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Macroalgal photosynthetic responses to light in relation to thallus morphology and depth zonation

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ABSTRACT: We show how photosynthesis and UV sensitivity of algae are related to thallus morphology and depth distributions. This was studied for typical depth zonations of red and brown macroalgae in the Skagerrak (ca. 25 psu) and the Baltic Sea (6.5 psu). The algae were collected from the water surface down to 20.5 m of depth, whereby each species was sampled at its maximum abundance depth. Altogether, we measured photosynthetic and respiratory rates of 19 red and 13 brown algal species as O_2 evolution at different light intensities. Photosynthesis versus irradiance curves (*PI* curves) showed that light-saturated net photosynthetic rates (P_{max}), respiratory rates in darkness (R_d) and the initial slope (α) were strongly related to algal morphology with higher values for thinner species. The compensation irradiance (I_c) and saturating irradiance (I_k) were strongly related to water depth with lower values at greater depth. A novel approach to analyse *PI* data with principal component analysis (PCA) is presented. The method makes it possible to assign a quantitative morphological gradient to algal species based on photosynthetic properties. Such a gradient can be used in ecological studies as an alternative to more subjective discrete subdivisions into functional-form groups. Another type of PCA analysis, with the relative shapes of the *PI* curves as input data, summarises α and convexity but discards all interference of morphology. This results in a gradient of genuine physiological responses, which in our study was strongly correlated to maximum abundance depth. The UV sensitivity of the same 32 algal species was determined as the change in net O_2 evolution after exposure to UV light and the recovery after this treatment. Deeper-growing algae were more sensitive to UV and species with thinner thalli recovered better after UV treatment in the Skagerrak. No such trends were observed for the algae in the northern Baltic Sea, which suggests that no real deep-water species occur here. This is further supported by the lack of a clear pattern in I_c and I_k values with depth for the algae in the Baltic Sea. Our results advocate that the reduced species diversity of the Baltic Sea is also coupled to a loss of functional groups in the sense of general photosynthetic performance and not only in the sense of pure morphology (loss of canopy-forming species).

KEY WORDS: Macroalgae · Depth zonation · Thallus morphology · Photosynthesis · Respiration · UV radiation · *PI* curve · PCA analysis

INTRODUCTION

The morphology of species is generally considered an important trait in algal ecology, e.g. to explain the outcome of interspecific competition (Lobban & Harrison 1997). Littler & Littler (1980) were the first to define functional-form groups for marine macroalgae. It is a well-known phenomenon that thin sheet-like and filamentous algae increasingly outcompete thick sheet-like algae with increasing eutrophication in coastal areas (Schramm & Nienhuis 1996), which is also the case in the Skagerrak (Johansson et al. 1998) and the Baltic Sea (Eriksson et al. 1998). One advantage of thin sheet-like and filamentous species in this case is the capability of fast growth, which is coupled to high photosynthetic rates per unit biomass (Littler et al. 1983, Falkowski & Raven 1997).

Photosynthetic properties, such as compensation and saturating irradiances, have been suggested to regu-

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late the zonation of macroalgae on rocky shores (Lüning 1981). Deeper-growing algae are generally more sensitive to light (due to lower compensation irradiances), which is considered an adaptation to low light levels at greater depth. Also, sensitivity to UV light may influence the zonation pattern (Bischof et al. 1998b). One would expect species growing closer to the surface to be more tolerant to UV and to recover better after periods of high UV radiation. Species with tougher and thicker thalli may also be less sensitive to UV radiation as a result of more protective tissue.

On the virtually atidal Swedish west coast, there is a strong trend of decreasing abundance of filamentous species and increasing abundance of leaf-like species with increasing water depth (Pedersén & Snoeijs 2001). On the Swedish Baltic Sea coast, this pattern becomes more diffuse. Here, the zonation is fundamentally different from that in the Skagerrak because the few species that can survive in the low salinity of the Baltic Sea have greatly extended depth distributions due to low competition (Snoeijs 1999). These field observations raise the question as to how photosynthesis and UV sensitivity of algae are related to thallus morphology and depth distributions. The aim of the present study was to investigate this for typical depth zonations of red and brown macroalgae in the Skagerrak and the Baltic Sea, and to elucidate the importance of algal responses to light in structuring the vegetation in the 2 areas.

MATERIALS AND METHODS

The sampling area in the Skagerrak was situated at the mouth of the Gullmar Fjord (58° 26′ N, 11° 42′ E, salinity ca. 25 psu at the surface, 33 psu below the halocline at ca. 15 m of water depth) and in the Baltic Sea at the island of Askö (58° 49′ 25″ N, 17° 38′ 25″ E, salinity 6.5 psu). The study in the Skagerrak was carried out from 15 to 21 June 2000 and in the Baltic Sea from 22 to 31 August 2000.

Altogether, 32 macroalgal species (19 rhodophytes and 13 phaeophytes) belonging to different functional-form groups as according to Littler & Littler (1980) were collected by snorkelling and SCUBA diving at their maximum abundance depth (Table 1). Maximum abundance depths were determined by estimating the highest percentage cover for each species along whole depth profiles while diving. Three of the species, *Dictyosiphon foeniculaceus*, *Fucus vesiculosus* and *Furcellaria lumbricalis*, were taken in both the Skagerrak and the Baltic Sea. For the Skagerrak, the species were selected to maximise the variation in water depth and thallus shape as much as possible for both red and brown algae. To provide an area-representative data set, only species that were common in the area were included. The Baltic Sea has very low macroalgal diversity (Snoeijs 1999), and all common red and brown species encountered in the Askö area during the study period were included.

