 and 2000 µmol photons m^{-2} s^{-1}, respectively. Data used to construct *P-E* curves were the means of the last 20 of a total of 30 O_2 records in each time period; this allowed for a 20 s lag phase for differences in gas exchange between species due to thallus thickness. The curves were fitted using the equation: $P_{net} = [P_{max} \times \tan h\ (\alpha \times E/P_{max})] + R_d$ (Jassby & Platt 1976, Henley 1993), employing the Levenberg–Marquardt algorithm for the parameter estimates P_{max} and α (P_{net} = net rate of photosynthesis, P_{max} = light-saturated photosynthetic rate, α = initial slope at limiting irradiance levels, E = irradiance, R_d = rate of respiration in darkness). The derived measures $E_c = -R_d/\alpha$ (compensation irradiance) and $E_k = P_{max}/\alpha$ (saturation irradiance) were calculated.

In the study on pigment dynamics each Light Pipette measurement consisted of a 1200 s programme including 600 s of darkness followed by 600 s of irradiance. Ten different irradiance levels (0, 10, 20, 50, 100, 300, 600, 900, 1500 and 2000 µmol photons m^{-2} s^{-1}) were used. Data used in the calculations were the last 360 s in each dark or light period, which allowed for a 240 s acclimation phase to light conditions. After incubation, the algae were transferred within 10 s to a freezer set to −86°C. Later, chlorophylls and carotenoids were extracted and analysed by high-performance liquid chromatography (HPLC) according to Ursi et al. (2003).

The sensitivity of *Cladophora glomerata* and *Ulva procera* to H_2O_2 in the NSW medium was measured as changes in *P-E* curves after the addition of 20 and

100 µM H_2O_2 to the NSW. A method using luminol-dependent chemiluminescence (LDC) was used to determine the concentrations of H_2O_2 in the seawater medium (modified after Glazener et al. 1991). A 5 mM luminol (5-amino-2,3-dihydro-1,4-phtalazinedone) solution of pH 7.6 was prepared in 1 ml of 1 M NaOH and 9 ml of 0.4 M Mops (3-N-morpholino propane sulfonic acid, pH 7.0). A horseradish peroxidase solution was prepared in 0.1 M phosphate buffer (pH 7.0) with an enzyme activity of 28 U ml^{-1}. Then, 16 µl luminol solution and 48 µl peroxidase solution were mixed, and 1 ml seawater was added. LDC was measured with a luminometer (LKB 1250, Wallac) equipped with a flat-bed recorder (Kipp & Zonen). A standard curve was prepared based on solutions with different concentrations of H_2O_2.

To study the effect of a strong external source of oxidative stress, the algae were exposed to UV-B radiation. An UV lamp providing 1.58 W m^{-2} UV-A (315 to 400 nm) and 2.45 W m^{-2} UV-B (280 to 315 nm), i.e. close to natural levels for UV-B at the water surface, but only ca. 4% of natural UV-A levels (Dring et al. 1996), was inserted into a special construction in front of the incubation chamber of the Light Pipette. Then, 5 successive Light Pipette runs were made with the same thallus at a constant irradiance of 300 µmol photons m^{-2} s^{-1}. This experiment was carried out for *Cladophora glomerata* and *Ulva procera*, and for comparison also with another *Ulva* species, *U. intestinalis* L., which is common in the Baltic Sea. Each run consisted of a 600 s long programme, and the seawater medium was exchanged between the runs to keep O_2 saturation <130% and to avoid carbon limitation. The first run without UV-B radiation acted as the control, Runs 2 to 4 included UV-B radiation. The fifth run without UV-B radiation was a postcontrol to record the degree of O_2 evolution recovery. Reference experiments consisting of 5 successive runs without UV-B radiation were performed as well. The UV-B effect was expressed as the O_2 evolution as percent of the control.

The occurrence of different carbon-uptake mechanisms in the 2 species was studied by a pH-drift technique in which photosynthetic carbon uptake was followed by pH increase in the seawater medium, as previously described in detail by Choo et al. (2002), Snoeijs et al. (2002) and Ray et al. (2003). The pH was recorded every minute for 7 h in nutrient-enriched, filtered NSW during photosynthesis of *Cladophora glomerata* and *Ulva procera* in closed glass flasks with pH electrodes inserted in a computerised set-up, with and without the addition of inhibitors for specific carbon-uptake mechanisms. Each experiment was carried out on 2 consecutive days using the same algal thalli. The first day consisted of a 7 h run without inhibitor to activate and stabilise the algae (Choo et al. 2002), and the second day consisted of a 7 h run with or without inhibitor. The data presented are only those of the second day. During the experiments, the temperature was kept at 25 to 26°C by air-fans. Light was supplied at 300 µmol photons m^{-2} s^{-1} by 4 daylight fluorescent tubes placed on both sides of the flasks. Acetazolamide (AZ, Sigma), an inhibitor of periplasmic carbonic anhydrase (CA) (Moroney et al. 1985, Björk et al. 1992), was prepared as a 50 mM stock solution in 0.5 M NaOH. A final concentration of 0.2 mM AZ was added to the seawater medium in the experiments. A 20 mM stock solution of 4,4′-diisothiocyanato-stilbene 2,2′-disulfonic acid (DIDS, Sigma), which inhibits the action of an anion exchange protein (AE; Drechsler et al. 1993), was prepared in distilled water. A final concentration of 0.3 mM DIDS was added to the seawater medium in the experiments. Orthovanadate (VAN, Sigma), an inhibitor of P-type H^+-ATPases (proton pump; Gilmour et al. 1985), was prepared as a 50 mM stock solution in distilled water and added to the seawater medium in a final concentration of 0.15 mM.

