Photosynthetic performance and impact of ultraviolet radiation on the reproductive cells of Antarctic macroalgae

Michael Y. Roleda[1,*], Katharina Zacher[2], Gabriela L. Campana[3], Angela Wulff[4], Dieter Hanelt[5], Maria Liliana Quartino[3] & Christian Wiencke[2]

[1]Institute for Polar Ecology, University of Kiel, Wischhofstr. 1-3, 24148 Kiel, Germany, mroleda@ipoe.uni-kiel.de; *corresponding author

[2]Alfred Wegener Institute for Polar and Marine Research, Am Handelshafen 12, 27570 Bremerhaven, Germany

[3]Instituto Antártico Argentino, Cerrito 1248 (1010), CA de Buenos Aires, Argentina

[4]Department of Marine Ecology, Marine Botany, Göteborg University, SE 40530 Göteborg, Sweden

[5]Department of Cell Biology / Phycology, University of Hamburg, Ohnhorststr. 18, 22609 Hamburg, Germany

Introduction

Macroalgal species inhabiting the polar regions of both Hemispheres are generally classified as being low light adapted (Kirst and Wiencke 1995). The radiation regime in high latitudes is subject to strong seasonal variation (polar days and nights) and also to changes caused by sea-ice conditions (Svendsen et al. 2002). This consequently affects algal productivity and population dynamics in the course of the year. The degree of UV-B (280- 315 nm) exposure is accordingly highly seasonal as affected by the sea-ice, prevailing weather conditions and the turbidity of the water column (Hanelt et al. 2001).

A yearly net springtime stratospheric ozone loss of 60- 70% over Antarctica has been a recurring phenomenon since its detection in the early 1980s that intensifies ambient UV-B radiation on the biosphere (Crutzen 1992; Herman *et al*. 1996). The area affected by ozone depletion has also expanded to 5 fold over the past decades in the continent. In this regard, it is necessary to study stress physiology on Antarctic primary producers.

The adverse effects of UV-B exposure on photosynthesis result from the absorption of high-energy radiation by biomolecules such as proteins and nucleic acids. The D1 protein in the core complex of photosystem II and the carbon dioxide-fixing enzyme RubisCO have been identified as major targets of UV exposure (Vass 1997; Bischof et al. 2000). Exposure to UVR may also generate reactive oxygen species contributing to the photooxidation of compo-nents of the photosynthetic machinery (e.g. pigments such as chlorophylls) (Bischof et al. 2003).

Existing Antarctic phycological studies show the lack of information on the effect of UVR on seaweeds (Wiencke 1996; Wiencke et al. 2006). The advance in Antarctic macroalgal research is primarily constrained by logistic difficulties.

This is in contrast to the more accessible Arctic locations where recent studies have shown that early life stages of macroalgae are most sensitive to UVR and their sensitivity is related to the depth distribution pattern of the adult sporophytes (Roleda *et al*. 2007).

No study has yet been conducted on the structural, biochemical and physiological responses of reproductive cells of Antarctic macroalgae exposed to UVR. This paper presents the physiological aspect with emphasis on the photosynthetic performance of the propagules of several macroalgal species exposed to light stress.

Materials and methods

Algal material

Fertile thalli of several macroalgal species (2 greens, 2 browns, and 3 reds) were collected in Peñon Uno and Peñon de Pesca around King George Island, Antarctica (62° 14'S, 58° 42'W) (Table 1). Blades with reproductive structures (n= 5) were thoroughly cleaned of epiphytes, washed with filtered seawater and processed for release of reproductive cells. Propagules released were maintained under low light condition (1- 2 µmol photon m^{-2} s^{-1}).

Table 1. Species collected around King George Island, their distribution zone, reproductive cell types isolated from different life-history stages and corresponding sizes of their propagules.