The O_2 evolution experiments were designed to measure the maximum photosynthetic and respiratory capacity of each algal species by selecting only young thallus parts. The O_2 measurements were carried out in an Illuminova™ Light Dispenser System ('Light Pipette'), equipped with a halogen lamp, and a patented IR deflector and waveband definer delimiting radiation between 400 and 700 nm. Pieces of thallus, varying between 0.01 g fresh weight (FW) for the finest filamentous species (*Pilayella littoralis*, *Sphacelaria cirrosa*) and 0.5 g FW for the thickest leathery species (*Laminaria hyperborea*), were incubated in filtered natural site water (NSW) of 100% O_2 saturation (equilibrated with air) in a 2.6 ml incubation chamber with an O_2 electrode (Microelectrodes™) inserted. To elucidate the range of pH drift (and thereby carbon availability) during one 20 min experimental run, a pH electrode (Microelectrodes™) was also inserted during the first experiments. pH varied little, the mean difference between minimum and maximum pH in 20 min was 0.08 ± 0.02 (n = 12 species of different morphologies and from different depths, start pH = 8.1) and hence, there was no necessity of buffering the seawater during the experiments.

For each species, 3 experiments were carried out, each on a different algal specimen. The 3 experiments were performed at different times of the day to minimise possible diel effects. All measurements were made within 15 h from collection, and during this period the algae were stored in flowing seawater at ca. 30 µmol photons m^{-2} s^{-1}. All experiments were carried out at 14°C, which was the approximate ambient temperature in the field at the time of the experiments in both areas. The salinity of the NSW used for incubation during the experiments was 25 psu in the Skagerrak and 6.5 psu in the Baltic Sea. Two species, *Laminaria hyperborea* and *Phyllophora crispa* (both of which mainly occur below the halocline in the Skagerrak), had higher respiration than photosynthesis in 25 psu, and therefore they were incubated in NSW of 33 psu. For species with flat thalli (sheet and thick leathery), the results were normalised to both dry weight (DW) and surface area (SA), but for the other species only to DW.

Two different types of experiments were carried out. The first type consisted of a 1200 s long computer-steered measuring sequence including 8 dark pulses and 7 light pulses of 80 s each. The % O_2 saturation and change in % O_2 saturation (photosynthetic rate) were recorded every 2 s. The photon flux density was increased for each light pulse and measured 10, 20, 50,

100, 300, 600 and 900 µmol photons m^{-2} s^{-1}, respectively. Data used to construct photosynthesis versus irradiance (*PI*) curves were the mean of the last 20 out of the total 40 O_2 records in each pulse; this allowed for a 40 s lag phase for differences in gas exchange between species due to thallus thickness. The curves were fitted using the equation $P_{net} = (P_{max} \times \tanh [\alpha \times \text{Irradiance}/P_{max}]) + R_d$ (Jassby & Platt 1976, Henley 1993) employing the Levenberg-Marquardt algorithm with standard error (SE) for the parameter estimates P_{max} and α.

The second type of experiment consisted of 5 successive runs with the same thallus piece after acclimation (until stable O_2 rates were reached) to 300 µmol photons m^{-2} s^{-1}. Each run consisted of a 600 s long sequence with O_2 recordings every second. The NSW was exchanged between the runs to keep O_2 saturation below 130 % and to avoid carbon limitation. During all runs, constant irradiation of 300 µmol photons m^{-2} s^{-1} was provided. Runs 2 to 4 included ultraviolet (UV) radiation at 1.58 W m^{-2} UV A (320 to 400 nm) and 2.45 W m^{-2} UV B (280 to 320 nm), i.e. close to natural

Table 1. List of the investigated algal species, including abbreviations, maximum abundance depths and functional-form groups according to Littler et al. (1983). The species are arranged by decreasing maximum abundance depth within areas and algal groups

Species	Abbreviation	Maximum abundance depth	Functional-form group
Skagerrak			
Rhodophyta			
Polysiphonia brodiaei (Dillwyn) Spreng.	Pol bro	0.25	Filamentous
Porphyra umbilicalis (L.) J. Agardh	Por umb	0.25	Sheet
Chondrus crispus Stackh.	Cho cri	1.5	Thick leathery
Furcellaria lumbricalis (Huds.) J. V. Lamour	Fur lum	2.5	Coarsely branched
Gracilaria verrucosa (Huds.) Papenf.	Gra ver	2.5	Coarsely branched
Spermothamnion repens (Dillwyn) Rosenv.	Spe rep	7.0	Filamentous
Cystoclonium purpureum (Huds.) Batters	Cys pur	4.5	Coarsely branched
Membranoptera alata (Huds.) Stackh.	Mem ala	4.5	Coarsely branched
Brongniartella byssoides (Gooden & Woodw.) F. Schmitz	Bro bys	5.0	Filamentous
Dilsea carnosa (Schmidel) Kuntze	Dil car	13.0	Thick leathery
Lomentaria clavellosa (Turner) Gaillon	Lom cla	17.0	Filamentous
Phycodrys rubens (L.) Batters	Phy rub	17.0	Sheet
Phyllophora crispa (Huds.) P. S. Dixon	Phy cri	20.5	Thick leathery
Phaeophyta			
Ascophyllum nodosum (L.) LeJol	Asc nod	0.5	Thick leathery
Dictyosiphon foeniculaceus (Huds.) Grev.	Dic foe	0.5	Filamentous
Fucus serratus L.	Fuc ser	0.5	Thick leathery
Fucus vesiculosus L.	Fuc ves	0.5	Thick leathery
Sargassum muticum (Yendo) Fensholt	Sar mut	2.0	Coarsely branched
Halidrys siliquosa (L.) Lyngb.	Hal sil	3.5	Thick leathery
Sphacelaria cirrosa (Roth.) C. Agardh	Sph cir	3.5	Filamentous
Laminaria saccharina (L.) J. V. Lamour	Lam sac	4.5	Thick leathery
Desmarestia aculeata (L.) J. V. Lamour	Des acu	11.0	Coarsely branched
Laminaria hyperborea (Gunnerus) Foslie	Lam hyp	14.5	Thick leathery
Baltic Sea			
Rhodophyta			
Ceramium tenuicorne (Kütz.) Wærn	Cer ten	4.5	Filamentous
Ceramium nodulosum (Lightf.) Ducluz	Cer nod	5.0	Filamentous
Furcellaria lumbricalis (Huds.) J. V. Lamour	Fur lum	5.5	Coarsely branched
Polysiphonia fucoides (Huds.) Grev.	Pol fuc	8.5	Filamentous
Rhodomela confervoides (Huds.) P. C. Silva	Rho con	8.5	Coarsely branched
Coccotylus truncatus (Pall.) M. J. Wynne & J. M. Heine	Coc tru	12.0	Thick leathery
Phyllophora pseudoceranoides (S. G. Gmel.) Newroth & A. R. A. Taylor	Phy pse	12.0	Thick leathery
Phaeophyta			
Chorda filum (L.) Stackh.	Cho fil	0.25	Coarsely branched
Dictyosiphon foeniculaceus (Huds.) Grev.	Dic foe	0.25	Filamentous
Fucus vesiculosus L.	Fuc ves	2.5	Thick leathery
Pilayella littoralis (L.) Kjellm.	Pil lit	8.0	Filamentous
Sphacelaria arctica Harv.	Sph arc	14.0	Filamentous