Sensitivity of photosynthesis to AZ was studied by performing 3 successive Light Pipette runs with the same thallus at a constant irradiation of 300 µmol photons m^{-2} s^{-1}. Each run consisted of a 600 s long sequence, with O_2 recordings every second. The seawater medium was exchanged between the runs to keep O_2 saturation <130% and to avoid carbon limitation. The first run without AZ acted as a control; in the second run, 0.2 mM AZ was added to the seawater medium; the third run, without AZ, was a postcontrol to show that it was possible to wash away AZ. The AZ effect was expressed as the O_2 evolution in percent of the control. Reference experiments consisting of 3 successive runs without AZ radiation were performed as well.

For statistical data elaboration (*t*-test and repeated-measures ANOVA) STATISTICA software was used. Significance was accepted at $p < 0.05$.

RESULTS

Morphology and nutrient contents

The tube-like thallus of *Ulva procera* was very thin and similar to the uniseriate thallus of *Cladophora glomerata*. At the sampling site, the richly branched tufts of both species were ca. 20 cm high and it was difficult to distinguish the 2 species *in situ*; the only macroscopic difference was the slightly darker green colour of *U. procera*. Epiphyte cover was low on both species. The DW/WW ratio, %C and %N of *C. glomerata* and *U. procera* did not differ significantly between the species (Table 1). The %P was significantly lower in *U. procera* (0.14%) than in *C. glomerata* (0.26%), and, consequently, the N/P ratio was higher in *U. procera*.

Table 1. *Cladophora glomerata* and *Ulva procera*. Comparisons of the nutrient contents and ratios of the thalli used in the experiments, given as overall mean ± SD (n = 4 d) based on daily means of 3 replicate algal thalli measured on 25, 27, 29 and 31 July. *t*-tests were performed to test for differences in the means of the 2 species. DW: dry weight; WW: wet weight

Property	*t*-test p-value	*C. glomerata*	*U. procera*
DW/WW	0.347	0.12 ± 0.02	0.11 ± 0.02
%C	0.166	31.05 ± 2.20	33.20 ± 1.60
%N	0.737	2.09 ± 0.60	1.96 ± 0.39
%P	0.001	0.26 ± 0.03	0.14 ± 0.03
C/N (on a molar basis)	0.524	18.4 ± 4.4	20.4 ± 3.7
N/P (on a molar basis)	0.017	17.8 ± 3.1	32.0 ± 8.1

P-E curves

Ulva procera had higher weight-specific P_{max} and α values, indicating a higher efficiency of photosynthesis in *U. procera* (Table 2). Also chl *a*-specific α was higher in *U. procera*, but chl *a*-specific P_{max} was not significantly different in the 2 species. The coefficients of variance (CV) for P_{max} and α showed larger variation between days in *U. procera* (CV = 27 and 23 %, respectively than in *C. glomerata* (CV = 9 and 5 %, respectively). Chl *a*-specific R_d was higher in *C. glomerata*. The affinity for light of *U. procera* was higher than that of *C. glomerata*, as shown by its more than 3 time lower E_c, while saturation irradiance (E_k) was similar for both species. The *P-E* curves did not indicate chronic photoinhibition (manifested by P_{max} decrease) at the studied irradiance levels of 0 to 2000 µmol photons m^{-2} s^{-1}.

Table 2. *Cladophora glomerata* and *Ulva procera*. Comparisons of the photosynthetic properties extracted from *P-E* curves for algae taken directly from the field on 24 July, 31 July, 1 August and 2 August 2002. The properties are given as overall mean ± SD (n = 4 d), based on daily means of 3 to 5 replicate algal thalli measured on 4 different days. P_{max}: light-saturated photosynthetic rate; R_d: respiration rate in darkness; α: initial slope of photosynthesis; $E_c = -R_d/\alpha$ (compensation irradiance); $E_k = P_{max}/\alpha$ (saturation irradiance). *t*-tests were performed to test for differences in the means of the 2 species

Measured and calculated photosynthetic properties	*t*-test p-value	*C. glomerata*	*U. procera*
P_{max}			
(µmol O_2 [kg DW]$^{-1}$ s^{-1})	0.007	69 ± 6	157 ± 43
(µmol O_2 [mg chl *a*]$^{-1}$ h^{-1})	0.293	125 ± 11	150 ± 41
R_d			
(µmol O_2 [kg DW]$^{-1}$ s^{-1})	0.408	−19 ± 6	−16 ± 3
(µmol O_2 [mg chl *a*]$^{-1}$ h^{-1})	0.012	−34 ± 10	−15 ± 3
α			
(µmol O_2 [kg DW]$^{-1}$ [µmol photons m^{-2}]$^{-1}$)	0.002	0.39 ± 0.02	1.09 ± 0.25
(mmol O_2 [mg chl *a*]$^{-1}$ [µmol photons m^{-2}]$^{-1}$)	0.036	0.20 ± 0.03	0.29 ± 0.07
E_c			
(µmol photons m^{-2} s^{-1})	0.008	50 ± 18	15 ± 5
E_k			
(µmol photons m^{-2} s^{-1})	0.437	183 ± 27	153 ± 65

