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The susceptibility of spores and propagules of Antarctic seaweeds to UV and photosynthetically active radiation — Field versus laboratory experiments

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ABSTRACT

The Western Antarctic Peninsula is strongly affected by stratospheric ozone depletion, leading to higher UVB radiation (UVBR) on the Earth surface. It is furthermore experiencing the fastest rates of global warming worldwide, resulting in an increased sediment run-off from glacial melting, altering the underwater light climate. Very little is known of how Antarctic organisms can cope with this rapidly changing environment. Seaweeds play an essential role within the Antarctic coastal ecosystems, building highly complex and productive underwater communities. The unicellular spores are the most sensitive stage in their life-cycle, forming the bottle-neck for successful recruitment. To supplement the very rare field experiments on seaweed propagules, three ecologically important Antarctic seaweeds (*Adenocystis utricularis*, *Himantothallus grandifolius*, *Iridaea cordata*) were investigated. The germination of spores after exposure in the field to different water depths to three light treatments (PAR; PAR + UVA; PAR + UVA + UVB) was recorded. In parallel, spores were exposed to the same treatments under artificial radiation in the laboratory for different periods. Germination of the intertidal species *A. utricularis* was not affected by the treatments. In spores of *I. cordata* and *H. grandifolius* depth was a major factor for successful germination. High PAR fluxes at 1 and 2 m water depth inhibited germination significantly. UVR further lowered germination in *H. grandifolius* while in *I. cordata* UVBR had a negative impact only in the laboratory experiment. The results show that already the unicellular life stage expresses strong species-specific susceptibility to changes in the radiation climate. Not only UVR but also the high PAR fluxes in the field are important factors in determining the upper distribution limit of Antarctic seaweeds and laboratory experiments show stronger UVB effects as studies under natural radiation.

1. Introduction

Ecological effects of global environmental changes on Antarctic organisms, particularly the increase in ultraviolet-B radiation (UVBR, 280–315 nm) caused by stratospheric ozone depletion (Farman et al., 1985; Weatherhead and Andersen, 2006), and rising temperatures due to global warming (IPCC, 2001) are of considerable concern (Roleda et al., 2007a). The Western Antarctic Peninsula (WAP) belongs to the most rapidly warming regions on earth, with a rise of surface air temperature of 3.4 °C (Vaughan et al., 2003) per century, compared to a global mean increase of 0.6 °C (Turner et al., 2007). One of the consequences of the local warming trend is a significant increase in land and sea ice melting, which intensifies the sediment run-off from the glaciers into the oceanic system during the melting season (spring–summer; Cook et al., 2005; Turner et al., 2007), affecting the underwater light climate in the proximity to the glaciers with unknown consequences for the primary producers (Schloss et al., 2002).

At the WAP, seaweeds constitute a year-round essential carbon sink through production of high amounts of biomass with maximum wet biomass in the sublittoral of over 10 kg fresh weight m^{-2} (Gómez et al., 2009; Quartino and Boraso de Zaixso, 2008). In some Antarctic areas the phytoplankton productivity is very low and it is postulated that the benthic primary producers (seaweeds and benthic microalgae) form an important food source for the heterotrophic community (Schloss et al., 2002). In this way, seaweeds are crucial for the diversity and stability of the polar coastal ecosystems. Due to retreating glaciers, new areas in the upper subtidal and intertidal will be accessible for seaweed colonization in the future, thereby altering the oceanic food web (Quartino et al., 2013).

As the penetration of light into the water column is altered by an accelerated glacial melting due to global warming, both, the upper and lower depth distribution limit of seaweeds might be modified. At the study site King George Island, Antarctica, the number of annual fresh water discharge days and daily discharge volume has doubled within the period from 2002 to 2006 (Eraso and Dominguez, 2007). While the lower depth distribution limit of the seaweeds depends on the capacity of the species to maintain a positive carbon balance (Gómez

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et al., 1997), the upper limit is determined by the capability to cope with excessive photosynthetically active radiation (PAR 400–700 nm) and the tolerance to UV radiation (UVR 280–400 nm, Bischof et al., 2006; Hanelt, 1998; Wiencke et al., 2004, 2006). Negative effects of UVR on seaweeds are, among others, the inhibition of photosynthesis or even photodamage, protein breakdown and the damage of the DNA resulting in lower germination and growth rates (reviewed in Bischof et al., 2006; Karsten et al., 2009; Roleda et al., 2007a).

The upper depth distribution of seaweeds can be determined by the susceptibility of their early life history stages (unicellular spores and propagules) to environmental perturbations (Swanson and Druehl, 2000; Wiencke et al., 2000). These stages are known to be the bottle neck for the successful recruitment of the species because they are more vulnerable to changes in the abiotic environment compared to the mature sporophytes in their life history (Agrawal, 2009; Coelho et al., 2000; Cordi et al., 2001; Roleda et al., 2007a; Véliz et al., 2006; Wiencke et al., 2006). It is therefore necessary to understand the physiological limits of the early developmental stages of the important seaweed species to be able to identify the main factors leading to a successful recruitment.

Most of the studies on young developmental stages have been performed under laboratory conditions with unnatural ratios between PAR, UVA and UVB radiation. Experiments on young developmental algal stages under ambient solar radiation in Antarctica are very rare (but see Zacher et al., 2007a; Zacher and Campana, 2008 working on early successional communities). In laboratory experiments UVR was shown to negatively affect the photosynthetic efficiency of *Adenocystis utricularis* zoospores, additionally damaging the DNA by forming cyclobutane pyrimidine dimers (CPDs). However, a full recovery is observed after 48 h under low light (Zacher et al., 2007a, 2007b). The subtidal red alga *Gigartina skottsbergii* and the endemic brown algae *Ascoseira mirabilis* were not able to repair their DNA damage completely after 8 h of exposure to 0.4 W m^{-2} UVBR but fully recovered after shorter times of exposure (Roleda et al., 2007b, 2008). In other regions of the Earth some experiments on the high PAR and UV tolerance of young developmental stages have been performed with inconsistent results (Hanelt et al., 1997; Jiang and Gao, 2008; Steinhoff et al., 2011; Wiencke et al., 2006). While Wiencke et al. (2006) and Steinhoff et al. (2011) found a decreased spore germination of subtidal species due to UVR and not under high PAR, Hanelt et al. (1997) and Jiang and Gao (2008) found a strong photoinhibition of photosynthesis due to high PAR and a weaker additional inhibition due to UVR.