levels for UV B at the water surface, but only ca. 4 % of natural UV A levels (Dring et al. 1996). The first run was used as a control and the last run as a postcontrol (recovery test). The UV effect was expressed as the percentage O_2 evolution left after 30 min of UV treatment and the recovery was expressed as the percentage O_2 evolution (of the control) regained after 10 min postcontrol.

Statistics follow Fowler et al. (1998) and ter Braak & Šmilauer (1998), and were performed with the STATISTICA™ software. Significance was accepted at $p < 0.05$.

Table 2. Photosynthetic properties and PCA scores of the investigated algal species. The species are arranged by decreasing maximum abundance depth within areas and algal groups. See Table 1 for full names of species. P_{max} = light-saturated net photosynthetic rate in µmol O_2 kg DW^{-1} s^{-1}. R_d = rate of respiration in darkness in µmol O_2 kg DW^{-1} s^{-1}. α = initial slope at limiting irradiance levels in µmol O_2 kg DW^{-1} (µmol photons $m^{-2})^{-1}$. $I_c = R_d/\alpha$ = compensation irradiance in µmol photons m^{-2} s^{-1}. $I_k = P_{max}/\alpha$ = light saturation parameter in µmol photons m^{-2} s^{-1}. R-value = R-value of the Levenberg-Marquardt algorithm used to fit the *PI* curve. M-axis = Axis 1 in the PCA analysis with the original data. D-axis = Axis 1 in the PCA analysis with the relative data. UV treatm. = O_2 rate expressed as % of control after 30 min of UV treatment. UV recov. = O_2 rate expressed as % of control regained after 10 min post control. SE = standard error of the mean

Species	P_{max} ± SE	R_d ± SE	α ± SE	I_c	I_k	R-value	PCA score M-axis	PCA score D-axis	UV treatm.	UV recov.
Skagerrak										
Rhodophyta										
Pol bro	127.8 ± 8.1	−33.4 ± 8.9	0.60 ± 0.10	56	213	0.94	1.14	−0.99	55	28
Por umb	142.5 ± 9.6	−19.3 ± 3.6	0.52 ± 0.08	37	277	0.94	1.31	−1.22	44	6
Cho cri	36.3 ± 2.0	−6.7 ± 1.8	0.26 ± 0.04	26	139	0.93	−0.81	−0.17	42	21
Fur lum	22.0 ± 1.3	−2.6 ± 0.2	0.13 ± 0.02	19	164	0.93	−1.17	−0.59	50	4
Gra ver	66.6 ± 3.6	−10.2 ± 1.3	0.36 ± 0.06	29	186	0.94	−0.16	−0.72	26	21
Spe rep	135.0 ± 6.8	−36.0 ± 1.6	1.31 ± 0.19	28	103	0.93	1.66	0.60	43	29
Cys pur	105.6 ± 2.7	−24.1 ± 0.1	0.76 ± 0.06	32	139	0.98	0.83	−0.18	23	11
Mem ala	78.9 ± 2.1	−13.8 ± 3.0	1.10 ± 0.09	13	72	0.98	0.36	1.30	34	20
Bro bys	96.5 ± 5.5	−19.5 ± 5.7	0.79 ± 0.13	25	122	0.92	0.66	0.16	16	31
Dil car	36.1 ± 1.7	−5.4 ± 1.3	0.38 ± 0.05	14	95	0.94	−0.77	0.60	56	43
Lom cla	128.5 ± 9.1	−32.1 ± 5.7	1.80 ± 0.38	18	72	0.85	1.67	1.10	8	1
Phy rub	87.1 ± 2.5	−21.3 ± 1.9	1.98 ± 0.19	11	44	0.96	0.69	1.96	4	4
Phy cri	43.7 ± 1.6	−4.1 ± 1.0	0.99 ± 0.13	4	44	0.92	-0.49	1.92	27	34
Phaeophyta										
Asc nod	20.4 ± 0.8	−3.8 ± 0.1	0.06 ± 0.01	62	336	0.98	−1.27	−1.57	49	47
Dic foe	166.0 ± 13.1	−35.2 ± 1.0	0.37 ± 0.05	95	446	0.95	1.37	−1.52	21	34
Fuc ser	47.6 ± 2.0	−10.3 ± 1.5	0.14 ± 0.01	71	329	0.98	−0.72	−1.49	74	66
Fuc ves	62.7 ± 3.7	−11.8 ± 1.4	0.20 ± 0.03	60	317	0.96	−0.41	−1.58	81	62
Sar mut	69.3 ± 3.4	−16.1 ± 1.5	0.29 ± 0.04	55	237	0.96	−0.18	−1.14	47	36
Hal sil	22.4 ± 1.2	−5.0 ± 0.4	0.15 ± 0.02	33	148	0.93	−1.15	−0.27	67	31
Sph cir	168.0 ± 7.6	−37.3 ± 1.4	1.24 ± 0.16	30	136	0.95	2.35	−0.20	40	21
Lam sac	37.3 ± 1.2	−11.4 ± 0.4	0.46 ± 0.04	25	81	0.97	−0.72	0.95	1	42
Des acu	81.2 ± 3.4	−15.2 ± 1.8	0.91 ± 0.11	17	89	0.95	0.37	0.80	22	30
Lam hyp	21.7 ± 0.8	−6.5 ± 1.3	0.15 ± 0.02	42	140	0.97	−1.16	−0.15	44	51
Baltic Sea										
Rhodophyta										
Cer ten	106.9 ± 3.9	−25.1 ± 2.7	1.15 ± 0.12	22	93	0.96	0.92	0.65	8	19
Cer nod	73.9 ± 1.9	−22.2 ± 1.4	0.69 ± 0.05	32	107	0.98	0.07	0.32	45	19
Fur lum	21.2 ± 1.0	−3.0 ± 0.9	0.18 ± 0.02	16	116	0.95	−1.17	0.05	60	21
Pol fuc	96.5 ± 7.1	−22.5 ± 6.0	0.96 ± 0.20	23	100	0.87	0.65	0.54	40	21
Rho con	45.7 ± 1.9	−15.2 ± 1.4	0.62 ± 0.08	24	74	0.95	−0.55	1.21	40	19
Coc tru	21.3 ± 1.0	−6.4 ± 0.9	0.31 ± 0.04	21	69	0.93	−1.15	1.25	32	50
Phy pse	39.7 ± 2.2	−10.7 ± 2.0	0.48 ± 0.08	22	82	0.91	−0.70	0.96	17	27
Phaeophyta										
Cho fil	17.3 ± 1.2	−4.3 ± 1.3	0.09 ± 0.02	46	184	0.92	−1.28	−0.61	25	51
Dic foe	120.5 ± 6.0	−25.7 ± 3.3	0.47 ± 0.06	55	256	0.96	0.81	−1.37	11	24
Fuc ves	54.0 ± 3.8	−9.3 ± 2.4	0.28 ± 0.06	34	195	0.91	−0.50	−0.89	51	34
Pil lit	96.2 ± 3.9	−17.2 ± 2.3	0.77 ± 0.09	22	124	0.96	0.58	0.10	51	38
Sph arc	25.7 ± 0.8	−7.7 ± 1.4	0.23 ± 0.02	34	113	0.97	−1.07	0.19	63	23