Carbon uptake

All tested inhibitors significantly reduced the pH increase in the medium during photosynthesis in the pH-drift experiments (Fig. 1; tested by repeated-

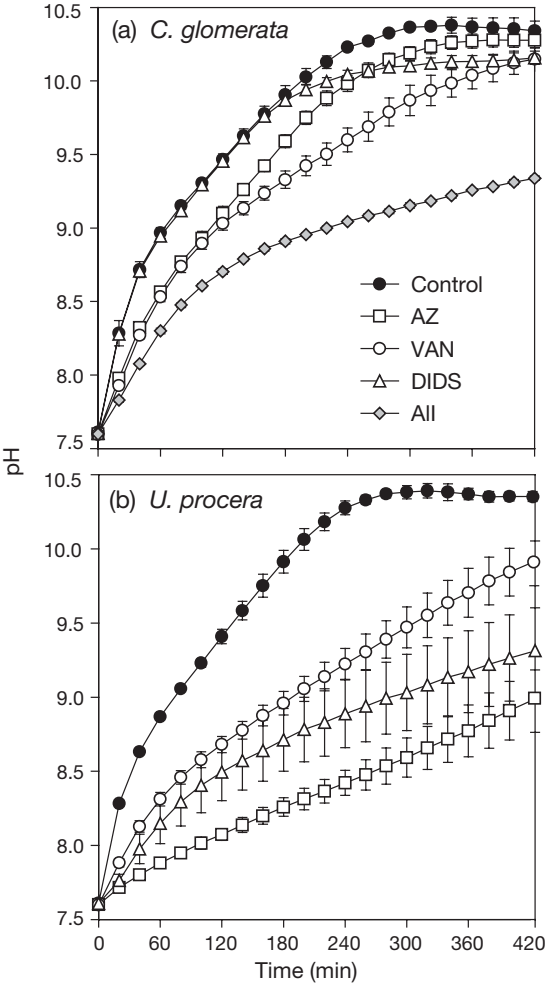

Fig. 1. *Cladophora glomerata* and *Ulva procera*. Changes in pH recorded in the seawater medium during pH-drift experiments with (a) *C. glomerata* and (b) *U. procera* with different inhibitor treatments: control (without inhibitor), 0.2 mM acetazolamide (AZ), 0.15 mM vanadate (VAN) and 0.3 mM 4,4′-diisothiocyanato-stilbene-2,2′-disulfonic acid (DIDS). *C. glomerata* was also treated with all 3 inhibitors in combination (All). Error bars show 1 standard error of the mean (not visible when very small)

measures ANOVA with time as the repeated-measures variable). The specific inhibitors AZ, VAN and DIDS identified the occurrence of 3 carbon-uptake mechanisms in both *Cladophora glomerata* and *Ulva procera*: an AZ-sensitive periplasmic CA, a VAN-sensitive P-type H^+-ATPase (proton pump) and a DIDS-sensitive AE. In *C. glomerata*, the inhibitory effects of each of the inhibitors AZ, DIDS and VAN were small and inhibition by DIDS was only found at pH > 9.8. After 7 h there were no significant differences between the AZ treatment and the control (*t*-test, pH 10.28 to 10.34) or between the VAN and DIDS treatments (*t*-test, pH 10.15 to 10.16) (Fig. 1a). This suggests that within 7 h the proton pump and AE can compensate for the absence of periplasmic CA, but that CA cannot fully compensate for the absence of the proton pump or AE at high pH. When all 3 inhibitors (AZ, VAN and DIDS) were used in combination in *C. glomerata*, a large inhibition of carbon uptake occurred. In *U. procera*, carbon uptake was highly dependent on periplasmic CA; when this enzyme was blocked, AE and the proton pump could not, or at least not within 7 h, compensate for the loss in carbon uptake (Fig. 1b). Similarly, when AE was blocked, CA and the proton pump could not compensate for the loss in carbon uptake. Blocking the proton pump had the least effect on carbon uptake in *U. procera*; after 7 h the pH had risen to 9.9 in the VAN treatment. The effect of AZ on O_2 evolution confirmed the pH-drift results that CA is more important for carbon uptake in *U. procera* than in *C. glomerata*; 0.2 mM AZ blocked 41 ± 6% of the O_2 evolution rate in *U. procera* compared with only 16 ± 9% in *C. glomerata*.

Table 3. *Cladophora glomerata* and *Ulva procera*. Pigment contents and ratios that did not vary with irradiance treatment (ANOVA, $p > 0.05$). The data are overall means ± SD (n = 10) calculated from treatment means (n = 3) for the 10 irradiance treatments. *t*-tests were performed to test for differences in the means of the 2 species. DW: dry weight.