To our knowledge, no data have been published so far on the germination of Antarctic seaweeds under ambient solar radiation, even though this region exhibits the strongest degree of stratospheric ozone depletion worldwide. In order to get deeper insights in the high PAR and UV tolerance of Antarctic seaweeds, the spore germination of the inter- to subtidal *Iridaea cordata* (Rhodophyta), the inter- to upper subtidal *Adenocystis utricularis* and the Antarctic endemic subtidal *Himantothallus grandifolius* (both Phaeophyceae) was investigated in Potter Cove, King George Island, Antarctica. Spores were exposed for ~24 h to i) PAR (P), ii) PAR + UVAR (PA) and iii) PAR + UVAR + UVBR (PAB) in different water depths (1, 2, 4 and 8 m) in the field and germination rates were subsequently determined after exposure to low light in the laboratory. For comparative reasons the same species were simultaneously exposed under laboratory conditions, where the different depths were simulated by different periods of exposure (1, 2, 4 and 8 h).

The study aimed at answering several questions:

1. Which wavelength range exerts the strongest effects on the germination of Antarctic propagules?
2. Is there a possible alteration in the upper vertical distribution limit of the subtidal species due to an increased sediment inflow during summer?
3. Are laboratory experiments suitable to provide results which can be used to predict the performance in the field?

2. Materials and methods

2.1. Algal material

Fertile specimens of the brown algae *A. utricularis* (Bory) Skottsberg, *H. grandifolius* (A.Gepp and E.S.Gepp) Zinova and the red alga *I. cordata* (Turner) Bory de Saint-Vincent were collected in November 2008 (*A. utricularis* and *I. cordata*) and February 2010 (*H. grandifolius*) at Potter Cove (King George Island, South Shetland Islands, 62°14.80′S, 58°41.26′W) during two expeditions. *Adenocystis utricularis* and *I. cordata* were collected in the intertidal, whereas *H. grandifolius* grows in the subtidal and was collected by SCUBA diving at approx. 10 m depth. After collection, the specimens were brought immediately to the nearby laboratory and kept at ~2 °C under low light conditions until further processing.

2.2. Spore release

Numerous individuals of each species were divided randomly in 5 replicates and prepared for spore release by blotting with tissue paper and treating the different species in the following ways: *I. cordata* tetrasporophytes were cut into smaller pieces and put into glass flasks with filtered seawater (0.2 μm) for collection of spores after a few days. Complete thalli of *A. utricularis* and fertile tissue of *H. grandifolius* (cut with a razor blade) were kept in darkness in moist chambers overnight or a few days at <5 °C. Spore release was obtained by flooding the algae with filtered, slightly warmer seawater in photo-dishes according to Clayton and Wiencke (1986). The initial spore density of brown algae was counted by the use of a Neubauer-chamber (Brand, Wertheim, Germany) and of the red alga by a Rafter chamber (Sedgewick-Rafter Cell S50 spore counter, Graticules Ltd., Tonbridge, UK), respectively. Initial spore densities for *A. utricularis* spore suspension were (zoospore length around 4 μm) approx. 1.8×10^5 spores ml^{-1}, for *H. grandifolius* spore suspension (zoospore length around 4 μm) approx. 1.42×10^5 spores ml^{-1} and for *I. cordata* tetraspore suspension (mean diameter 20 μm) approx. 6000 spores ml^{-1}. Spore solutions were then divided and diluted between the field and the laboratory approach. The spore solution of the same species was exposed in the field and under laboratory conditions at the same date, whereas spores of different species were exposed at different dates due to different times of fertility. *Himantothallus grandifolius* e.g. gets fertile in austral summer to autumn, and was investigated in 2010 whereas fertile *I. cordata* and *A. utricularis* were collected in spring 2008.

2.3. Field experiment

The field experimental units consisted of an aluminum frame (~1 m × 1 m) with a black plastic bottom and a top of UV-transparent Plexiglas (GS 2458, Röhm, Darmstadt, Germany). It contained 16 Petri dishes (53 × 12 mm) arranged in a 4 × 4 grid. Petri dishes were filled with the spore solutions and exposed to three different light treatments and four depths (1, 2, 4 and 8 m) in a two-factorial design (n = 5, *I. cordata* and *A. utricularis* and n = 4, *H. grandifolius*). Three kinds of filter foils were used to obtain the different light treatments (see Bischof et al. 2002 for details): 1. Ultraphan transparent (Digefra GmbH, Germany), 2. Folanorm 320 (Folex GmbH, Germany), and 3. Ultraphan URUV farblos, corresponding to the PAR + UVAR + UVBR (PAB, 280 to 700 nm), PAR + UVAR (PA, 320 to 700 nm) and PAR (P, 400 to 700 nm) treatments, respectively. The cut-off wavelengths of the available filter-material were slightly different from the definition of CIE (Commission Internationale De l'Éclairage, UVB = 280–315 nm, UVA = 315–400 nm) but are for practical reasons commonly used in environmental science (Franklin et al., 2003). Experimental units were

exposed for about 24 h in the field using weights and buoys. Irradiance in the field was measured continuously during the duration of the experiments using UVA and UVB data loggers (X-2000-14, Gigahertz-Optik, Puchheim, Germany) in underwater housings mounted at the experimental units at each depth. PAR profiles were measured once during each experiment around noon between 0 and 10 m depth with a LiCor data logger (LI-1400, Li-Cor, Lincoln, USA) equipped with an underwater PAR sensor (LI-192). Diffuse vertical attenuation coefficients of downward irradiance (Kd) for PAR, UVAR and UVBR during the three field experiments were determined using the following formula (after Kirk, 1994) for the measurement at noon:

$$Kd = \ln\left[Ed_{(z2)}/Ed_{(z1)}\right] \times (z_1 - z_2)^{-1}$$

where $Ed_{(z1)}$ and $Ed_{(z2)}$ are the respective irradiances at depths z_1 (1 m) and z_2 (8 m).

2.4. Laboratory experiments

In the laboratory, light was provided by white fluorescent lamps (Osram, L65 Watt/25S, Germany), emitting background photosynthetically active radiation (PAR) and by UV lamps (Q-Panel UV-A-340, 40 W, Cleveland, USA), emitting a spectrum qualitatively similar to solar radiation in the range of 295 to 340 nm. The same light treatments (PAB, PA and P) as in the field were performed using the same filter material. Irradiation in the laboratory was measured below the cut-off filters using a Solar Light PMA 2100 radiometer equipped with a UVA (PMA 2110) and a UVB broad-band sensor (PMA 2106; Solar Light, Philadelphia, USA). PAR was measured using a flat-head LICOR 190 SA quantum sensor (cosine corrected) connected to a LICOR LI-1400 datalogger. For germination measurements, the spore suspension was put into small Petri dishes (n = 5, *I. cordata* and *A. utricularis* and n = 4, *H. grandifolius*), which were subsequently exposed to the three radiation conditions for 1, 2, 4 and 8 h at approx. 2 °C.