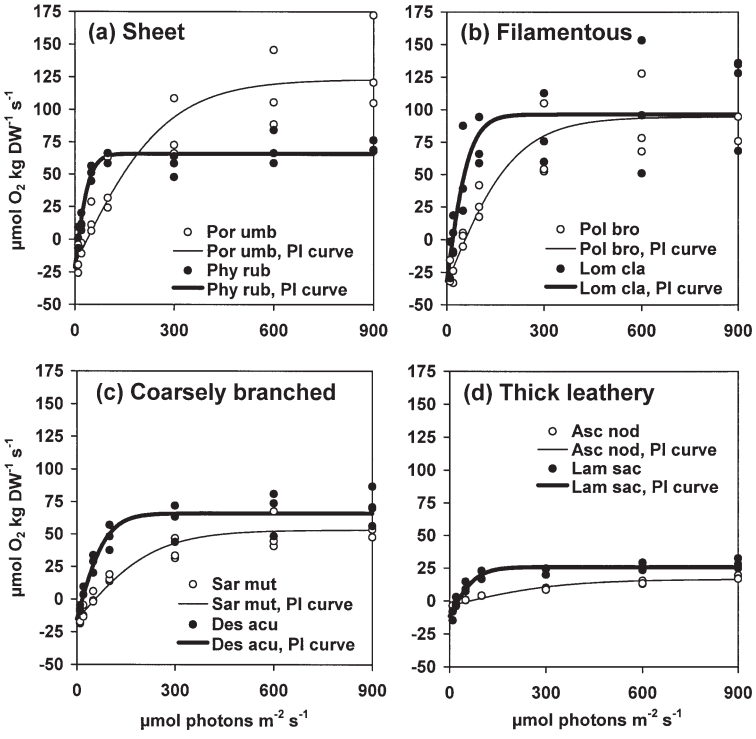

Fig. 1. Measured O_2 evolution (circles) and *PI* curves for 8 macroalgal species from the Skagerrak selected pairwise by morphology: (a) sheet, (b) filamentous, (c) coarsely branched and (d) thick leathery. See Table 1 for full names of species. Within pairs, the species are selected according to large differences in maximum abundance depth. Thick lines and filled circles represent deeper-growing species

RESULTS

The photosynthetic properties of the investigated algal species normalised to DW are given in Table 2. To illustrate the range of differences between the species, Fig. 1 shows the *PI* curves for 8 species from the Skagerrak selected pairwise by morphology and within the pairs, according to large differences in maximum abundance depth. Differences in morphology are reflected by high P_{max} and R_d for algae with high surface to volume ratios (sheets and filamentous), and lower P_{max} and R_d for algae with low surface to volume ratios (coarsely branched and thick leathery). A striking feature is the shape of the curve, with higher α and lower I_k for the deeper-growing species. The comparison of P_{max}, R_d and α between species is greatly dependent on the normalisation used. This is illustrated in Fig. 2 by the example of *Fucus vesiculosus* and *Porphyra umbilicalis*, 2 species growing close to each other at the upper water fringe in the Skagerrak.

When DW was used, *P. umbilicalis* had the highest P_{max}, R_d and α, but when SA was used, *F. vesiculosus* had the highest values. However, the relative shape of the curve, as well as I_c and I_k, were the same for each species, irrespective of normalisation. For the whole data set (n = 35), Pearson correlation coefficients (r_P, $p < 0.05$) showed that P_{max} and R_d were strongly correlated ($r_P = -0.94$), as well as I_c and I_k ($r_P = 0.93$). α was weakly correlated to P_{max} ($r_P = 0.59$), R_d ($r_P = -0.63$), I_c ($r_P = -0.47$) and I_k ($r_P = -0.51$). No significant correlations were found between P_{max} or R_d and I_c or I_k. Maximum abundance depth was not correlated to P_{max} or R_d, but it was significantly ($p < 0.05$) correlated to α ($r_P = 0.48$), I_c ($r_P = -0.62$) and I_k ($r_P = -0.69$).