Class/Species	Distribution zone	Reproductive cell type	Cell size (µm)
ULVOPHYCEAE			
Monostroma hariotii Gain	eulittoral	gamete	7‡
Urospora penicilliformis (Roth) Areschoug	eulittoral	zoospore	6; 20‡
PHAEOPHYCEAE			
Adenocystis utricularis (Bory de Saint-Vincent) Skottsberg	eulittoral	zoospore	4‡
Ascoseira mirabilis Skottsberg	sublittoral	gamete	3
BANGIOPHYCEAE			
Porphyra endiviifolium (A. Gepp & E.S. Gepp) Y.M. Chamberlain	supralittoral	monospore	15
FLORIDOPHYCEAE			
Iridaea cordata (Turner) Bory de Saint-Vincent	eulittoral	tetraspore	22
	sublittoral	tetraspore	20
Gigartina skottsbergii Setchell & N.L. Gardner	sublittoral	tetraspore	23
	sublittoral	carpospore	27

Cell sizes are in diameter, ‡ cell length

The initial density and cell size of reproductive cells was counted and measured by use of a Sedgewick-Rafter Cell S50 spore counter (Graticules Ltd., Tonbridge, England) observed under a light microscope (Zeiss Axioab, Ger-

many). Stock suspensions were diluted with filtered seawater to obtain cell densities necessary for the desired background fluorescence for photosynthetic measurements among the five replicates.

Irradiation treatments

Photosynthetically active radiation (PAR, 400- 700 nm) was provided by white fluorescent tubes (Osram, L65 Watt/25S, Munich, Germany). Ultraviolet radiation (UVR, 280- 400 nm) was generated by UVA-340 fluorescent tubes (Q-Panel, Cleveland,OH, USA). Cell culture dishes were covered with one of the following filters to cut off different wavelength ranges from the spectrum emitted by the fluorescent tubes: Ultraphan transparent (Digefra GmbH, Germany), Folanorm (Folex GmbH, Germany) or Ultraphan URUV farblos corresponding to the PAR + UV-A + UV-B (PAB), PAR + UV-A (PA) and PAR (P) treatments, respectively. Ultraviolet radiation was measured using a Solar Light PMA 2100 radiometer equipped with the UV-A sensor PMA 2110 and the UV-B Sensor PMA 2106 (Solar light, Philadelphia, USA). Ultraviolet radiation below the UV-transparent filter was 4.34 W m^{-2} UV-A and 0.40 W m^{-2} UV-B. Photosythetically active radiation was adjusted using a cosine quantum sensor attached to a LI-COR data logger (LI-1000, LI-COR Biosciences, Lincoln, Nebraska, USA) to be 22 µmol photon m^{-2} s^{-1} (~ 4.73 W m^{-2}).

Chlorophyll fluorescence measurements

Photosynthetic parameters were measured as variable fluorescence of photosystem II (PSII) using a Water Pulse Amplitude Modulation fluorometer (Water-PAM) connected to a PC with WinControl software (Heinz Walz GmbH, Effeltrich, Germany). After propagule release and adjustment of cell density (not exceeding 1 h after spore release), optimum quantum yield (F_v/F_m, n= 5) and photosynthesis-irradiance curve (P-I curve in terms of relative electron transport rate, rETR = PFR x $\Delta F/F_{m'}$, n= 3) were measured at time zero as described by Roleda et al. (2006a). The hyperbolic tangent model of (Jassby and Platt 1976) was used to estimate P-I curve parameters described as:

$$rETR = rETR_{max} * \tan h (\alpha * I_{PAR} * rETR_{max}^{-1})$$

where $rETR_{max}$ is the maximum relative electron transport rate, tan h is the hyperbolic tangent function, α is the initial slope of the curve at pre-saturation irradiance (as a measure for the electron transport efficiency) and *I* is the photon fluence rate of PAR. The saturation irradiance for electron transport (I_k) was calculated as the intercept between α and the ETR_{max} values. Curve fit was calculated with the Solver module of MS-Excel using the least square method comparing differences between measured and calculated data.