The doses of the different treatments in the field and in the laboratory are shown in Table 1.

After exposure in the field or in the laboratory the Petri dishes were removed from the treatment and exposed to dim white light (10–15 μmol photons m^{-2} s^{-1}) in the laboratory until germination started. Germination rates were determined microscopically by the use of an Axioplan microscope (Zeiss, Göttingen, Germany) equipped with a 20× and 40× seawater immersion objective lens. A spore was classified as germinated, if at least a germ-tube was formed (brown algal spores) or cell division was visible (red algal spores). A minimum of 300 spores were examined per sample. In *A. utricularis* germination was counted after 3 days, in *H. grandifolius* after 5 days and in *I. cordata* after 20 days.

2.5. Statistics

A two-way ANOVA was performed to test for the interactive effects of depth/dose and light treatment on the germination of the different species. Germination data were arcsin transformed. Prior to analysis, data were tested for homogeneity of variances (Cochran's test). Heteroscedastic data were analyzed by the non-parametric Kruskal–Wallis test. Post-hoc comparisons were performed with Duncans or Newman–Keuls test. Statistica™ 6.0 software package was used.

3. Results

3.1. Irradiance measurements

Fig. 1 shows the underwater PAR profiles measured during the three field experiments around noon. Although during the experiment with *I. cordata* maximum values measured in air were much higher than in the other two experiments (1650 μmol photon m^{-2} s^{-1} versus 540 in *A. utricularis* and 755 μmol photon m^{-2} s^{-1} in *H. grandifolius*, respectively), PAR values in the water column were very similar from 3 m downwards and lowest in the *I. cordata* experiment at 10 m depth (Fig. 1). This is also reflected in the Kd values ranging between 0.13 (*A. utricularis* and *H. grandifolius* experiment) and 0.21 (*I. cordata* experiment), demonstrating a higher turbidity in the experiment with *I. cordata* compared to the other measurements. At 8 m depth there were still 158, 137 and 184 μmol photon m^{-2} s^{-1} PAR measured around noon. Maximal PAR values in the laboratory experiment were lower than those in the field (constant 51 μmol photon m^{-2} s^{-1}).

Fig. 2 shows the underwater UVAR and UVBR at the four depths during the experimental period in the field. There is a clear difference between the radiation regimes at the various depths. Highest values of underwater UVAR and UVBR during the experiments were measured in mid-November at 1 m depth (36.9 W m^{-2} and 1.21 W m^{-2}, respectively). In February values were lower, reaching maxima of 15.7 UVAR and 0.6 W m^{-2} UVBR at 1 m depth (Table 1, Fig. 2). Lowest values were measured at 8 m depth with maxima of 4.8 W m^{-2} UVAR and 0.06 W m^{-2} UVBR (Table 1). Total doses of UVAR and UVBR at 1 and 8 m ranged between 605 and 57 kJ, and 19 and 0.5 kJ during the field experiments (Table 1). UVA and UVB doses in the field and laboratory experiments differed most strongly in the UVA doses which were lower in the laboratory experiments (Table 1). UVB doses were comparable between the field and laboratory approaches (Table 1).

3.2. Germination experiments

Generally, the germination rate of *A. utricularis* spores was high three days after the release, reaching >80% in all treatments. Germination was not affected by light treatment or depth, even though a higher germination rate after 8 h of exposure was measured in the laboratory experiment (two-way ANOVA, Table 2, Fig. 3a + b). No significant interactions between light treatment and depth/dose were found (Table 2).

The germination rate of *H. grandifolius* spores was lower compared to *A. utricularis* five days after release, reaching maximum values of 67% at 8 m depth in the field experiment (Fig. 3c). Lowest germination rates (<15%) were recorded at 1 and 2 m during the field experiment (Fig. 3c). The Kruskal–Wallis test showed a strong influence of the depth on germination. Germination rates were significantly higher at 2 m compared to 1 m and at 4 and 8 m depth compared to exposures at 1 and 2 m depth (Newman–Keuls test, Table 2, Fig. 3c). The light treatments with UVAR (PA) and UVAR + UVBR (PAB) showed a significantly

Table 1
UVA and UVB doses (kJ) in the field and laboratory experiments and maximal intensities measured in the field at 1, 2, 4 and 8 m and intensities applied in the laboratory approach (values give the ranges of the three experiments).

	Field				Laboratory			
	1 m	2 m[a]	4 m	8 m	8 h	4 h	2 h	1 h
UVA kJ	522–605	442–465	200–263	57–105	138–200	69–100	35–50	17–25
UVB kJ	19–21	13–14	4.0–5.9	0.5–1.3	10.3–19.7	5.1–9.9	2.6–4.9	1.3–2.5
UVA W m^{-2}	15.7–36.9	20.7–22.7	6.6–15.0	1.9–4.8	4.8–6.9			
UVB W m^{-2}	0.6–1.21	0.63	0.15–0.35	0.02–0.06	0.4–0.7			

[a] In the experiment with *H. grandifolius* the 2 m logger failed, only values from the other two field experiments are available for this depth.

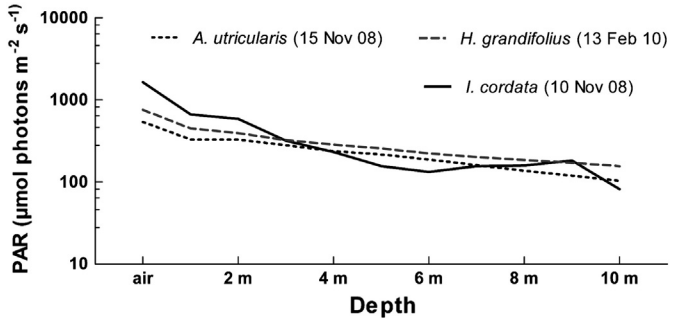

Fig. 1. Underwater PAR (photosynthetic active radiation, 400–700 nm) profiles (0 to 10 m) from the three field experiments measured around noon in µmol photon m^{-2} s^{-1} (logarithmic scale).

Table 2
Two-way ANOVA or non-parametric Kruskal–Wallis (*in italic*) test of the field and laboratory (LAB) experiments on light treatment and depth/doses effects on the germination of *A. utricularis*, *H. grandifolius* and *I. cordata*. Data were arcsin transformed prior to analysis, nt = not tested because variances were not homogenous after transformation, ns = not significant.