Pigments	*t*-test p-value	*C. glomerata*	*U. procera*
µmol pigment (g DW)$^{-1}$			
Chl *a*	<0.001	2.22 ± 0.10	4.23 ± 0.69
Chl *b*	<0.001	1.58 ± 0.11	4.99 ± 0.82
Total carotenoids	0.005	3.52 ± 0.20	4.24 ± 0.68
mol carotenoid (mol chl *a*)$^{-1}$			
Neoxanthin	0.001	0.094 ± 0.005	0.085 ± 0.005
Lutein	0.062	0.462 ± 0.021	0.482 ± 0.024
Sum of violaxanthin, antheraxanthin and zeaxanthin	<0.001	0.574 ± 0.023	0.200 ± 0.019
α-Carotene	<0.001	0.127 ± 0.013	0.040 ± 0.005
β-Carotene	<0.001	0.326 ± 0.015	0.183 ± 0.013
Chl *b*/Chl *a* (mol/mol)	<0.001	0.708 ± 0.028	1.182 ± 0.053
Chl *a*/Total carotenoids (mol/mol)	<0.001	0.635 ± 0.020	1.017 ± 0.057
Chl *a*/Total carotenes (mol/mol)	<0.001	2.218 ± 0.110	4.519 ± 0.303
Chl *a*/Total xanthophylls (mol/mol)	<0.001	0.890 ± 0.027	1.315 ± 0.076

Pigment dynamics

Ulva procera had higher chlorophyll and carotenoid concentrations per unit DW; however, per unit chl *a* carotenoid concentrations were almost 2 times higher in *Cladophora glomerata* (Table 3). During the pigment dynamics experiments, O_2 production was higher in *U. procera* than in *C. glomerata* at irradiances above E_k (Fig. 2a,b). All pigment concentrations or ratios remained unchanged during the short-term (10 min) exposures to different irradiation levels varying from 0 to 2000 µmol photons m^{-2} s^{-1} (ANOVA, $p > 0.05$), except for violaxanthin, antheraxanthin and zeaxanthin in *C. glomerata*. The sum of these 3 xanthophylls remained unchanged as well (Table 3), while they performed the interconversions typical of the xanthophyll cycle with increasing light, i.e. decreases in violaxanthin and antheraxanthin and an increase in zeaxanthin (Fig. 2c). *U. procera* also possessed these 3 xanthophylls, but in lower concentrations, and no xanthophyll cycling was detected (Fig. 2d).

Sensitivity to H_2O_2

The H_2O_2 additions significantly affected the *P-E* curves of *Cladophora glomerata* negatively, but had no significant effect on the *P-E* curves of *Ulva procera* (Fig. 3; repeated-measures ANOVA). In 20 and 100 µM H_2O_2, respectively, *C. glomerata* had a 9 and 25% lower P_{max}, 23 and 34% lower α, 79 and 112% higher R_d and 125 and 231% higher E_c (*t*-tests, $p < 0.05$), but E_k was not affected. In *U. procera*, none of these photosynthetic parameters was affected by the H_2O_2 treatments (*t*-tests, $p > 0.05$). The NSW had an initial H_2O_2 concentration of 0.28 ± 0.05 µM; after the 15-min incubations without addition of H_2O_2, this had increased to 1.06 ± 0.30 µM for *C. glomerata* and to 0.44 ± 0.14 µM for *U. procera*. In the 20 µM H_2O_2 treatment, the concentrations decreased to 6.8 ± 0.6 µM for *C. glomerata*