Fig. 3 shows a comparison of photosynthetic properties between the Skagerrak and the Baltic Sea for the different functional-form groups. Significant differences were found between the means of P_{max}, R_d and α as a result of functional-form group (sheets excluded because of too few observations) and area (Skagerrak or Baltic Sea) by 2-way ANOVA ($p < 0.05$), but not for the means of I_c and I_k ($p > 0.05$). Pairwise comparisons rendered significant differences between the 2 areas only for P_{max} in the filamentous and coarsely branched groups, and for R_d in the filamentous group (unpaired *t*-tests, $p < 0.05$; Fig. 3). Despite a general tendency to lower mean values of α, I_c and I_k in the Baltic Sea, the differences were not significant because of large variation within the functional-form groups.

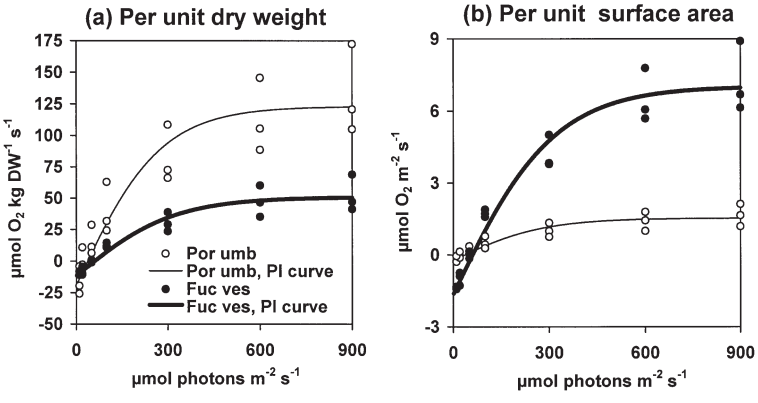

Fig. 2. Measured O_2 evolution (circles) and *PI* curves for 2 species co-occurring in the upper littoral zone of the Skagerrak, *Fucus vesiculosus* (thick lines, filled circles) and *Porphyra umbilicalis* (thin lines, open circles) normalised to (a) dry weight and (b) surface area

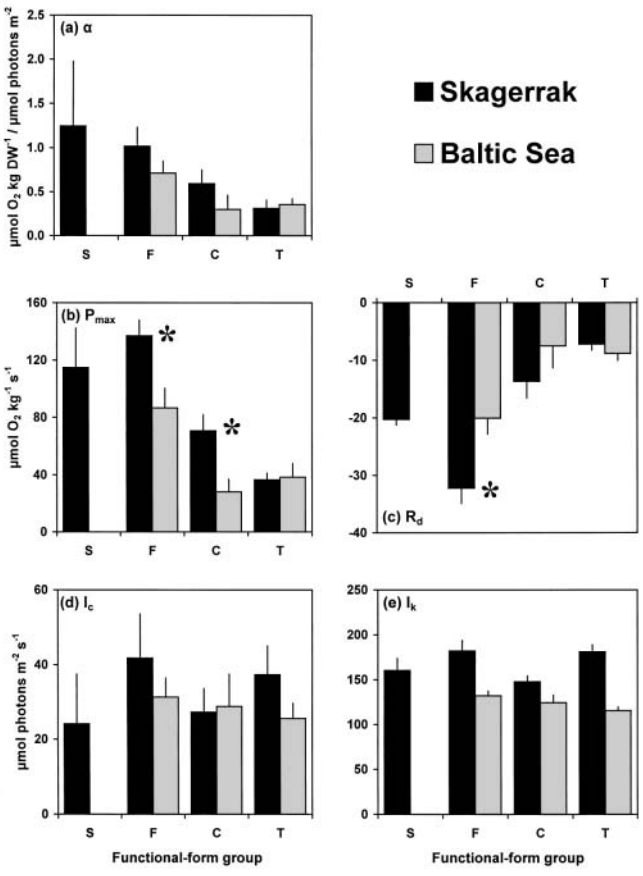

Fig. 3. Comparisons of photosynthetic properties between the Skagerrak and the Baltic Sea for different functional-form groups: S = sheet, F = filamentous, C = coarsely branched, T = thick leathery. Photosynthetic properties are expressed as mean ± SE. Skagerrak: S: n = 2, F: n = 6, C: n = 6, T = 9; Baltic Sea: S: n = 0, F: n = 6, C: n = 3, T: n = 3. (a) Initial slope at limiting irradiance levels, α; (b) light-saturated net photosynthetic rate, $P_{max;}$ (c) rate of respiration in darkness, R_d; (d) compensation irradiance, I_c (= R_d/α); (e) light saturation parameter, I_k (= P_{max}/α). * Significant differences ($p < 0.05$, unpaired *t*-test)

Two principal components analyses (PCA) runs were carried out on the triplicate O_2 exchange rates at the 7 irradiances (n = 3 × 7 data points per species). The first data set, using the original data, yielded eigenvalues of 0.94 and 0.05 for the first 2 ordination axes, respectively. The second data set, using the relative proportions of O_2 rates in each of the 7 irradiances within each experiment related to 0 irradiance, yielded eigenvalues of 0.86 and 0.09 for the first 2 ordination axes, respectively. This shows that in both analyses the first axis explains almost all variation in the data. The second data set only included data on the shape of the curve irrespective of P_{max} and R_d, and is therefore related to α and convexity (the sharpness of transition from photon flux density limitation to saturation). When using the original data, Axis 1 (hereafter referred to as the 'M-axis') showed a gradient in morphology with thicker thalli to the left of the ordination and thin thalli to the right (Fig. 4a). The only exception in this pattern is *Sphacelaria arctica*, a filamentous species scoring in the left of the ordination. This species contained intertwined sediment grains, which may have affected its DW. The M-axis was strongly correlated (n = 35, $p < 0.05$) to P_{max} ($r_P = 0.98$), R_d ($r_P = -0.94$) and α ($r_P = 0.72$). Axis 2 was correlated (n = 35, $p < 0.05$) to water depth ($r_P = 0.72$; Fig. 4c), as well as to α ($r_P = 0.67$), I_c ($r_P = -0.77$) and I_k ($r_P = -0.83$). No pattern was found in the ordination for sampling area (Fig. 4e). When using the relative data, Axis 1 (hereafter referred to as the 'D-axis') showed a gradient in water depth with shallow water to the left of the ordination and deep water to the right ($r_P = 0.80$; Fig. 4d), and was related to α ($r_P = 0.62$), I_c ($r_P = -0.83$) and I_k ($r_P = -0.91$) as well (all correlation coefficients n = 35, $p < 0.05$). Sampling area was related to Axis 2 (Fig. 4f) and no pattern was found for morphology (Fig. 4b). These results show that more detailed algal photosynthetic responses to light can be assessed when the effect of algal morphology is deleted from *PI* data. In our case, these detailed responses consist of differences between the 2 investigated sea areas, which are probably related to the generally lower I_c and I_k of the Baltic Sea algae (Fig. 3d,e).