Species	Source of variation	Field experiment		Laboratory experiment	
		F-value	*P*-value	*F*-value	*P*-value
A. utricularis	Light treatment (A)	0.518	ns	2.241	ns
	Depth/dose (B)	2.786	ns	3.174	0.032429
	A × B	0.888	ns	0.558	ns
H. grandifolius	Light treatment (A)	3.739	0.033464	30.660	<0.00001
	Depth/dose (B)	129.950	*<0.00001*	2.998	0.043291
	A × B	0.939	ns	2.201	ns
I. cordata	Light treatment (A)	3.120	ns	3.490	0.038462
	Depth/dose (B)	23.722	*<0.00001*	0.983	ns
	A × B	2.336	nt	0.146	ns

lower germination rate than the P treatment in the field experiment (Duncan's test, Table 2). In the laboratory experiment germination was significantly lower under the PAB treatment compared to the P and PA treatments (Table 2, Fig. 3d). Interestingly, germination rates were lower under short term exposure (lower dose) for 2 h than for 4 and 8 h (Fig. 3d). No significant interactions between light treatment and depth/dose were found.

Iridaea cordata tetraspores showed lowest germination rates compared to the other two species after 20 d (maximum 47% in the laboratory experiment, Fig. 3f). Germination was significantly reduced at 1 m depth compared to 2, 4 and 8 m and at 2 m compared to 4 and 8 m depth (Kruskal–Wallis and Duncan's test, Table 2, Fig. 3e). Germination was not significantly affected by the light treatment in the field experiment, but was significantly higher in the P treatments compared to the PAB treatments in the laboratory (two-way ANOVA and Duncan's test, Table 2, Fig. 3f). No effects of the dose were detected.

4. Discussion

The main results of this first field study on the light susceptibility of Antarctic macroalgal spores demonstrate the extreme tolerance of the intertidal *A. utricularis* zoospores to high PAR and UV radiation and a lower tolerance of the upper to lower subtidal *I. cordata* and *H. grandifolius* spores. The results reflect the actual position of these algae on the shore and confirm that the PAR and UV tolerance of the

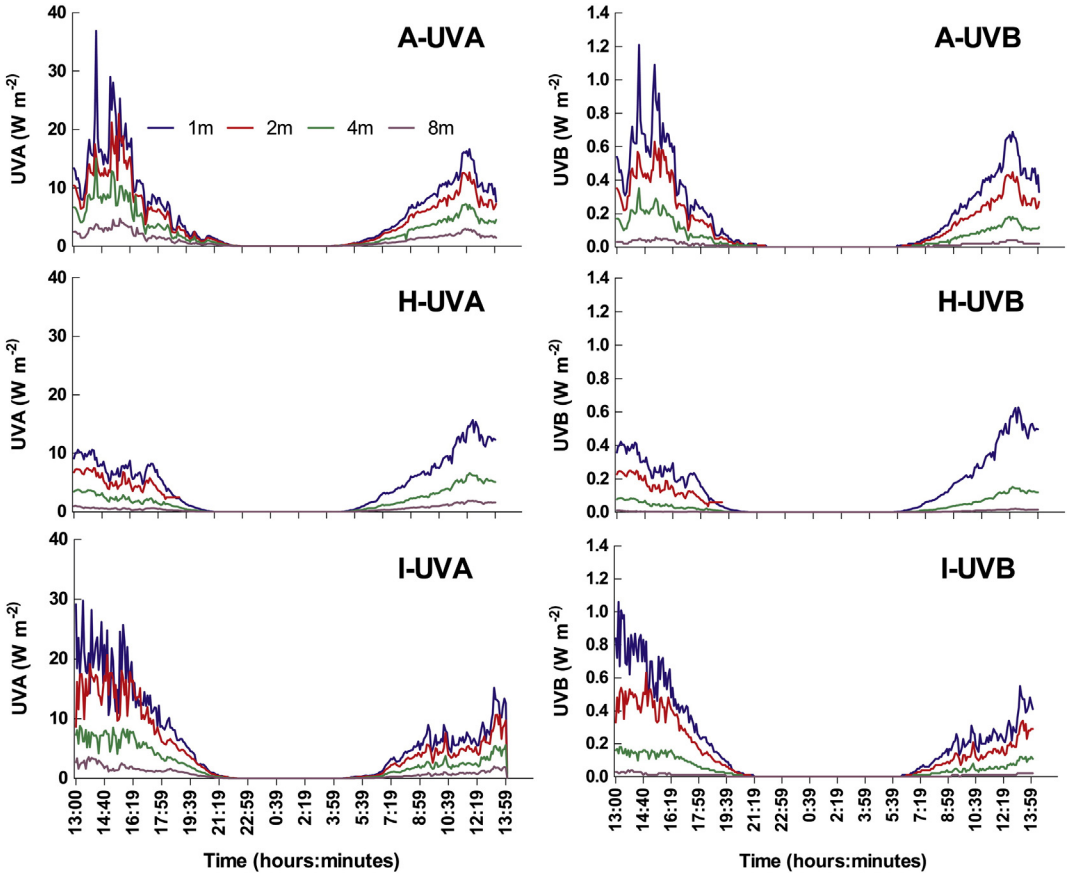

Fig. 2. Underwater UVA and UVB radiation during the field experiments A-UVA + A-UVB *A. utricularis* (15.–16.11.2008), H-UVA + H-UVB *H. grandifolius* (13–14.02.2010) and I-UVA + I-UVB *I. cordata* (10.–11.11.2008) at 1, 2, 4 and 8 m depth. The 2 m sensor in the experiment with *H. grandifolius* failed after some hours.