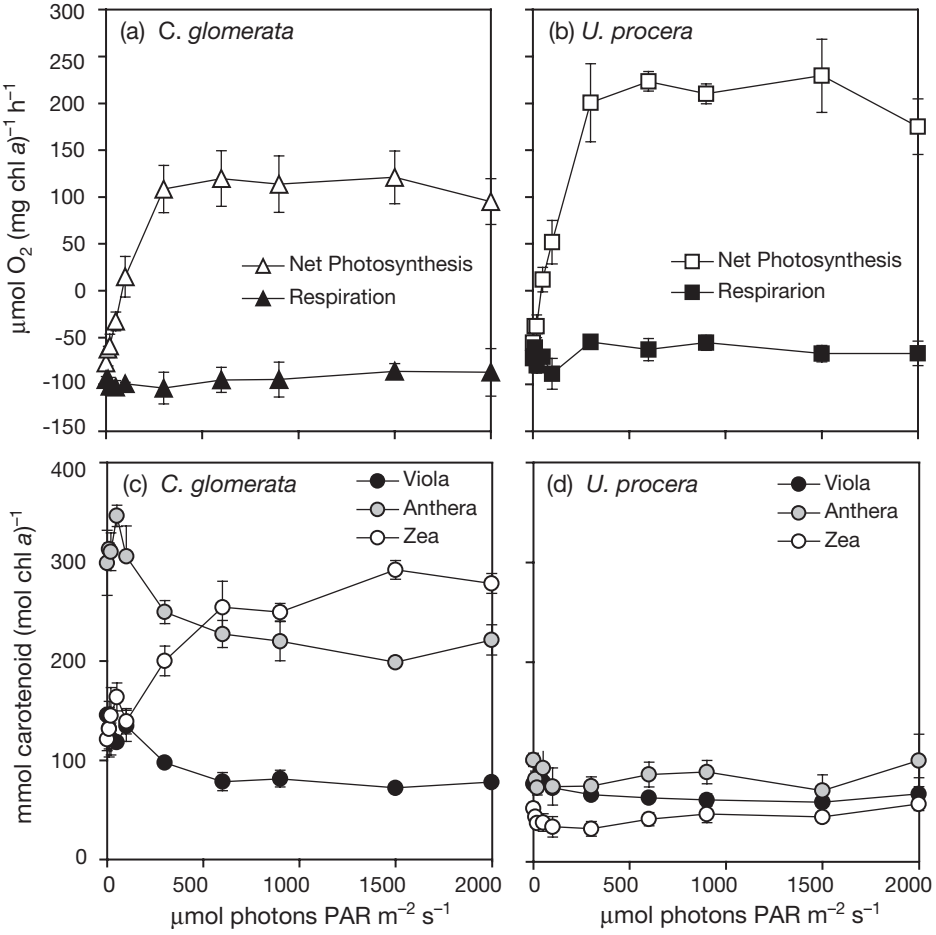

Fig. 2. *Cladophora glomerata* and *Ulva procera*. Results of the pigment dynamics experiments, showing (a,b) O_2 evolution and (c,d) changes in the chl *a*-specific concentrations of the xanthophylls violaxanthin (Viola), antheraxanthin (Anthera) and zeaxanthin (Zea) in (a,c) *C. glomerata* and (b,d) *U. procera*. Error bars show 1 standard error of the mean (not visible when very small). PAR: photosynthetically active radiation

and to 6.0 ± 0.6 µM for *U. procera*. In the 100 µM H_2O_2 treatment, the concentrations decreased to 14.6 ± 1.5 µM for *C. glomerata* and to 15.7 ± 0.5 µM for *U. procera*. In control experiments without algae, the H_2O_2 concentrations decreased by ca. 50%, probably by chemical degradation. These results show that photosynthesis in *C. glomerata* was negatively affected by H_2O_2, but not in *U. procera*, and that both species were able to scavenge H_2O_2 added to the seawater. Maximum H_2O_2 levels in seawater taken within the dense algal belt at the sampling site varied between 1 and 15 µM (measured on different days at noon).

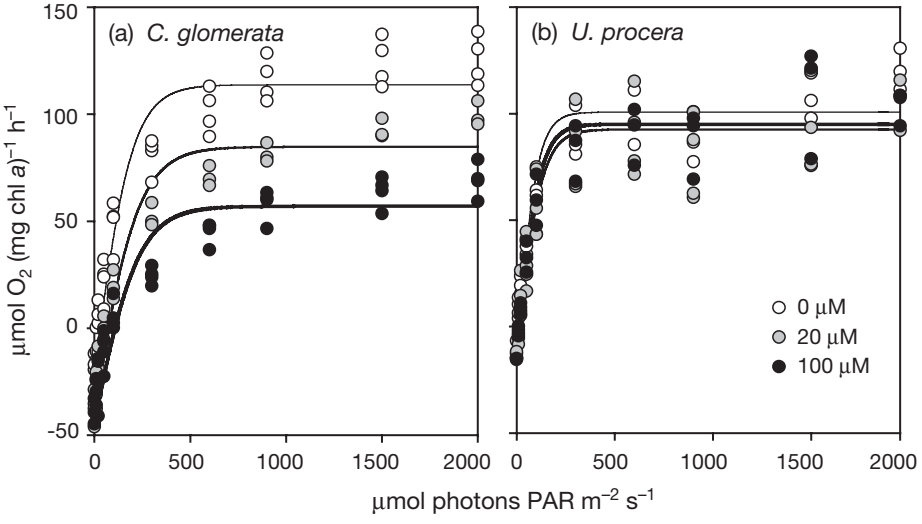

Fig. 3. *Cladophora glomerata* and *Ulva procera*. Sensitivity of the photosynthesis of (a) *C. glomerata* and (b) *U. procera* to H_2O_2 in NSW (natural seawater): *P-E* curves with 0, 20 and 100 µM H_2O_2 added to the NSW medium. PAR: photosynthetically active radiation

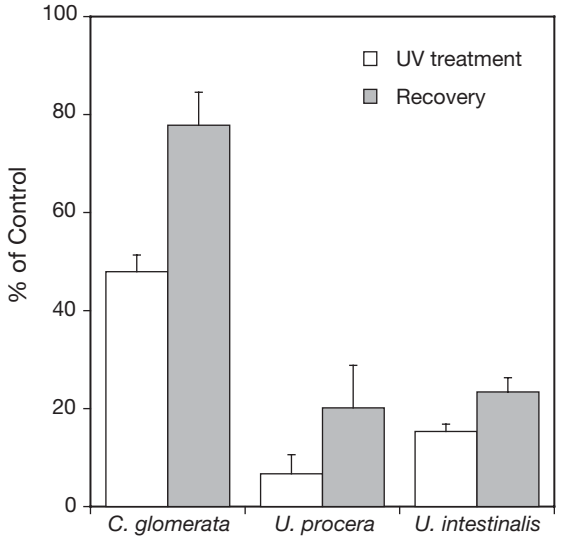

Fig. 4. The effect of UV-B radiation on the photosynthesis of *Cladophora glomerata*, *Ulva procera* and *U. intestinalis* expressed as O_2 evolution in percent of the control. O_2 evolution was measured on the same algal thalli before (control), immediately after 30 min of ultraviolet treatment (UV treatment) and after 10 min of photosynthetically active radiation after the ultraviolet treatment (recovery). Error bars show 1 standard error of the mean

Sensitivity to UV-B radiation

The photosynthesis of *Cladophora glomerata*, *Ulva procera* and *Ulva intestinalis* was inhibited by UV-B radiation; the strongest inhibition occurred in the 2 *Ulva* species (Fig. 4). The 30 min UV treatment reduced O_2 evolution by 52 ± 6% in *C. glomerata* and by 93 ± 7% in *U. procera*. The same pattern was observed in the recovery treatment during which *C. glomerata* regained its photosynthesis to 78 ± 7% of the control, while *U. procera* only recovered to 20 ± 9% of the control.

