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Ultraviolet radiation and consumer effects on a field-grown intertidal macroalgal assemblage in Antarctica

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Abstract

Ultraviolet radiation (UVR) research on marine macroalgae has hithero focussed on physiological effects at the organism level, while little is known on the impact of UV radiation on macroalgal assemblages and even less on interactive effects with other community drivers, e.g. consumers. Field experiments on macrobenthos are scarce, particularly in the Antarctic region. Therefore, the effects of UVR and consumers (mainly limpets were excluded) on early successional stages of a hard bottom macroalgal community on King George Island, Antarctica, were studied. In a two-factorial design experimental units [(1) ambient radiation, 280–700 nm; (2) ambient minus UVB, 320–700 nm and (3) ambient minus UVR, 400–700 nm vs. consumer–no consumer] were installed between November 2004 and March 2005 ($n = 4$ plus controls). Dry mass, species richness, diversity and composition of macroalgal assemblages developing on ceramic tiles were followed. Consumers significantly suppressed green algal recruits and total algal biomass but increased macroalgal richness and diversity. Both UVA and UVB radiation negatively affected macroalgal succession. UVR decreased the density of *Monostroma hariotii* germlings in the first 10 weeks of the experiment, whereas the density of red algal recruits was significantly depressed by UVR at the end of the study. After 106 days macroalgal diversity was significantly higher in UV depleted than in UV-exposed assemblages. Furthermore, species richness was significantly lower in the UV treatments and species composition differed significantly between the UV-depleted and the UV-exposed treatment. Marine macroalgae are very important primary producers in coastal ecosystems, serving as food for herbivores and as habitat for many organisms. Both, UVR and consumers significantly shape macroalgal succession in the Antarctic intertidal. Consumers, particularly limpets can mediate negative effects of ambient UVR on richness and diversity till a certain level. UVB radiation in general and an increase of this short wavelength due to stratospheric ozone depletion in particular may have the potential to affect the zonation, composition and diversity of Antarctic intertidal seaweeds altering trophic interactions in this system.

Keywords: Antarctica, diversity, grazing, hard bottom community, King George Island, macroalgal recruitment, ozone depletion, UV radiation

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Introduction

The ozone layer protects all living organisms from excessive ultraviolet B radiation (UVB, 280–320 nm). Owing to anthropogenic emission of ozone-depleting substances a decline in stratospheric ozone concentrations was detected in the early 1980s (Farman *et al.*, 1985). During Antarctic spring, the ozone concentration can decrease by >50%, consequently increasing the UVB radiation reaching the Earth's surface (WMO,

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2003). Little improvement is expected for total column ozone in that region for the next several decades (Weatherhead & Andersen, 2006). Although the release of ozone-depleting substances is declining, whether or not ozone levels will ever recover to pre-1980s values is unknown (Weatherhead & Andersen, 2006).

The timing of the ozone depletion over Antarctica is crucial for aquatic organisms, as it coincides with the break up of sea ice, (i.e. the phase of highest water transparency; Karentz, 2003), and the season with strongest growth and reproduction for most macroalgal species Wiencke *et al*., (2007). Macroalgae are the major primary producers on intertidal rocky shores, providing food and shelter for a variety of associated species (Iken, 1996). Changes in macroalgal productivity or diversity are known to severely affect the structure of coastal marine food webs (Santas *et al*., 1998). Compared with algae from subtidal habitats, specimens from the intertidal are exposed to higher UVB regimes. Consequently, changes in species composition and species interactions due to UVR should firstly be recognized within eulittoral communities (Wahl *et al*., 2004).

Most UVR studies on marine macroalgae have been conducted in the laboratory, using artificial irradiance and focusing on physiological effects at the organism level. These studies indicate adverse UVB effects on macroalgal DNA (van de Poll *et al*., 2001; Roleda *et al*., 2004, 2005), growth (reviewed in Franklin & Forster, 1997), photosynthesis (Dring *et al*., 1996; Hanelt *et al*., 1997) and an influence on the vertical zonation of macroalgae (e.g. Wiencke *et al*., 2004; Bischof *et al*., 2006 for a review). Early developmental stages of macroalgae are regarded as most susceptible to UV stress (reviewed in Coelho *et al*., 2000), and, therefore, harmful UV effects should be most severe during early succession.