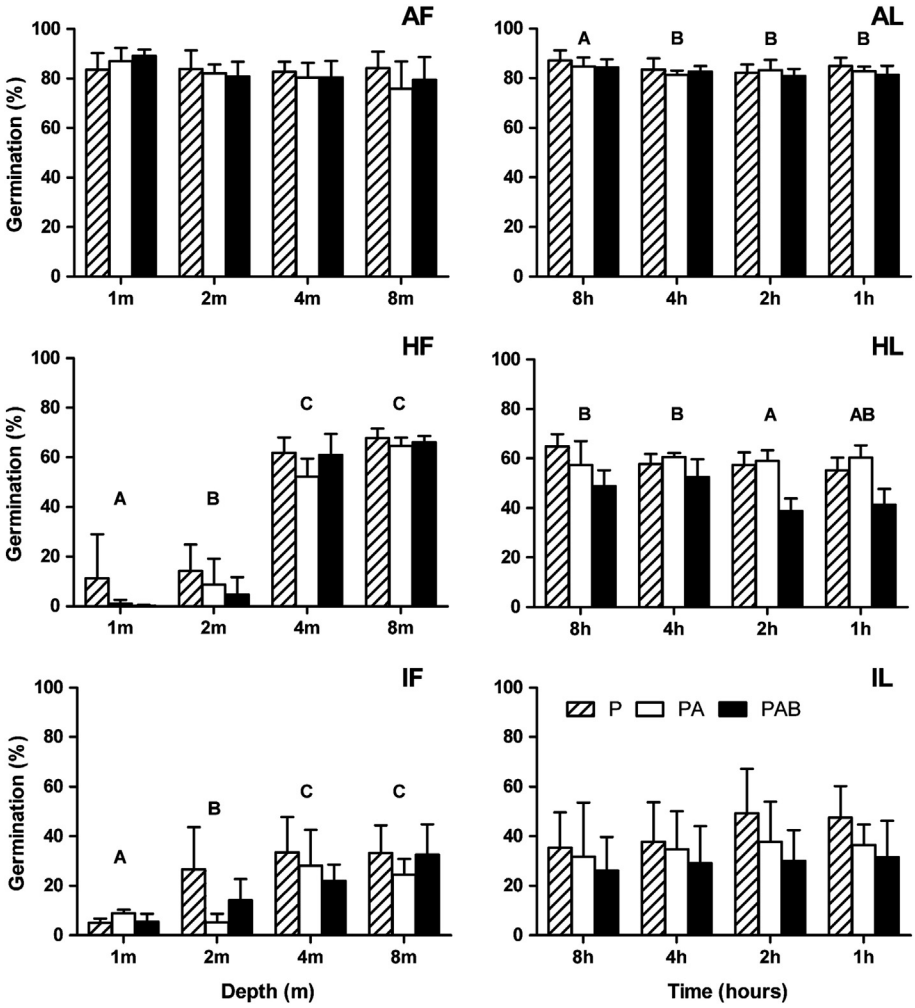

Fig. 3. Germination of *A. utricularis* (AF + AL), *H. grandifolius* (HF + HL) and *I. cordata* (IF + IL) after exposure in the field in different water depths (AF, HF, IF = field) and in the laboratory for different periods (AL, HL, IL = lab). P = PAR, PA = PAR + UVA, PAB = PAR + UVA + UVB. Shown is the mean germination ± SD. Letters indicate significant differences between the depth/doses (two-way ANOVA).

unicellular developmental stages is one important factor (among others) for the successful recruitment of the algae at a certain depth, thereby participating in the determination of the vertical distribution of the species.

In contrast to other field studies performed on Arctic seaweeds (Steinhoff et al., 2011; Wiencke et al., 2006) germination was strongly inhibited by high PAR in the subtidal species (*H. grandifolius* 1 and 2 m; *I. cordata* 1 m). PAR intensities during the field studies could reach maximum values of ~600 μmol m^{-2} s^{-1} at 2 m water depth (experiment with *I. cordata*) when the vertical attenuation coefficient (K_d) as an indicator of water turbidity was quite low, meaning that PAR could penetrate relatively deep into the water column. In the studies on Arctic spores PAR values and doses were lower. In the study by Wiencke et al. (2006) with much higher K_d values (between 0.67 and 1.28 for UVBR) and by Steinhoff et al. (2011) the high PAR treatment was around 400 μmol m^{-2} s^{-1} during the day, possibly leading to the different results for the subtidal species. High PAR intensities are known to exert negative effects on the photosynthesis and growth of sporophytes and gametophytes of seaweeds (Aguilera et al., 1999; Dring et al., 2001; Hanelt et al., 1997) In *Saccharina latissima* (formerly *Laminaria saccharina*) exposure to 500 μmol m^{-2} s^{-1} PAR for 2 h led to a severe photoinhibition of photosynthesis in sporophytes and gametophytes (Hanelt et al., 1997). Young sporophytes did not recover under low light, indicating photodamage. Spores were not tested in this study, but as the resistance to high light levels was related to changes in the thallus structure during the development of the sporophytes (Hanelt et al., 1997), the photosynthesis of the unicellular spore is considered even more vulnerable to high PAR than the one of gametophytes and sporophytes. It was high PAR as well that accounted for most of the reduction of the effective quantum yield in the conchocelis phase of *Porphyra haitanensis* (Jiang and Gao, 2008). During laboratory exposure to relatively low PAR the optimum quantum yield (F_v/F_m) of *A. utricularis* zoospores did not change (Zacher et al., 2007b), whereas in *I. cordata* spores a decrease of F_v/F_m was measured over time (Zacher et al., 2009). This confirms a stronger sensitivity of *I. cordata*.

Additional UV radiation did not significantly affect the germination of *A. utricularis* and *I. cordata* spores in the field reconfirming former studies on the photosynthetic performance of spores from these species (Zacher et al., 2007b, 2009) and of adult field material (Hanelt et al., 1994; Rautenberger and Bischof, 2008). An initially lower optimum quantum yield (F_v/F_m) under the UV treatment was followed by a complete recovery, suggesting that photosynthesis is down-regulated (dynamic photoinhibition) and no photodamage of photosystem II occurred (Hanelt et al., 1994).

On the other hand the germination of *H. grandifolius* spores was negatively affected by UV radiation in the field experiments. However, no additional UVB radiation effect on germination in comparison with the UVA treatment is detectable, a fact consistent to the study on Arctic zoospore germination (Wiencke et al., 2006). Apparently, the strong UVB effects found in many laboratory studies are most likely caused

by the unnatural PAR to UVA to UVB ratios (e.g. Roleda et al., 2005; Wiencke et al., 2000). In contrast to our field study *H. grandifolius* and *I. cordata* germination was negatively affected by UVB radiation in the laboratory experiments. While in the laboratory experiment the UVA to UVB ratio was 10–12 to 1, in the field the UVA is much higher in relation to the UVB part of the spectrum. It was even increasing with depth due to a higher UVB attenuation in the water column (between 24 and 95 to 1 in our experiment). Furthermore the PAR radiation in the laboratory experiment was much lower than that in the field. That fact generally leads to an overestimation of UVB effects in laboratory studies which in the field are masked or overrun by PAR and/or UVA effects. Another reason of not detecting UVB effects in the field might be a better stimulation of the blue-light dependent photolyase, repairing UV induced DNA lesions by absorbing light between 350 and 450 nm (Hada et al., 2000; Pakker et al., 2000).