Controls measured at time zero were filled into corresponding culture dishes. To evaluate the effect of different radiation treatments and exposure times, 5 ml of fresh reproductive cell suspension were filled into each 35mm x 10mm cell culture dish (Corning™, Corning Inc., NY, USA) and exposed under

the three radiation conditions for 4 hours (n= 5) at 2 ± 1.5 °C. After exposure treatment, F_v/F_m was determined and the suspension was returned to the same culture dish and cultivated under dim white light (4 ± 1 µmol photons m^{-2} s^{-1}) at the same temperature for recovery. Time zero control was also maintained at the same condition. Measurements of photosynthetic recovery were made after 24- 48 hours in dim white light condition. Settled and germinating zygotes were slowly re-suspended by sucking and jetting the medium against the bottom of the culture dish using Eppendorf pipettes. Optimum quantum yields were expressed as percent of control.

Results

The I_k values of propagules investigated varied between species, reproductive cell type and habitat. Saturating irradiance (I_k) was highest in the zoospores of the eulittoral green macroalga *Urospora penicilliformis* and lowest in the monospores of supralittoral red macroalga *Porphyra endiviifolium* (Table 2). Comparison between eulittoral and sublittoral *Iridaea cordata* showed comparable I_k values (38- 39 µmol photon m^{-2} s^{-1}), while diploid carpospores of *Gigartina skottsbergii* have higher a I_k value compared to its haploid tetra-spores. Comparison between different groups of algae showed a generally higher I_k in green (83- 87 µmol photon m^{-2} s^{-1}) followed by brown (52- 64 µmol photon m^{-2} s^{-1}) and lower in red (33- 54 µmol photon m^{-2} s^{-1}) macroalgae.

Table 2. Photosynthesis-irradiance curve parameters estimated using the hyperbolic tangent equation of Jassby and Platt 1976, and mean optimum quantum yield (F_v/F_m) of propagules immediately after release and after post cultivation in dim white light (4 ± 1 µmol photons m^{-2} s^{-1}) for 24- 48 h.

Class/Species	P-I curve parameters			Photosynthetic efficiency (F_v/F_m)	
	I_k	Alpha	$rETR_{max}$	After release	After post cultivation
ULVOPHYCEAE					
M. hariotii	83	0.06	5.41	0.288±0.04	0.397±0.15
U. penicilliformis	87	0.16	14.14	0.501±0.04	0.511±0.04
PHAEOPHYCEAE					
A. utricularis	64	0.14	9.04	0.462±0.11	0.601±0.04
A. mirabilis	52	0.10	4.99	0.400±0.06	0.446±0.05
BANGIOPHYCEAE					
P. endiviifolium	33	0.12	4.07	0.488±0.04	0.249±0.02
FLORIDOPHYCEAE					
I. cordata (eulittoral)	39	0.15	6.01	0.476±0.04	0.448±0.07
I. cordata (sublittoral)	38	0.11	4.28	0.445±0.04	0.523±0.02
G. skottsbergii (tetraspore)	44	0.13	5.60	0.307±0.07	0.371±0.05
G. skottsbergii (carpospore)	54	0.13	6.87	0.403±0.03	0.434±0.02

I_k (µmol photon m^{-2} s^{-1}) is the light intensity at which the initial slope of the curve ($\propto$) intercepts the horizontal asymptote of the maximum relative electron transport rate ($rETR_{max}$).

The slope alpha (α), a parameter for the performance of both light-harvesting and photosynthetic conversion efficiency, is characterized by a gradual increase (α= 0.06) of rETR in gametes of *Monostroma hariottii* and a steep increase (α= 0.16) in zoospores of *U*. *penicilliformis* at lower photon flux density (PFD). Photosynthetic capacity, expressed as $rETR_{max}$, was highest in *U*. *penicilliformis* and lowest in *P. endiviifolium* (Table 2).