However, in laboratory studies with single species it is not possible to detect synergistic or indirect UV effects on the community level. Furthermore, in laboratory studies unnatural ratios of UVB, UVA and photosynthetically active radiation (PAR, 400–700 nm) have been applied with a possible overestimation of UVB effects. Predictions of ecosystem response to UVR cannot be made by single trophic-level assessments. Different UV sensitivities of (e.g. algae and consumers) may lead to strong interactive effects as shown by Bothwell *et al*., (1994). In the marine environment, only few studies on interactive effects exist, demonstrating the significance of climatic (e.g. temperature, UVR) and ecological factors (e.g. grazing) as important drivers on macroalgal recruitment (Lotze *et al*., 1999; Lotze & Worm, 2002). Recently, the effects of UVR on the succession of field grown marine macrobenthic communities were investigated in temperate and tropical regions. In these experiments, UVR was identified as a significant, but nonpersistent driver of community structure during early successional stages in macrobenthic assemblages (Lotze *et al*., 2002; Molis & Wahl, 2004 but see Dobretsov *et al*., 2005).

Studying UV effects on Antarctic macroalgal assemblages is particularly important due to the severe ozone depletion over this region (WMO, 2003). However, to our knowledge only few field studies investigated effects of UVR on Antarctic algal assemblages (Wahl *et al*., 2004, Fairhead *et al*., 2006). To date, studies testing for interactions between UV effects and other ecologically important factors are missing.

In the light of this, we designed a two-factorial field-experiment to test the separate and combined effects of UVR and consumers on the early succession of an Antarctic intertidal macroalgal assemblage. The main questions were (1) whether UVR and consumer treatments influence biomass, the structure, and diversity of the macroalgal assemblage, (2) whether there is a difference between UVA and UVB radiation effects and (3) whether interactive effects of UV radiation and consumers affect macroalgal community structure.

Materials and methods

Study site

The field experiment was conducted at a rocky intertidal platform at Peñón Uno, Maxwell Bay, King George Island, Antarctica (62°14′S, 58°41′W). The substratum consists of andensitic bedrock (G. Kleinschmidt, personal communication) and boulder fields. Intertidal Antarctic seaweed communities consist mainly of annual or pseudoperennial species and richness is low in comparison with temperate or tropical ecosystems (Wiencke & Clayton, 2002). Epibenthic communities are characterized by Rhodophyta [e.g. *Iridaea cordata* Turner (Bory)], Heterokontophyta [e.g. *Adenocystis utricularis* (Bory) Skottsberg] and Chlorophyta (e.g. *Monostroma hariotii* Gain, Iken, 1996), as well as mobile consumers, mostly gastropods and amphipods (Ferraz Nonato *et al*., 2000). In the present study, the gastropod *Nacella concinna* Strebel among other, smaller gastropods like *Laevilacunaria antarctica* Martens and *L. umbilicata* Pfeffer was found very frequently and was according to its biomass the most important grazer on macrolagae in the intertidal. Dominant amphipod species in the area are *Gondogeneia antarctica* Chevreux and *Djerboa furcipes* Chevreux (Jazdzewski *et al*., 2001; B. Obermüller, personal communication). During the sampling period, the maximal tidal range was about 2 m at a sea surface temperature between −1.8 °C (spring) and 2 °C (summer). Water transparency was strongly variable, depending on glacial freshwater input and wind

direction. UV transparency of the water body was highest in spring (e.g. November 28, 2003) with a maximal 1% depth at 16 m for UVB radiation, 19 m for UVA radiation and >20 m for PAR (400–700 nm). Minimum concentrations of nitrate, phosphate and silicate were recorded in February at nonlimiting algal growth levels of 15, 2 and 47 μmol, respectively (Schloss *et al*., 2002).

Experimental design and set-up

Using a randomized block design, we tested in a two-factorial experiment the effects of consumers (two levels, fixed) and UV radiation (three levels, fixed) on the succession of a macroalgal assemblage ($n = 4$).