Although Antarctic seaweeds are characterized as low light adapted (Wiencke et al., 1993) and show strong photoinhibition during high light stress, *A. utricularis* sporophytes were shown to be able to cope with excessive light and optimize their photosynthesis under these conditions (Hanelt et al., 1994). The responses of *A. utricularis* to a changing light regime during the study by Hanelt et al. (1994) were very fast even under low temperatures, thereby making this alga well adapted to its intertidal habitat with extreme alterations in temperature and light. The different PAR susceptibilities of the investigated species might be explained by a higher content of xanthophyll cycle pigments in *A. utricularis* in comparison with the other two species (Hanelt et al., 1994). In the intertidal brown alga *Dictyota dichotoma* the conversion of violaxanthin to zeaxanthin is responsible for an increase in thermal energy dissipation as a protection from excessive irradiation (Uhrmacher et al., 1995). Whether this is also true for the zoospores of the species in our study remains to be tested.

The different UV susceptibilities of the investigated species could have been caused by an uneven increase of the activities of repair mechanisms. DNA damage can be repaired under the influence of photolyase enzymes (light-dependent), nucleotide excision and recombination repair (light-independent; van de Poll et al., 2002). The dimerization of the DNA due to UVB radiation and its repair was found in many seaweeds and their spores (Roleda et al., 2007a, 2007b; van de Poll et al., 2002; Zacher et al., 2007b, 2009). It was shown that haploid spores are very efficient in DNA damage repair and that the most efficient repair occurred in eulittoral species in comparison to sublittoral ones (Roleda et al., 2006, 2007a, 2008).

Another reason for the different tolerances for PAR and UV radiation within the different species might be the ability of producing photoprotective substances. For kelp zoospores from the Northern Hemisphere it was shown that the mother plant exudates phlorotannins (polyphenolic substances) during the release of the spores (Müller et al., 2009; Steinhoff et al., 2011). Because phlorotannins absorb in the UVB range, UV protective environments can be formed, preventing UV induced cell damage (Roleda et al., 2006; Swanson and Druehl, 2002). Phlorotannins were found in both brown algal species tested here (*A. utricularis* and *H. grandifolius*) (Iken et al., 2007). However, whether an exudation during spore release really takes place remains to be tested for these species. The red alga *I. cordata* on the other hand, contains UV absorbing mycosporine-like amino acids (MAAs; Hoyer et al., 2001). In the spores of this species the MAAs shinorine (λ_{max} = 334 nm) and palythine (λ_{max} = 320 nm) were determined and higher concentrations of palythine compared to shinorine were found (Zacher et al., 2009). Under natural solar radiation, the UVA wavelengths were shown to exhibit the highest efficiency on the synthesis of both MAAs in the red alga *Chondrus crispus* (Kräbs et al., 2002), possibly explaining our findings of UV effects in the laboratory (with less UVA) but not in the field.

A. utricularis and *I. cordata* are fertile during the whole Antarctic spring/summer (Müller, 1984), whereas *H. grandifolius* releases spores mostly in summer (Wiencke, 1996; Wiencke and Clayton, 1990), when water turbidity due to melt water is usually higher at coastal areas and UVB radiation is lower than in spring during the time of strongest stratospheric ozone depletion (Weatherhead and Andersen, 2006). At Potter Cove, King George Island, *H. grandifolius* is usually observed to grow from 7 to 10 m downwards (Quartino et al., 2001; Wiencke and Clayton, 2002), while in the current experiments it was already able to successfully germinate at 4 m water depth. A successful recruitment is also dependent on other factors such as interspecific competition with other dominant Antarctic species. Klöser et al. (1994) found *H. grandifolius* only below a *Desmarestia* belt at the mouth of Potter Cove whereas in areas inside Potter Cove *H. grandifolius* is more abundant than *Desmarestia* (Quartino et al., 2013) and already found together with *Desmarestia* species at 3 m water depth where turbidity is high (Quartino, personal communication). This is an indication that a change in abiotic conditions may lead to changes in the community structure especially at more affected sites and that a recruitment higher up the shore is possible at turbid sites. Surely, other abiotic and biotic factors despite the light climate such as substrate, slope and ice disturbance affect the survival of the species at a specific site.

In conclusion, photosynthetically active radiation (400–700 nm) was mainly responsible for the germination success of the species at a certain depth, whereas the UV part of the spectrum had no or only a minor impact.

Our results further show the importance of field experiments to get ecologically relevant results. Laboratory experiments tend to overestimate UVB effects but can serve as mechanistic studies.

While a change in depth distribution of *A. utricularis* due to a change in the light regime is unlikely, the upper distribution limit of *I. cordata* and *H. grandifolius* is a function of both, PAR and UVR. A changing underwater light climate due to increasing sedimentation will allow an upward shift of these species at the shore (as already observed in the inner Potter Cover (Quartino, personal communication)).

Global change, however, will have multiple effects on the marine ecosystems interacting in a manifold and yet mostly unknown way. There is a special need for experiments on multiple stressors, such as temperature, light, disturbance and sedimentation combined with biotic factors such as grazing and competition which are simultaneously acting on organisms. These data are urgently needed in order to get more realistic results to fit future models calculating the outcome of global climate change on the coastal ecosystems.

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References

Agrawal, S.C., 2009. Factors affecting spore germination in algae — review. Folia Microbiol. 54 (4), 273–302.

Aguilera, J., Karsten, U., Lippert, H., Vögle, B., Philipp, E., Hanelt, D., Wiencke, C., 1999. Effects of solar radiation on growth, photosynthesis and respiration of marine macroalgae from the Arctic. Mar. Ecol. Prog. Ser. 191, 109–119.

Bischof, K., Kräbs, G., Wiencke, C., Hanelt, D., 2002. Solar ultraviolet radiation affects the activity of ribulose-1,5-bisphosphate carboxylase-oxygenase and the composition of photosynthetic and xanthophyll cycle pigments in the intertidal green alga Ulva lactuca L. Planta 215, 502–509.

Bischof, K., Gómez, I., Molis, M., Hanelt, D., Karsten, U., Lüder, U., Roleda, M.Y., Zacher, K., Wiencke, C., 2006. Ultraviolet radiation shapes seaweed communities. Rev. Environ. Sci. Biotechnol. 5, 141–166.