Optimum quantum yield of the PSII (F_v/F_m) of freshly released reproductive cells was likewise highest in *U*. *penicilliformis* (0.501 $\pm$ 0.04) and lowest in *M. hariotii* (0.288 $\pm$ 0.04). In brown and red macroalgae, higher F_v/F_m was observed in supra- and eulittoral (*Adenocystis utricularis*, *P*. *endiviifolium* and *I*. *cordata*) compared to sublittoral (*Ascoseira mirabilis* and *G*. *skottsbergii*) species (Table 2). Post cultivation in dim white light (4 µmol photon m^{-2} s^{-1}) generally showed an increase in the photosynthetic efficiencies of germinating cells except for *P. endiviifolium* (Table 2).

Exposure to 4 hours of different light treatments consisting of PAR only (P), PAR+UV-A (PA) and PAR+UV-A+UV-B (PAB) showed species-specific response in F_v/F_m, expressed as percent of control (Fig. 1). All species, except *U*. *penicilliformis* and *A*. *utricularis* (Fig. 1B-C), were photoinhibited after exposure to a PAR fluence of 6.8 x 10^4 J m^{-2}. A 50% decrease in F_v/F_m was observed in other supra- and eulittoral species (*M*. *hariotii*, *P*. *endiviifolium* and *I*. *cordata* [int]; Fig. 1A, 1E-F), and 70- 87% decrease in F_v/F_m of sublittoral species (*A*. *mirabilis*, *I*. *cordata* [sub] and *G*. *skottsbergii*; Fig. 1D, 1G, 1H-I).

Relative to PAR treatment, light supplemented with UVR further reduced photosynthetic efficiency of propagules by 18- 65% in the PA and 26- 78% in the PAB treatment. The monospores of the supralittoral species *P*. *endiviifolium* were most tolerant to UVR with minimal additional photoinhibition of 18% and 26% in PA and PAB treatments respectively (Fig. 1E). Tetraspores of the subtidal *I*. *cordata* were most susceptible to PA treatment with additional 65% photoinhibition (Fig. 1G) while gametes of the sublittoral *A*. *mirabilis* were most susceptible to the impact of PAB with additional 78% reduction in their photosynthetic efficiency (Fig. 1D).

Post cultivation in dim white light (4 µmol photon m^{-2} s^{-1}) allowed repro-ductive cells of all species investigated to recover their photosynthetic efficiencies. Recovery was relatively more efficient in supra- and eulittoral species (Fig. 1A-C, E-F) compared to sublittoral species (Fig. 1D, G-I). Moreover, photosynthetic recovery was also higher in diploid carpospores compared to haploid tetraspores of *G*. *skottsbergii* (Fig. 1H-I).

Discussion

This study reports on the latest advances of phycological research in Antarctica with emphasis on the photosynthetic activity of reproductive cells of several macroalgae. The impact of exposure to varying spectral composition on the photosynthesis of propagules showed a species-specific relation to the zonation pattern of the parental plants and the corresponding life-history cell types.