The experiment was run from November 28, 2004 to March 14, 2005 (106 days). A pilot-study was performed the year before from December 20, 2003 to March 9, 2004 (74 days). Thirty-two PVC cages (50 cm × 50 cm × 12 cm, including the control treatments) were fixed to the substratum at Peñón Uno at a minimal distance of 1 m to each other in the lower eulittoral (Fig. 1). Consequently, cages were submerged at a maximum depth of 2 m. Cages were either open to all sides (open cage) or closed with plastic mesh (1 mm mesh size) to exclude macrograzers, mainly limpets (closed cage). To test for cage artefacts, partially open cages (half cages, equipped with PAB filters, $n = 4$) were deployed by cutting two holes (~15 cm × 5 cm = 25%) into each sidewall. Using cut-off filters as cage tops, ambient UV radiation levels were manipulated (see below for details). Open cages without filter (= full sunlight, $n = 4$) were used as procedural controls to test for filter artefacts.

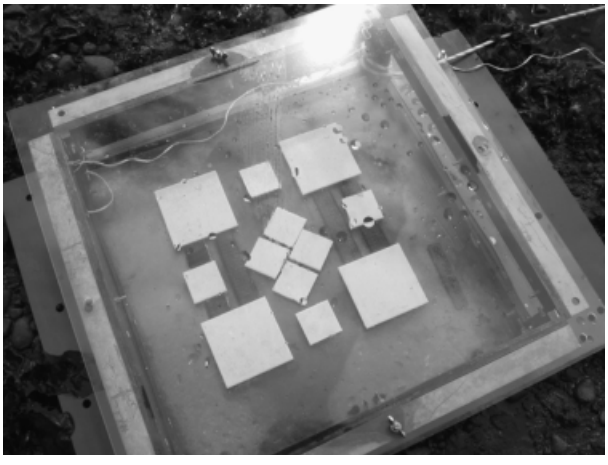

Fig. 1 Open cage allowing free access for consumers. Spatial arrangement of large and small ceramic tiles for the macro- and microalgal assemblage, respectively. Large tiles were used for macroalgae recruit identification and biomass measurements, half of the remaining small tiles for postcultivation of macroalgae and the other half for the assessment of the microalgal assemblage.

Unglazed ceramic tiles served as settlement substrata and were attached with Velcro to cage bottoms (Fig. 1). Each cage contained four large (10 cm × 10 cm) and eight small tiles (5 cm × 5 cm). At each of four sampling events, one large and one small tile were randomly withdrawn from each cage to determine treatment effects on the macroalgal and microalgal community, respectively. The results from the microalgal experiment are presented elsewhere (Zacher *et al*., 2007). At the end of the experiment four small tiles remained and were returned to the laboratory at Bremerhaven, Germany for cultivation.

UV radiation treatments

Cut-off filters manipulated the ambient light regime in three ways. (1) P = PAR treatment (>400 nm): using a 3 mm thick Perspex sheet (GS 231, Röhm, Darmstadt Germany), radiation <400 nm was blocked, while filters were transparent for 91% of PAR. (2) PA = PAR + UVA treatment (>320 nm): using a 3 mm thick Perspex sheet (GS 2458, Röhm, Darmstadt Germany) and a 0.13 mm transparent polyester film (Folanorm-SF/AS, folex imaging GmbH, Cologue, Germany), radiation <320 nm was blocked, while 89% of PAR and UVA passed the filter. (3) PAB = PAR +UVA + UVB treatment (>280 nm): using a 3 mm thick Perspex sheet (GS 2458, Röhm) transmitting 92% of PAR and UV radiation. Transparency of the GS 231 and GS 2458 Perspex filters decreased on average by 1.11% (SD ± 0.01) and 1.31% (SD ± 0.01) per month, respectively. Therefore, only damaged filters were exchanged. Polyester films were exchanged biweekly to minimize aging and fouling effects on transparency. Filters were cleaned once or twice per week.

Radiation measurements

Weekly to biweekly, the radiation regime above the water surface, at 10 and 200 cm depth was recorded at a distance ~50 m to the experimental site with a LiCor data logger (LI-1400, Li-Cor, Lincoln, NE, USA) equipped with an underwater PAR sensor (LI-192) and a Solar Light (PMA2100, Solar Light Co. Inc., Philadelphia, PA, USA) equipped with a UVB (PMA2106-UW) and a UVA radiation (PMA2110-UW) broad-band sensor. Readings were taken ±1 h of local noon. Ambient UVA + UVB radiation was continuously recorded at the nearby (1.5 km) Dallmann Laboratory with a 32-channel single-photon counting spectroradiometer (Isitec, Bremerhaven, Germany). In addition, the weighted irradiance (minimal erythemal dose, UV_{ery}) was measured continuously next to the cages with two

ELUV-14 UV-dosimeters (ESYS, Berlin, Germany; El Naggar *et al*., 1995) to follow the underwater UV-regime and its relative changes during the experiment.