Clayton, M.N., Wiencke, C., 1986. Techniques and equipment for culturing Antarctic benthic marine algae, and for preparing specimens for electron microscopy. Ser. Cien. INACH 34, 93–97.
Coelho, S.M., Rijstenbil, J.W., Brown, M.T., 2000. Impacts of anthropogenic stresses on the early development stages of seaweeds. J. Aquat. Ecosyst. Stress Recovery 7, 317–333.
Cook, A.J., Fox, A.J., Vaughan, D.G., Ferrigno, J.G., 2005. Retreating glacier fronts on the Antarctic Peninsula over the past half-century. Science 308, 541–544.
Cordi, B., Donkina, M.E., Peloquinb, J., Pricec, D.N., Depledgea, M.H., 2001. The influence of UV-B radiation on the reproductive cells of the intertidal macroalga, *Enteromorpha intestinalis*. Aquat. Toxicol. 56, 1–11.
Dring, M.J., Wagner, A., Lüning, K., 2001. Contribution of the UV component of natural sunlight to photoinhibition of photosynthesis in six species of subtidal brown and red seaweeds. Plant Cell Environ. 24, 1153–1164.
Eraso, A., Dominguez, M.C., 2007. Physicochemical Characteristics of the Subglacier Discharge in Potter Cove, King George Island, Antarctica, vol. 45. University of Silesia, Wroclaw.
Farman, J., Gardiner, B., Shanklin, J., 1985. Large losses of total ozone in Antarctica reveal seasonal ClO_x/NO_x interactions. Nature 315, 207–210.
Franklin, L.A., Osmond, C.B., Larkum, A.W.D., 2003. Photoinhibition, UV-B and algal photosynthesis. In: Larkum, A.W.D., Douglas, S.E., Raven, J.A. (Eds.), Photosynthesis in Algae. Kluwer Academic Publishers, The Netherlands, pp. 351–384.
Gómez, I., Weykam, G., Klöser, H., Wiencke, C., 1997. Photosynthetic light requirements, metabolic carbon balance and zonation of sublittoral macroalgae from King George Island (Antarctica). Mar. Ecol. Prog. Ser. 148, 281–293.
Gómez, I., Wulff, A., Roleda, M.Y., Huovinen, P., Karsten, U., Quartino, M.L., Dunton, K., Wiencke, C., 2009. Light and temperature demands of marine benthic microalgae and seaweeds in polar regions. Bot. Mar. 52, 593–608.
Hada, M., Iida, Y., Takeuchi, Y., 2000. Action spectra of DNA photolyases for photorepair of cyclobutane pyrimidine dimers in sorghum and cucumber. Plant Cell Physiol. 41, 644–648.
Hanelt, D., 1998. Capability of dynamic photoinhibition in Arctic macroalgae is related to their depth distribution. Mar. Biol. 131, 361–369.
Hanelt, D., Jaramillo, M.J., Nultsch, W., Senger, S., Westermeier, R., 1994. Photoinhibition as a regulative mechanism of photosynthesis in marine algae of Antarctica. Ser. Cien. INACH 44, 67–77.
Hanelt, D., Wiencke, C., Karten, U., 1997. Photoinhibition and recovery after high light stress in different developmental and life-history stages of *Laminaria saccharina* (Phaeophyta). J. Phycol. 33, 387–395.
Hoyer, K., Karsten, U., Sawall, T., Wiencke, C., 2001. Photoprotective substances in Antarctic macroalgae and their variation with respect to depth distribution, different tissues and developmental stages. Mar. Ecol. Prog. Ser. 211, 117–129.
Iken, K., Amsler, C.D., Hubbard, J.M., McClintock, J.B., Bajer, B.J., 2007. Allocation patterns of phlorotannins in Antarctic brown algae. Phycologia 46, 386–395.
IPCC, 2001. Climate Change 2001: Third Assessment Report of the Intergovernmental Panel on Climate Change (IPCC), Cambridge University Press for the Intergovernmental Panel on Climate Change, Cambridge, UK.
Jiang, H., Gao, K., 2008. Effects of UV radiation on the photosynthesis of conchocelis of *Porphyra haitanensis* (Bangiales, Rhodophyta). Phycologia 47, 241–248.
Karsten, U., Wulff, A., Roleda, M.Y., Müller, R., Steinhoff, F.S., Fredersdorf, J., Wiencke, C., 2009. Physiological responses of polar benthic algae to ultraviolet radiation. Bot. Mar. 52, 639–654.
Kirk, J.T.O., 1994. Light and Photosynthesis in Aquatic Ecosystems, Cambridge University Press, Cambridge, UK.
Klöser, H., Mercuri, G., Laturnus, F., Quartino, M.L., Wiencke, C., 1994. On the competitive balance of macroalgae at Potter Cove (King George Island, South Shetlands). Polar Biol. 14, 11–16.
Kräbs, G., Bischof, K., Hanelt, D., Karsten, U., Wiencke, C., 2002. Wavelength-dependent induction of UV-absorbing mycosporine-like amino acids in the red alga *Chondrus chrispus* under natural solar radiation. J. Exp. Mar. Biol. Ecol. 268, 69–82.
Müller, D.G., 1984. Culture studies on the life history of *Adenocystis utricularis* (Phaeophyceae, Dictyosiphonales). Phycologia 23, 87–94.
Müller, R., Wiecnke, C., Bischof, K., Krock, B., 2009. Zoospores of three Arctic Laminariales under different UV radiation and temperature conditions: exceptional spectral absorbance properties and lack of phlorotannin induction. Photochem. Photobiol. 85, 970–977.
Pakker, H., Beekmann, C.A.C., Breeman, A.M., 2000. Efficient photoreactivation of UVBR-induced DNA damage in the sublittoral macroalga *Rhodymenia pseudopalmata* (Rhodophyta). Eur. J. Phycol. 35, 109–114.
Quartino, M.L., Boraso de Zaixso, A.L., 2008. Summer macroalgal biomass in Potter Cove, South Shetland Islands, Antarctica: its production and flux to the ecosystem. Polar Biol. 31, 281–294.
Quartino, M.L., Klöser, H., Schloss, I.R., Wiencke, C., 2001. Biomass and associations of benthic marine macroalgae from the inner Potter Cove (King George Island, Antarctica) related to depth and substrate. Polar Biol. 24, 349–355.
Quartino, M.L., Deregibus, D., Campana, G.L., Latorre, G.E.J., Momo, F.R., 2013. Evidence of macroalgal colonization on newly ice-free areas following glacial retreat in Potter Cove (South Shetland Islands), Antarctica. PLoS One 8 (3), e58223.
Rautenberger, R., Bischof, K., 2008. UV-susceptibility of photosynthesis of adult sporophytes of four brown Antarctic macroalgae (Phaeophyceae). Ber. Polarforsch. Meeresforsch. 571, 263–269.