UV sensitivity clearly showed different patterns for the Skagerrak and the Baltic Sea. The Skagerrak algae reflected a depth gradient with algae growing deeper being more negatively affected by UV radiation. In Fig. 5, the effects of UV treatment and subsequent recovery are plotted against the scores on the M- and D-axes obtained by the PCA analyses (Table 2, Fig. 4) for the different species. For the Skagerrak algae (n = 23), UV sensitivity was correlated to depth ($r_P = -0.61$, $p < 0.05$; Fig. 4b), but not to morphology ($p > 0.05$). Recovery after UV treatment was correlated to morphology ($r_P = -0.48$, $p < 0.05$; Fig. 4a), but not to depth ($p > 0.05$). No significant patterns of UV sensitivity with the M- or D-axes were found for the Baltic Sea algae (n = 12, $p > 0.05$).

DISCUSSION

Methodology

We used a novel data analysis approach by applying PCA to original *PI* data in 2 different ways. Thus, we were able to detach morphological impacts from genuine physiological responses to light and to obtain separate species rankings for both events. The possibility of quantifying a gradient in the morphology of species

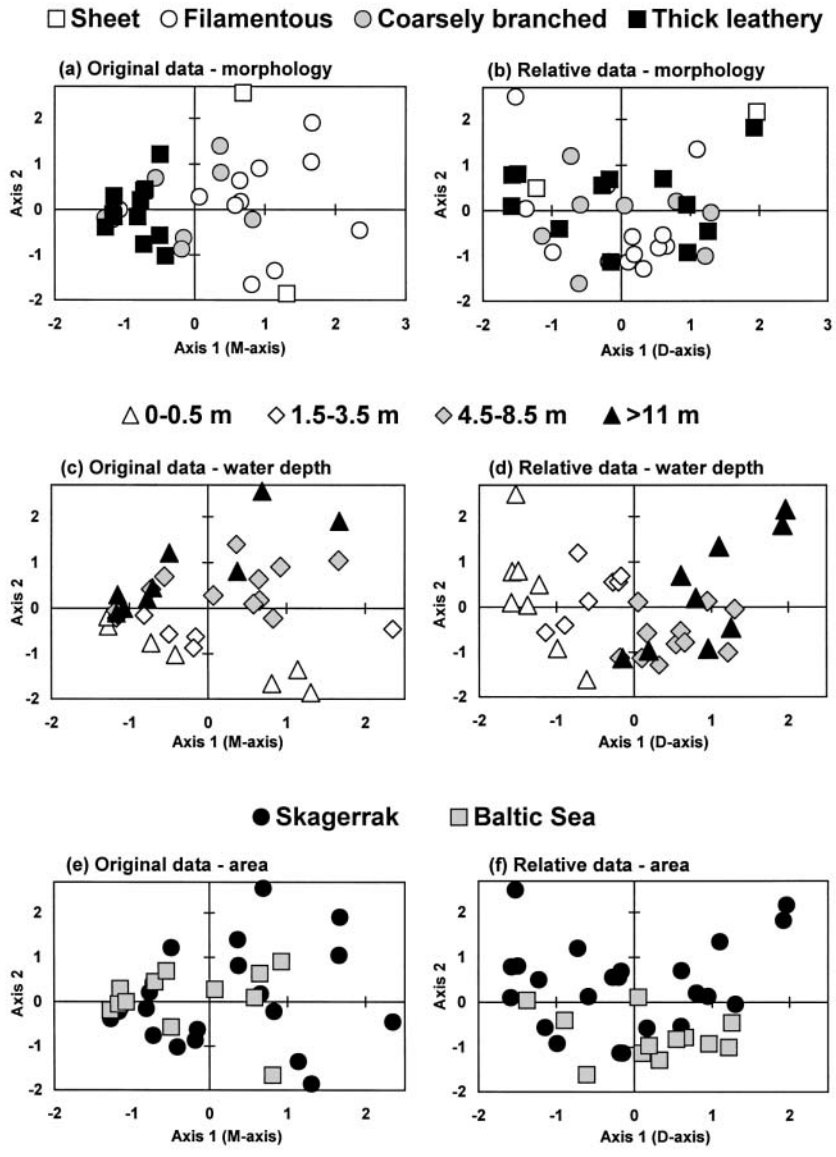

Fig. 4. PCA ordination plots: (a), (c), (e) Analyses with original data, eigenvalues for Axis 1 (M-axis) = 0.94 and for Axis 2 = 0.05; (b), (d), (f) analyses with relative data, eigenvalues for Axis 1 (D-axis) = 0.86 and for Axis 2 = 0.09. (a), (b) PCA score symbols show morphology; (c), (d) PCA score symbols show water depth intervals; (e), (f) PCA score symbols show sampling area

on the basis of their photosynthetic performances is a clear advantage in algal ecology because the attribution to functional-form groups (Littler & Littler 1980) contains a dimension of subjectivity. The shape of a *PI* curve irrespective of normalisation and thus, irrespective of morphology, as we used to assess physiological responses (the relative data set), provides an ideal tool to compare photosynthetic capacity under different environmental conditions within and between species in ecological studies. The advantage of the PCA method is that measured data are analysed. Modelled *PI* curves often build in either fixed convexity or require complicated algorithms in which one has to subjectively decide on the level of convexity (Henley 1993). Although P_{max} and R_d extracted from *PI* curve models provide good measures of morphological impacts and I_c and I_k of physiological responses, it is an advantage to be able to use measured data. We found that α is a measure of photosynthetic performance that combines both morphology and physiology; in our data set, it most strongly reflected morphology. An absolute requirement for this type of measurements is high accuracy and reproducibility of photosynthetic readings under highly controlled light conditions. When measuring O_2 evolution in small thallus pieces over short time periods, the light pipette is superior in this respect. When whole thalli of large algae are to be compared, larger incubations must be used, which will not provide the same accuracy as a result of self-shading, problems with stirring, etc.