DISCUSSION

Species of the freshwater genus *Cladophora* and the marine genus *Ulva* are notorious opportunists (Raffaelli et al. 1998). They cause nuisance blooms in lakes and shallow marine areas when general conditions for algal growth become favourable, e.g. by increased nutrient availability (Kamer et al. 2001, Gordillo et al. 2003) or increased water temperature (Snoeijs & Prentice 1989). In a wide ecological sense, these short-lived, fast-growing easy colonisers are classified as r-strategists. Our study deals with a subdivision within this group of r-strategists into persistent and ephemeral species, with emphasis on ecophysiological aspects. In the brackish Baltic Sea, 1 *Cladophora* and 1 *Ulva* species meet and coexist in a conspicuous belt on rocky coasts. Even a simple comparison of the variability of photosynthetic rates measured on different days (Table 2, Figs. 2 & 3) identifies *C. glomerata* as the more stable species compared with *U. procera*. In the highly dynamic hydrolittoral zone of the northern Baltic Sea, *C. glomerata* usually persists throughout the summer, while *U. procera* appears to arrive with favourable and leave with unfavourable conditions. When conditions are favourable, *U. procera* seems to be able to successfully compete with *C. glomerata* for nutrients and space when they coexist and both are in good vigour.

In comparison with the weight-specific photosynthetic properties of 12 red and brown macroalgal species growing at Askö and measured with the same photosynthetic equipment as used in the present study (Johansson & Snoeijs 2002), the α and P_{max} values of *Ulva procera* were the highest measured. The α and P_{max} values of the red algae *Ceramium tenuicorne* (Kütz.) Wærn, *Ceramium nodulosum* (Lightf.) Ducluz, *Polysiphonia fucoides* (Huds.) Grev. and the brown algae *Dictyosiphon foeniculaceus* (Huds.) Grev. and *Pilayella littoralis* (L.) Kjellm. were all higher than those of *Cladophora glomerata*. These observations indicate that the differences in photosynthesis between *U. procera* and *C. glomerata* are not caused by morphology because the 3 above-mentioned red algae all have a coarser filamentous thallus structure than *C. glomerata*. The relatively low photosynthetic capacity of *C. glomerata* (for a thin-filamentous species in the area) could not be explained by detrimental conditions either, as the algal belt was well-developed at the sampling site. Neither could it be caused by nutrient limitation because the tissue C, N and P levels of *C. glomerata* were well balanced (Table 1), while those of *U. procera* indicated P-limitation (Björnsäter & Wheeler 1990, Lohman & Priscu 1992, Planas et al. 1996, Altamirano et al. 2000). A factor that partly explains the difference in photosynthetic capacity between the 2 species is the much higher chlorophyll level per unit DW in *U. procera*. A plausible functional explanation is that *C. glomerata* is adapted to keep its photosynthesis at a stable high (but not too high) level to be able to maintain its thallus also when carbon and other nutrients are less readily available in the dense belts. Thus, the ephemeral life form of *U. procera* may be partly driven by a lower capability of nutrient storage compared with *C. glomerata*.

Figueroa et al. (2003) compared photosynthetic properties and pigment composition of 2 morphologically similar *Ulva* species, the subtidal *U. rotundata* Bliding (shade adapted) and the intertidal *U. olivascens* P. A. Dangeard (sun adapted). The sun-adapted species showed lower pigment contents, lower α, higher P_{max} (all weight specific) and higher E_c and E_k. Lower α

values in combination with higher P_{max}, E_c and E_k were also typically found for the intertidal red alga *Porphyra umbilicalis* (L.) J. Ag. compared with the deep-growing red alga *Phycodrys rubens* (L.) Batters, which has a similar morphology (Johansson & Snoeijs 2002). Another parameter that can be used to distinguish sun- and shade-adapted green algae is the ratio chl *b*/chl *a*, which is lower in sun-adapted algae (Lüning 1990, p. 307). In our case, *Cladophora glomerata* had lower pigment contents per unit weight, lower chl *b*/chl *a*, lower α and higher E_c, but also lower P_{max}, while E_k did not differ between the 2 species. From these measurements it can be concluded that *C. glomerata* has more features in common with sun-adapted algae, and *U. procera*, with shade-adapted algae. The main difference between *U. procera* and 'real' shade-adapted algae is its high P_{max}, which is a major feature of its ephemeral life form, while a lower P_{max} fits the more persistent *C. glomerata*. In the field, neither of the 2 species was observed to be typically growing in the understorey of the other. However, its higher sensitivity to light may provide *U. procera* with the ability to invade already dense algal belts by fragments or spores, or to persist as fragments in the understorey where light penetration is limited. In this way *U. procera* would be able to easily re-establish when conditions become favourable again. The low E_c of *U. procera* (15) is comparable to that of deep-growing marine red algae such as *Dilsea carnosa* (Schmidel) Kuntze and *Phycodrys rubens* (L.) Batters, which, in the Skagerrak, have mean depth distributions of 13 and 17 m, respectively (Johansson & Snoeijs 2002). The E_c of *C. glomerata* (50) was high compared to the values of the other 12 previously studied species from Askö, most of which had an E_c of around 25 (Johansson & Snoeijs 2002).