Roleda, M.Y., Wiencke, C., Hanelt, D., van de Poll, W.H., Gruber, A., 2005. Sensitivity of Laminariales zoospore from Helgoland (North Sea) to ultraviolet and photosynthetically active radiation: implications for depth distribution and seasonal reproduction. Plant Cell Environ. 28, 466–479.
Roleda, M.Y., Wiencke, C., Lüder, U., 2006. Impact of ultraviolet radiation on cell structure, UV-absorbing compounds, photosynthesis, DNA damage, and germination in zoospores of Arctic *Saccorhiza dermatodea*. J. Exp. Bot. 57, 3847–3856.
Roleda, M.Y., Wiencke, C., Hanelt, D., Bischof, K., 2007a. Sensitivity of early life stages of macroalgae from the northern hemisphere to ultraviolet radiation. Photochem. Photobiol. 83, 1–12.
Roleda, M.Y., Zacher, K., Wulff, A., Hanelt, D., Wiencke, C., 2007b. Photosynthetic performance, DNA damage and repair in gametes of the endemic Antarctic brown alga *Ascoseira mirabilis* exposed to ultraviolet radiation. Austral Ecol. 32, 917–926.
Roleda, M.Y., Zacher, K., Wulff, A., Hanelt, D., Wiencke, C., 2008. Susceptibility of spores of different ploidy levels from Antarctic *Gigartina skottsbergii* (Gigartinales, Rhodophyta) to ultraviolet radiation. Phycologia 47, 361–370.
Schloss, I.R., Ferreyra, G.A., Ruiz-Pino, D., 2002. Phytoplankton biomass in Antarctic shelf zones: a conceptual model based on Potter Cove, King George Island. J. Mar. Syst. 36, 129–143.
Steinhoff, F., Wiencke, C., Wuttke, S., Bischof, K., 2011. Effects of water temperatures, UV radiation and low vs high PAR on phlorotannin content and germination in zoospores of *Saccorhiza dermatodea* (Tilopteridales, Phaeophyceae). Phycologia 50, 256–263.
Swanson, A.K., Druehl, L.D., 2000. Differential meiospore size and tolerance of ultraviolet light stress within and among kelp species along a depth gradient. Mar. Biol. 136, 657–664.
Swanson, A.K., Druehl, L.D., 2002. Induction, exudation and the UV protective role of kelp phlorotannins. Aquat. Bot. 73, 241–253.
Turner, J., Overland, J.E., Walsh, J.E., 2007. An Arctic and Antarctic perspective on recent climate change. Int. J. Climatol. 27, 277–293.
Uhrmacher, S., Hanelt, D., Nultsch, W., 1995. Zeaxanthin content and the degree of photoinhibition are linearly correlated in the brown alga *Dictyota dichotoma*. Mar. Biol. 123, 159–165.
Van de Poll, W.H., Hanelt, D., Hoyer, K., Buma, A.G.J., Breeman, A.M., 2002. Ultraviolet-B induced cyclobutane-pyrimidine dimer formation and repair in Arctic marine macrophytes. Photochem. Photobiol. 76, 493–501.
Vaughan, D.G., Marshall, G.J., Connolley, W.M., Parkinson, C., Mulvaney, R., Hodgson, D.A., King, J.C., Pudsey, C.J., Turner, J., 2003. Recent rapid regional climate warming on the Antarctic Peninsula. Clim. Change 60, 243–274.
Véliz, K., Edding, M., Tala, F., Gómez, I., 2006. Effects of ultraviolet radiation on different life cycle stages of the south Pacific kelps, *Lessonia nigrescens* and *Lessonia trabeculata* (Laminariales, Phaeophyceae). Mar. Biol. 149, 1015–1024.
Weatherhead, E.C., Andersen, S.B., 2006. The search for signs of recovery of the ozone layer. Nature 441, 39–45.
Wiencke, C., 1996. Recent advances in the investigation of Antarctic macroalgae. Polar Biol. 16, 231–240.
Wiencke, C., Clayton, M.N., 1990. Sexual reproduction, life history, and early development in culture of the Antarctic brown alga *Himantothallus grandifolius* (Desmarestiales, Pheophyceae). Phycologia 29, 9–18.
Wiencke, C., Clayton, M.N., 2002. In: Wägele, J.W. (Ed.), Synopsis of the Antarctic benthos: Antarctic Seaweeds. A.R.G. Ganter Verlag KG Ruggell, Lichtenstein.
Wiencke, C., Rahmel, J., Karsten, U., Weykam, G., Kirst, G.O., 1993. Photosynthesis of marine macroalga from Antarctica: light and temperature requirements. Bot. Acta 106, 78–87.
Wiencke, C., Gómez, I., Pakker, H., Flores-Moya, A., Altamirano, M., Hanelt, D., Bischof, K., Figueroa, F.L., 2000. Impact of UV-radiation on viability, photosynthetic characteristics and DNA of brown algal zoospores: implications for depth zonation. Mar. Ecol. Prog. Ser. 197, 217–229.
Wiencke, C., Clayton, M.N., Schoenwaelder, M., 2004. Sensitivity and acclimation to UV radiation of zoospores from five species of Laminariales from the Arctic. Mar. Biol. 145, 31–39.
Wiencke, C., Roleda, M.Y., Gruber, A., Clayton, M.N., Bischof, K., 2006. Susceptibility of zoospores to UV radiation determines upper depth distribution limit of Arctic kelps: evidence through field experiments. J. Ecol. 94, 455–463.
Zacher, K., Campana, G.L., 2008. UV radiation and consumer effects on an intertidal and subtidal macroalgal assemblage: a comparative study. In: Wiencke, C., Ferreyra, G., Abele, D., Marenssi, S. (Eds.), The Potter Cove Coastal Ecosystem, Antarctica. Synopsis of research Performed 1999–2006 at the Dallmann Laboratory and Jubany Station, King George Island (Isla 25 de Mayo). Ber. Polarforsch. Meeresforsch., 571, pp. 287–294.
Zacher, K., Wulff, A., Molis, M., Hanelt, D., Wiencke, C., 2007a. UV radiation and consumer effects on a field-grown intertidal macroalgal assemblages in Antarctica. Glob. Change Biol. 13, 1201–1215.
Zacher, K., Roleda, M.Y., Hanelt, D., Wiencke, C., 2007b. UV effects on photosynthesis and DNA in propagules of three Antarctic seaweeds (*Adenocystis utricularis*, *Monostroma hariotii* and *Porphyra endiviifolium*). Planta 225, 1505–1516.
Zacher, K., Roleda, M.Y., Wulff, A., Hanelt, D., Wiencke, C., 2009. Responses of Antarctic *Iridaea cordata* (Rhodophyta) tetraspores exposed to ultraviolet radiation. Phycol. Res. 57, 186–193.