Consumer abundance

Macrobenthic consumer density in each cage was estimated in January and March 2005 (by Scuba diving). In each cage, the individuals of each gastropod species were counted and the density of amphipods estimated in categories of tens. Consumers inside closed cages were also counted and occasionally found gastropods were removed. Amphipods entering or recruiting in the closed cages could not be removed and remained inside.

Sampling of macroalgae

The density (number cm^{-2}) of each macroalgal species was estimated on January 15 and 29, February 16 and March 3, 2004 (i.e. 26, 40, 58 and 74 days after starting the pilot study) and January 10, February 7 and 24 and March 14, 2005 (i.e. 43, 71, 88 and 106 days after starting the experiment). At the final sampling, four small tiles from each cage were transported in seawater filled plastic bags to Bremerhaven, Germany and cultivated under fluctuating Antarctic daylength (10–30 $\mu mol\,m^{-2}\,s^{-1}$) at 0 °C in a constant temperature room until most macroalgal germlings could be identified. Species identified after postcultivation served as qualitative data only and not for the statistical tests. All large tiles were sampled immediately after collection from the field at the Dallmann Laboratory. Recruit density of macroalgae was determined by counting individual germlings in five subsamples per tile ($\sim$50 mm^2) using a stereomicroscope (×16 magnification), leaving a border of 1 cm unsampled to avoid edge effects. Biomass of the community was measured as dry mass, by removing and drying (48 h at 80 °C) all organisms from the tile. We calculated Shannon diversity H' and Margalef species richness d (PRIMER™ 5 software package, Plymouth Marine Laboratory).

Data analysis

A *t*-test was performed to test for differences between two independent groups (e.g. test for cage or filter artefacts). Repeated measures (RM) ANOVA was used to test for the overall effects of consumers and UV radiation over time. Because the assumption of sphericity was not met (Mauchley's test) adjusted univariate *F*-ratios (Greenhouse–Geyser and Huynh–Feldt) were used (Quinn & Keough, 2002). Outcome was the same as in the RM ANOVA, therefore, we refer in the following to the former test. For separate sampling dates, a two-way ANOVA was performed to test for the effects of consumers and UV radiation on biomass, density of red and green algal recruits, species richness d and diversity H' at a Bonferroni corrected significance level ($\alpha = 0.0125$) in order to lower the probability of making a type I error (Quinn & Keough, 2002). Before analysis, data were tested for homogeneity of variances (Cochran's test). Heteroscedastic data after ln- or square-root transformation were analyzed by the non-parametric Kruskal–Wallis test. *Post hoc* comparisons were performed with Newman–Keuls test using STATISTICA™ 6.0 software package. Species composition of communities was compared by ANOSIM, and in case of significance, followed by SIMPER to quantify the relative contribution of species to observed dissimilarities among treatments (PRIMER™ 5 software package, Plymouth Marine Laboratory). ANOSIM used a Bray–Curtis similarity matrix based on fourth root transformed density data. Results from ANOSIM were illustrated with MDS-plots.

Results

Radiation measurements

Figure 2 shows the maximal UVA and UVB irradiances measured during April 2004 and April 2005. Peak values of UVA and UVB radiation in the air were recorded in December (Fig. 2), coinciding with the highest values of underwater UVB irradiance determined as UV_{ery} (Fig. 3). Lowest underwater UVB values during the experiment were measured in February and March 2005 (Fig. 3). Maximum UV exposure on the tiles was reached during low tide on December 14, 2004 (around noon) were the cages were exposed to 44 $W\,m^{-2}$ UVA and 2.3 $W\,m^{-2}$ UVB, respectively. On average, $7.3 \pm 5.7\%$ (mean $\pm$ SD) of surface UVB, $13 \pm 9.8\%$ of UVA and $30 \pm 11.4\%$ of PAR reached 200 cm water depth close to the experimental site around noon (Table 1).