Our pH-drift experiments showed that both *Cladophora glomerata* and *Ulva procera* possess highly efficient carbon-uptake systems, active up to pH ~10.4 when carbon occurred as HCO_3^- (~10%) and CO_3^{2-} (~90%) in the brackish Baltic Sea water. Three carbon-uptake mechanisms were identified by specific inhibitors in both species: an AZ-sensitive periplasmic CA, a VAN-sensitive proton pump and a DIDS-sensitive AE. In our previous studies of carbon-uptake mechanisms in marine and brackish-water algae, we measured alkalinity during pH-drift as well, which made it possible to calculate the carbon uptake from changes in pH and alkalinity at a specific temperature and salinity (Choo et al. 2002, Snoeijs et al. 2002, Ray et al. 2003). In such calculations it is also necessary to correct for the buffer capacity of the inhibitors AZ and VAN in seawater of a given salinity. However, in the present comparison of the strategies of the 2 species we only wished to know which mechanisms of carbon uptake were available to *C. glomerata* and *U. procera* from the sampling site and to obtain a rough measure of the relative magnitudes of the inhibitor effects.

Algae which cannot raise the pH above 9 in a closed system are considered incapable of HCO_3^- membrane transport (Maberly 1990). *Cladophora glomerata* possesses several options for HCO_3^- transport because during photosynthesis and carbon uptake the pH could be raised far above 9 when CA, AE, or a proton pump were blocked. This includes uptake of HCO_3^- because inhibition of the enzyme necessary for the conversion of HCO_3^- to CO_2 (CA) still resulted in high carbon uptake rates. When CA, AE and a proton pump were blocked simultaneously, no HCO_3^- was transported. In similar experiments with combinations of inhibitors it was found that *C. glomerata* could not raise the pH above 9 by periplasmic CA alone (DIDS + VAN treatment) or by AE alone (AZ + VAN treatment), but that HCO_3^- could be transported when a proton pump was active (AZ + DIDS treatment) (Choo 2001). In *Ulva procera*, HCO_3^- utilisation was highly dependent on periplasmic CA; when this enzyme was blocked, AE and the proton pump could not compensate for the loss in carbon uptake. The only possibility for *U. procera* to utilise HCO_3^- (pH raise above 9) was when both CA and AE were available to the alga (VAN treatment). When both CA and the proton pump (DIDS treatment) were available, HCO_3^- still could not be utilised by *U. procera* (no pH raise above 9). These results suggest that a proton pump is involved in HCO_3^- transport in *C. glomerata*, while in *U. procera* a proton pump transporting only CO_2 seemed to be present. Thus, for HCO_3^- transport, *U. procera* appears to be solely dependent on its AE, as previously shown for *U. intestinalis* by Larsson et al. (1997). *C. glomerata* possesses several possible mechanisms and has therefore a more flexible carbon uptake. As *C. glomerata* relies more on its proton pump than *U. procera* and because CO_2 can be transported over all the cell membranes in *U. procera* for direct use in rubisco (HCO_3^- has to be converted to CO_2 by intracellular CA), it is probable that the carbon-uptake system of *C. glomerata* requires more energy. However, our results also suggest that *C. glomerata* has a carbon-uptake system which is better adapted for persistence in dense algal belts with high pH and carbon limitation than that of *U. procera*. Carbon limitation, and limitation of other nutrients (P?), during fast growth of *U. procera* may be the reason for its often observed sudden disappearance from the upper littoral.

While *Cladophora glomerata* can cope better with high light stress in the upper littoral zone, the more low-light-adapted *Ulva procera* removes excessive absorbed energy by the water–water cycle (Asada 1999) and produces high amounts of H_2O_2. This H_2O_2

is removed through diffusion out of the cells into the seawater. We showed that H_2O_2 in the seawater medium was harmful to the photosynthesis of *C. glomerata*, but not to that of *U. procera*. This suggests that H_2O_2 may be involved in direct competition between *U. procera* and *C. glomerata* as an allelochemical because *U. procera* releases much higher levels of H_2O_2 to the seawater medium than *C. glomerata* at high irradiation and carbon deficiency (Abrahamsson et al. 2003, Choo et al. 2004). High release of H_2O_2 may, together with intercalary growth (Table 4) and an ephemeral life form, prevent the growth of epiphytes. In the Baltic Sea, *U. procera* usually has conspicuously fewer epiphytes (mainly diatoms) than *C. glomerata* (Snoeijs 1999). Collén & Pedersén (1996) studied the toxicity of H_2O_2 on *U. rigida* and found that photosynthesis and carbon uptake were inhibited at a concentration of 1000 µM H_2O_2 in seawater, but not at 100 µM. However, the unicellular green alga *Euglena gracilis* decreased in growth by 5 to 45% at 100 µM H_2O_2 (Radtke et al. 1992). *U. rigida* is a close relative of *U. procera* and also releases high amounts of H_2O_2 during stress conditions. It seems logical that these species have no or very low sensitivity to H_2O_2 in the seawater, while other species, such as *C. glomerata*, are more sensitive. If H_2O_2 indeed functions as an allelochemical, as suggested by our results, it is a cheap investment for *Ulva* species because H_2O_2 is also a cellular waste product, and lowers the costs of intracellular defence against oxidative stress (enzymes such as catalase and ascorbate peroxidase) because H_2O_2 just diffuses out of the cells.