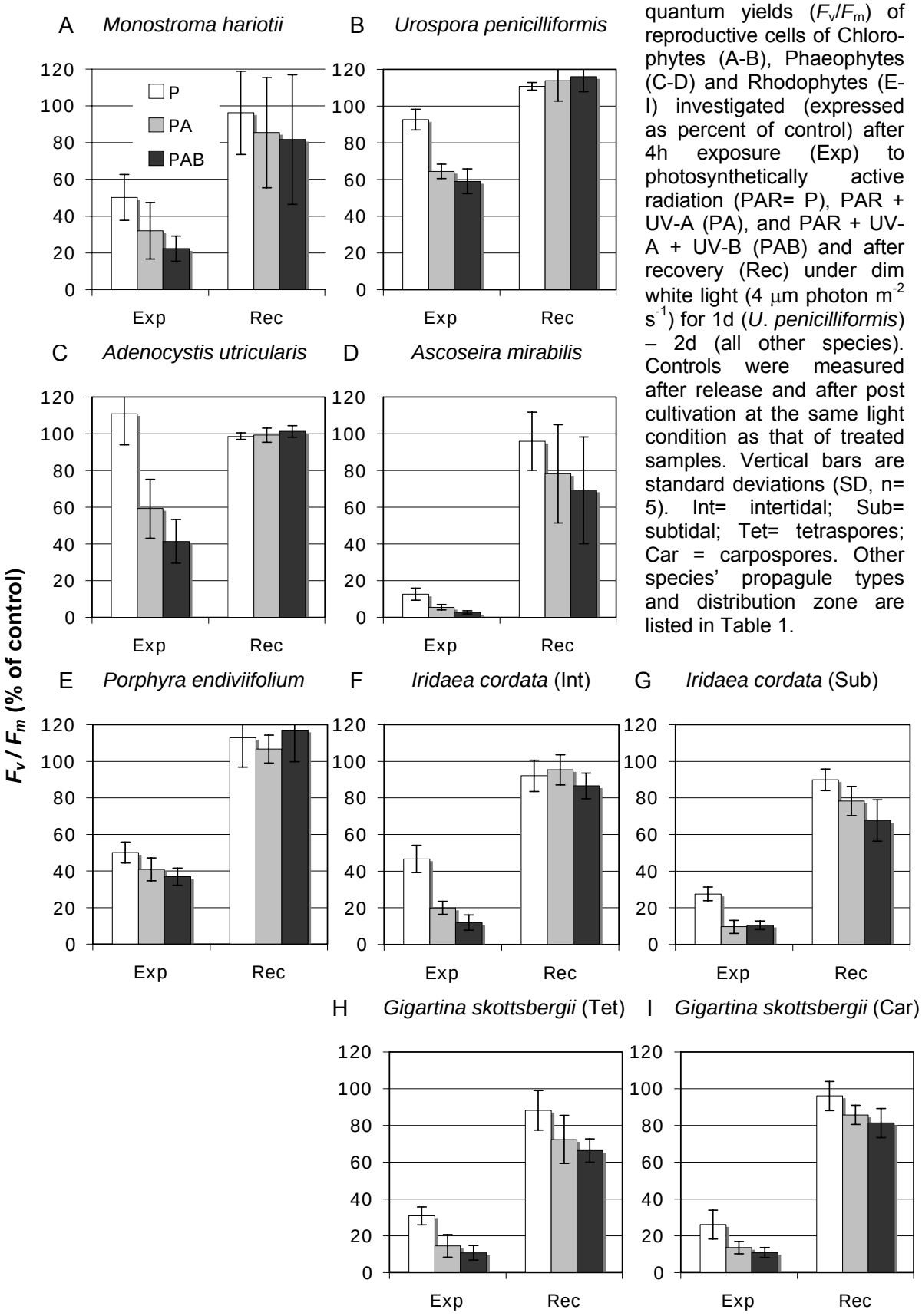

Figure 1. Mean optimum quantum yields (F_v/F_m) of reproductive cells of Chlorophytes (A-B), Phaeophytes (C-D) and Rhodophytes (E-I) investigated (expressed as percent of control) after 4h exposure (Exp) to photosynthetically active radiation (PAR= P), PAR + UV-A (PA), and PAR + UV-A + UV-B (PAB) and after recovery (Rec) under dim white light (4 μm photon m^{-2} s^{-1}) for 1d (*U. penicilliformis*) – 2d (all other species). Controls were measured after release and after post cultivation at the same light condition as that of treated samples. Vertical bars are standard deviations (SD, n= 5). Int= intertidal; Sub= subtidal; Tet= tetraspores; Car = carpospores. Other species' propagule types and distribution zone are listed in Table 1.