Morphology

We found that the photosynthetic properties P_{max} and α are highly dependent on thallus morphology with higher and faster O_2 production rates for thinner and filamentous species, and lower rates for coarser and thicker species when normalised to biomass (DW) and opposite when normalised to algal SA. The same type of relationships were described for 5 green-algal species by Arnold & Murray (1980) as well as by Littler (1980) for 45 species of marine macroalgae from field incubations. Also between congeneric species, such as in the polymorphic genus *Caulerpa* (Gacia et al. 1996) and within the thallus of single specimens of *Sargassum polyceratium* Mont. (Kilar et al. 1989), strong relationships can be found between morphology and primary productivity. We have not considered whole thalli or intraspecific variation in our study, but we related the morphology of the incubated thallus pieces to their photosynthetic performance. Peckol & Ramus (1988) found that thin flat species had higher photosynthetic capacity and higher pigment content (per

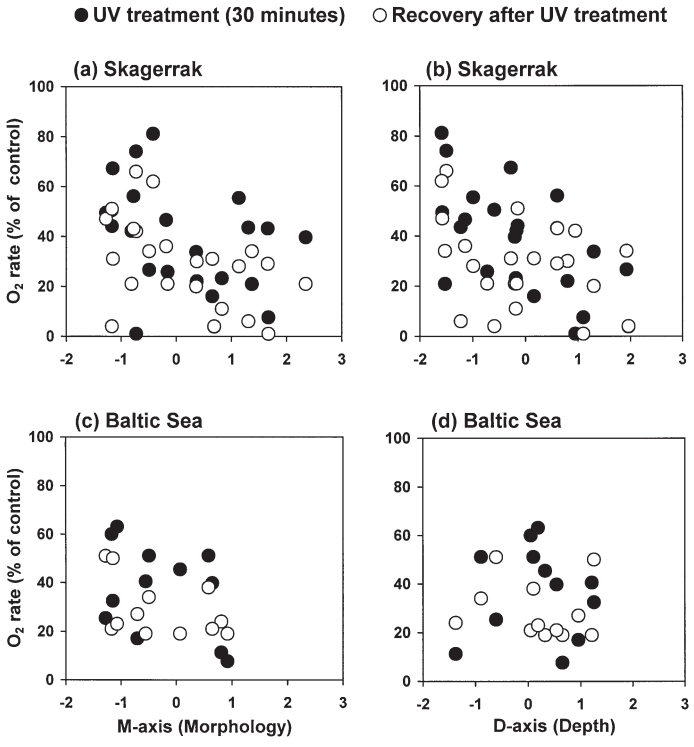

Fig. 5. UV sensitivity of the algae from the Skagerrak and the Baltic Sea. Expressed as O_2 rates in % of the control run after 30 min of UV treatment and 10 min of recovery after this UV treatment plotted against PCA scores (Table 2) of (a), (c) Axis 1 of the analysis with original data set illustrating a morphology gradient (M-axis), and (b), (d) Axis 1 of the analysis with the relative data set illustrating a depth gradient (D-axis)

unit biomass) than species with calcified, coarsely branched or leathery thalli. Also in our data, the underlying principle of the different photosynthetic rates obtained for species belonging to different functional-form groups can to a large extent be explained by the relation between photosynthetically active tissue and total biomass. However, specific action spectra for different species may also interfere (Lüning & Dring 1985, Talarico & Maranzana 2000). The increase in respiratory rates in our data was in concert with increased photosynthetic rates. This is a direct consequence of increased photosynthesis because more carbon skeletons are needed to keep the balance between light uptake and carbon fixation.

Depth zonation

Shade-adaptation in algae includes a high sensitivity to light and thus, low compensation irradiance (I_c) values (Lüning 1990). Therefore, deeper-growing algal species are expected to have lower I_c and species growing higher up in the littoral higher I_c, as we convincingly showed in our study. Also, within-species I_c can decrease as an acclimation to ambient light with water depth as shown for example by Gómez et al. (1997) for 5 Antarctic macroalgal species. However, most published records of I_c do not clearly reflect the relationship with depth in the zonation of algal species (see overview in Lüning 1981). We partly contribute our clear results to the sampling strategy of taking each species at its carefully estimated maximum abundance depth. The lack of clear data in the literature is most probably due to scattered temporal and spatial samplings of algal species and poor irradiance control at low light levels. We collected *PI* data within short time intervals (on average 3 species d^{-1}) and with high precision in irradiance control. By doing so, we found a good correlation between sampling depth and I_c (r_P = 0.62). In the PCA analysis, after correcting for algal morphology, we obtained a depth gradient (D-axis, relative data set), which had an even stronger correlation with sampling depth (r_P = 0.80). Markager & Sand-Jensen (1992) estimated the I_c for growth in laboratory-grown algal thalli from the relationship between specific growth rate (mol C mol C^{-1} d^{-1}) and irradiance. Their I_c for growth was of course much lower than our photosynthetic I_c for the 2 species that overlap between the studies: *Fucus serratus* (1.12 and 71 µmol photons m^{-2} s^{-1}, respectively) and *Chondrus crispus* (0.44 and 26). However, proportionally the 2 measures give surprisingly similar results in correctly reflecting the lower position of *Chondrus crispus* in the littoral zonation. Previously published light levels for the light saturation parameter (I_k) often do reflect the relationship with depth in the zonation of algal species (see overview in Lüning 1981), and are of the same order of magnitude as our values, i.e. 400 to 500 µmol photons m^{-2} s^{-1} for species typical of the upper littoral and below 100 µmol photons m^{-2} s^{-1} for species typical of the lower littoral. Exceptions to the general pattern are few in our data set. One is *Membranoptera alata*, which, relative to its maximum abundance depth, had low I_c, low I_k and a high score on the D-axis. This may be explained by the fact that *M. alata* is a sciaphilic species, typically found in the undergrowth vegetation of canopy-forming algae. Dark respiration versus depth has not been intensively studied in macroalgae. Some evidence indicates that algae living in deep habitats exhibit very low respiratory activity, a strategy to avoid excessive carbon losses (Littler et al. 1986, Lüning 1990). However, in our data, R_d was strongly correlated to morphology as discussed above, but not at all to sampling depth.