Lower defence against oxidative stress might explain the higher sensitivity of *Ulva procera* to UV-B radiation in our study. Algal sensitivity to UV-B radiation has been suggested to be related to oxidative stress tolerance (Aguilera et al. 2002, White & Jahnke 2002). UV-B radiation causes downregulation and damage to photosystem II (PS II), which has been shown to increase the production of harmful reactive oxygen species and the activities of antioxidant enzymes in algae (Malanga & Puntarulo 1995, Lorenz et al. 1997). *U. procera* has lower activities of the antioxidant enzymes ascorbate peroxidase and catalase than *Cladophora glomerata* (Choo et al. 2004) and lacks the xanthophyll cycle which protects PS II from

Table 4. *Cladophora glomerata* and *Ulva procera*. Comparisons of life forms, morphology and ecophysiological traits during the highest level of algal seasonal growth in July to August. DW: dry weight; CA: periplasmic carbonic anhydrase

	C. glomerata	*U. procera*
Life form	Annual, stays attached throughout summer	Ephemeral, can appear and disappear from week to week
Thallus	Thin filamentous, branched, larger cells apical growth	Thin filamentous, branched, smaller cells, intercalary growth
	High P concentration, low pigment concentrations per unit DW	Low P concentration, high pigment concentrations per unit DW
Photosynthesis and respiration (normalised to DW)	Low P_{max} Low α High E_c	High P_{max} High α Low E_c
Photosynthesis and respiration (normalised to chl *a*)	High R_d Low α High E_c	Low R_d High α Low E_c
Carbon uptake	Proton pump transports HCO_3^- HCO_3^- utilisation is not dependent on CA	Proton pump does not transport HCO_3^- HCO_3^- utilisation is dependent on CA
Sensitivity to oxidative stress	Low temperature + high irradiance causes less lipid damage[a]	Low temperature + high irradiance causes more lipid damage[a]
	UV-B radiation has a weaker negative effect on photosynthesis	UV-B radiation has a stronger negative effect on photosynthesis
	Fast recovery after UV-B treatment	Slow recovery after UV-B treatment
Defences against oxidative stress	High carotenoids/chl *a* ratios Active xanthophyll cycle	Low carotenoids/chl *a* ratios No xanthophyll cycle
	High intracellular activities of the enzymes catalase and ascorbate peroxidase[a] Low excretion of H_2O_2[a]	Low intracellular activities of the enzymes catalase and ascorbate peroxidase[a] High excretion of H_2O_2[a]

[a]Data from Choo et al. (2004)

oxidative damage (Asada 1999). Low recovery of photosynthesis in *U. procera* also shows that the damage to PS II was more severe than that in *C. glomerata*, where photosynthesis is quickly restored. In general, algae growing near the water surface need strong protective mechanisms against UV-B radiation, and this is considered a factor affecting the vertical distribution of macroalgae (Bischof et al. 1998, Johansson & Snoeijs 2002, Figueroa et al. 2003). The high sensitivity of *U. procera* to UV-B (93 ± 7 % of photosynthesis lost after the 30-min treatment) is shared by its close relative *U. intestinalis* (85 ± 3 %). Only 5 out of 32 other algal species growing at water depths from 0.25 to 20.5 m that were tested by the same method lost >85 % of their photosynthesis (Johansson & Snoeijs 2002). Among these were some deep-water species, but also the filamentous brown alga *Dictyosiphon foeniculaceus*. This is surprising as *U. procera*, *U. intestinalis* and *D. foeniculaceus* occur in the upper littoral of the Baltic Sea, and it is possible that low resistance to UV-B radiation may be related to low defence against oxidative stress and an ephemeral life form.

From our experiments we can draw some conclusions that are valid when the *Cladophora*-belt is at its highest state of development in the Baltic Sea during summer. While the ecophysiological traits of *C. glomerata* seem to be directed to persistence (efficient carbon uptake and well-developed intracellular defences against oxidative stress, such as the xanthophyll cycle, enzymes and high carotenoid/chl *a* ratios), those of *Ulva procera* seem to be more engaged with large but short-term gains (efficient photosynthesis, high sensitivity to light, high pigment concentrations per unit DW, excretion of H_2O_2). This correlates with their different life strategies (summarised in Table 4). Ecological processes in algal belts are complicated, as shown by Lotze et al. (2000), who found that the combined effects of a propagule bank, herbivory and nutrients best explained the population development and dominance patterns of the 2 co-occurring bloom-forming macroalgae *Ulva intestinalis* and *Pilayella littoralis* in the southern Baltic Sea and that the magnitude of these effects varied with season. Our study shows that with this variety of factors the ecophysiological traits of the constituent species should also be integrated in order to explain population development and dominance patterns in macroalgal blooms.

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