The estimated slope (α) and saturating light intensity (I_k) derived from P-I curves showed that photosynthesis of reproductive cells of Antarctic macroalgae are shade adapted compared to adult plants (e.g. *U. penicilliformis*; Roleda and Campana, unpublished data). Low light adaptation of photosyn-thesis is observed to be the general characteristic feature of reproductive cells of macroalgae (Amsler and Neushul 1991; Roleda et al. 2004, 2005, 2006a, 2006b; Zacher et al. 2007). This might be related to the chlorophyll antenna size and number of chloroplast present in reproductive cells compared to multicellular macroscopic stages. Survival of propagules will therefore be dependent on their immediate settle-ment on substrate at depths or under algal canopies where the prevailing low-light microenvironment is suitable for their germination.

A photon fluence of 6.8 x 10^4 J m^{-2} PAR did not affect the F_v/F_m of zoospores of eulittoral species *U*. *penicilliformis* and *A*. *utricularis*. In spores and gametes of other species, the reduction of photosynthetic capacity and quantum efficiency when exposed to fluence of PAR exceeding their requirement is a protective strategy to dissipate excess energy absorbed by the photosystem II as heat to avoid photodamage. This is a regulative protective mechanism against excessive radiation also known as dynamic photoinhibition (Osmond 1994). This process may also be regulated by an increase in the zeaxanthin content of the PSII antenna (Adams and Demming-Adams 1992) and/or by increasing the amount of inactive PSII centres which dissipate a surplus of absorbed energy as heat to protect the photosynthetically active centres (Öquist and Chow 1992). In contrast, impairment of D1 protein leading to decrease in photosynthetic capacity is called chronic photoinhibition. This occurs in shade-adapted macroalgae growing in the lower sublittoral zone when exposed to high irradiances. These species have a lower ability to down-regulate photosynthesis through the protective dynamic photoinhibitory process (Hanelt et al. 2003).

Additional reduction of the photosynthetic efficiency was observed in all species exposed to light supplemented with UV-A and UV-A+UV-B. Mono-spores of supralittoral species *P*. *endiviifolium* were observed to be the most tolerant to UVR. Although the measurable effects of both PAR and UVR in the reduction of photosynthetic efficiency are similar, the mechanisms behind PAR- and UVR-induced inhibition of photosynthesis are different (Franklin et al. 2003). Photosynthetic performance may be additionally depressed in light treatments supplemented with UVR by possible damage to the oxidizing site and reaction center of PS II (Grzymski et al. 2001; Turcsányi and Vass 2002).

After photoinhibition, recovery of photosynthesis often requires dim white light condition (Hanelt et al. 1992). Full recovery of photosynthetic capacity was observed in supra- and eulittoral species after 24- 48 hours post-cultivation in low white light. Incomplete recovery was observed in sublittoral species especially in propagules exposed to UVR. Recovery of photosynthetic efficiency of zoospores of different kelp species varies between 8 and 24 hours in upper and lower sublittoral species respectively (Roleda et al. 2006a). Exposure to UVR was further observed to delay photosynthetic recovery of Arctic kelp zoospores (Roleda et al. 2006a). Comparison between species showed that intertidal *I*. *cordata* tetraspores were more tolerant to all light treatments compared to

tetraspores isolated from subtidal sporophytes. Higher recovery rates were also observed in spores of intertidal *I*. *cordata* pre-exposed to UVR. Depth related sensitivity of reproductive cells was previously reported in kelp zoospores isolated from sporophytes collected at different depth gradient (Swanson and Druehl 2000). Although the measured photoinhibition of photo-synthesis are similar between the diploid carpospores and haploid tetraspores of *G*. *skottsbergii*, more efficient recovery was observed in diploid carpospores compared to the haploid tetraspores.

The sensitivity of photosynthesis of reproductive cells of Antarctic macroalgae to PAR and UVR is related to the observed zonation pattern of the adult plants. This response was also reported in the early life stages of macroalgae from the northern Hemisphere (Roleda et al. 2007). The prevailing environmental factors in different habitats along the vertical gradient of the shore are important in conditioning the physiological optimum and conferring fitness for the survival of the organism. An increase in stratospheric ozone depletion and the corresponding increase in irradiance of UV-B on the biosphere might, however, re-shape seaweed community structure along coastal environments (cf Bischof et al. 2006).

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