Sensitivity to UV radiation

We found significant correlations between UV sensitivity and water depth (D-axis) in the Skagerrak, but not in the Baltic Sea. It is logical to assume that algae growing near the water surface need stronger protective mechanisms against UV than algae growing deeper down and protected by the water column. For example, *Porphyra umbilicalis* (upper littoral) lost ca. 50% of its photosynthetic capacity by the UV treatment, but *Phycodrys rubens* (similar morphology, lower littoral) lost more than 90%. A large difference in UV sensitivity between these 2 species was previously shown by Dring et al. (1996). They found that dark-adapted variable fluorescence (ratio of variable to maximal fluorescence, $F_v:F_m$) in *P. umbilicalis* was not affected by UV radiation, but $F_v:F_m$ in *Delesseria sanguinea* and 11 other red algal species from the North Sea decreased. Dring et al. (1996) were unable to find a direct correlation between UV sensitivity and the depth ranges of the species. However, 2 similar studies on Antarctic and Arctic algae did retrieve gradients in UV sensitivity that reflect zonation patterns in the field (Bischof et al. 1998b, 2000). Also, withinspecies sensitivity to UV radiation has previously been shown, e.g. for *Chondrus crispus* sampled from different depths at the French Atlantic coast (Sagert et al. 1997). It has also been shown that *Laminaria saccharina* can acclimate effectively to increasing irradiance levels for both PAR and UV radiation (Bischof et al. 1998a). Extrapolating these observations to our results would mean that PAR and UV radiation may be considered factors structuring algal zonation in the Skagerrak, but also that algae acclimate to the ambient light climate at different depths. However, sampling at maximum abundance depth, as we did, is presumably the best way to highlight differences between species. When comparing *P. rubens* with 2 other species typical of the lower littoral, but with tougher (*Phyllophora crispa*) or thicker (*Dilsea carnosa*) thalli and both less photosynthesis-inhibited by UV, the importance of morphology is also illustrated. However, it is possible that this is a short-term effect and that different responses with morphology will disappear with longer exposure to UV radiation than that provided in our short-term experiments.

Comparisons between the Skagerrak and the Baltic Sea

Both *Furcellaria lumbricalis* and *Fucus vesiculosus* have wider depth distributions and deeper depth limits in the Baltic Sea than in the Skagerrak (Waern 1965, Snoeijs 1999). These species also had higher PCA scores for the Baltic Sea than for the Skagerrak on the D-axis, suggesting that they are adapted to their increased maximum abundance depths. *Dictyosiphon foeniculaceus*, the third species found in both areas, grows close to the water surface in both the Skagerrak and the Baltic Sea, and (as expected) did not show a large difference in PCA scores. The PCA score for *Laminaria hyperborea* on the D-axis deviated from what would be expected according to its maximum abundance depth (Table 2). In the Skagerrak, the upper distributional limit of this species is set by low salinity in the surface water and not, as on Atlantic coasts, by the lowest tidal level. Our PCA results suggest that *L. hyperborea* is not fully adapted to the light levels at its maximum abundance depth in the Skagerrak and the high I_c also validates this assumption. The filamentous species *Sphacelaria arctica* also had a lower PCA score on the D-axis than would be expected since this is the deepest penetrating non-crustose species in the northern Baltic Sea. *S. arctica* also turned out to be remarkably insensitive to the UV treatment. This suggests that no real deep-water species occur in the northern Baltic Sea as is also shown by the lack of strong pattern in I_c and I_k values with depth for the algae in this area (Table 2). Together with the general lack of pattern in UV sensitivity of the Baltic Sea algae, this illustrates that the reduced species diversity is also coupled to a loss of functional groups in the sense of general photosynthetic performance and not only in the sense of pure morphology (loss of canopy-forming species).

We found lower P_{max} in the Baltic Sea than in the Skagerrak for the groups filamentous and coarsely branched algae, but there were no significant differences for α between the areas. This suggests that the number of photosynthetic reaction units in the algae was lower in the Baltic Sea, while the effective absorption cross-section of the reaction centres (antenna size) is about the same (Falkowski et al. 1980, Ramus 1981). If the algae in the Baltic Sea do possess fewer photosynthetic reaction units per unit DW, this indicates a more stressed situation and could explain their smaller thallus size compared to the Skagerrak algae. However, the number of photosynthetic reaction units and the antenna size are basic photoacclimation responses in algae, and may therefore in our data set, merely reflect differences in light climate (turbidity and/or season) between the areas.

The Skagerrak and the Baltic Sea algae were separated to some extent along Axis 2 in the PCA with the relative data set. This difference between the areas was possibly a seasonal effect since the Baltic Sea study was performed later in the summer. Light intensity is lower and day length is shorter in August than in June, and this will most certainly affect photosynthetic properties. King & Schramm (1976) presented some

seasonal data on photosynthetic rates from the western Baltic Sea in between the Skagerrak and the Askö area. In their study, it is apparent that large changes in *PI* responses can occur throughout the year. For summer annuals, like *Dictyosiphon foeniculaceus*, June and August represent youth and senescence, respectively, and differences in e.g. P_{max} and UV sensitivity between the areas might therefore also be attributed to factors related to ageing, such as thallus morphology.

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