Consumer abundance

The most abundant consumers during the experiment were amphipods (Table 2). Amphipod density in January was higher in half cages ($n = 4$) than in open cages (t-test = 2.78, $P = 0.032$), indicating cage artefacts. Furthermore, their density was significantly higher (about 100%) in closed cages in relation to open cages (t-test = −3.30, $P = 0.003$). In January, *N. concinna* and other gastropod densities in open and half cages showed no significant differences (t-test = 2.41, $P > 0.05$), thus no cage artefact was observed. Gastropod

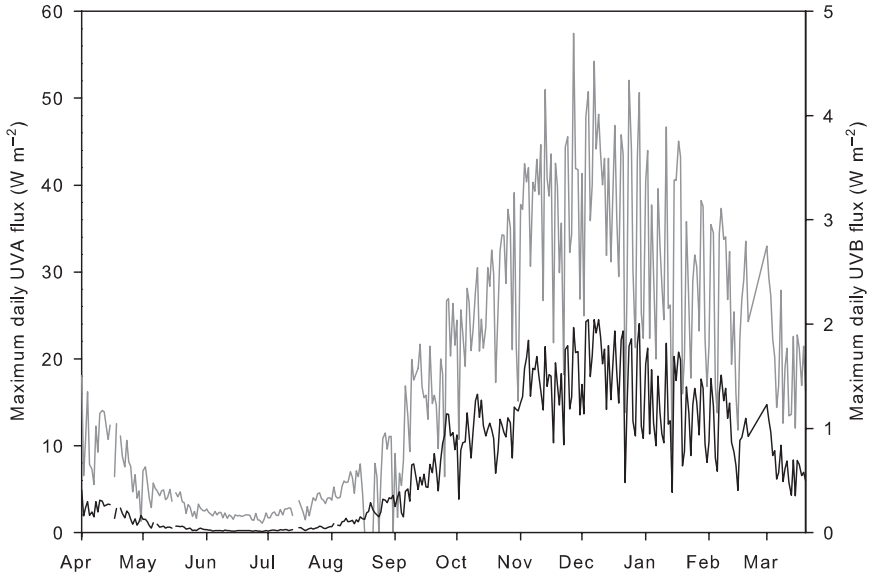

Fig. 2 Daily maximum ultraviolet A (UVA) and UVB irradiance from April 2004 to April 2005 measured at the Dallmann Laboratory (UVA gray line, UVB black line).

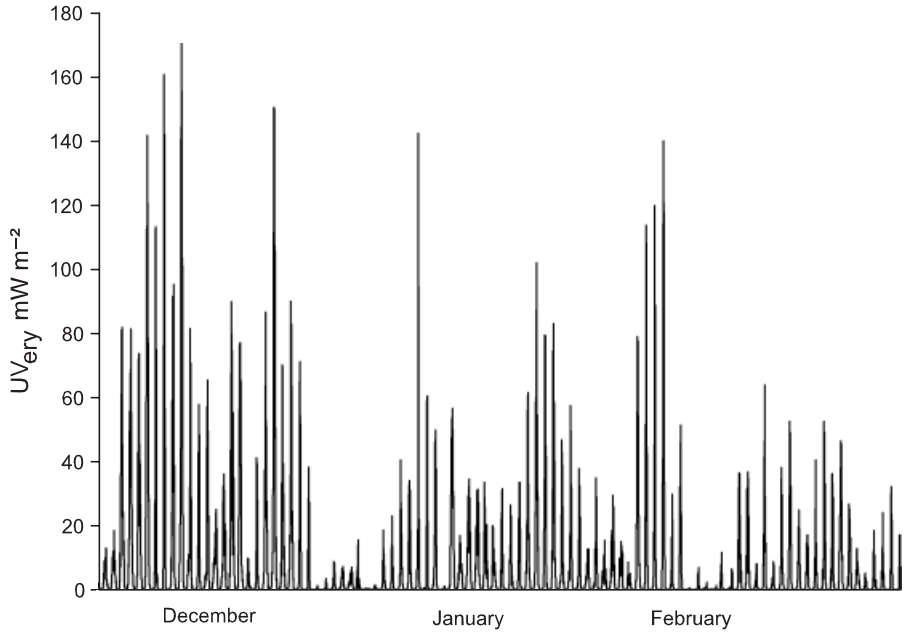

Fig. 3 Erythema weighted ultraviolet B (UVB) irradiance (UV_{ery}) during the duration of the experiment at Peñón Uno from December 2004 to March 2005. The sensor was located close to the cages with a maximal water column on top of 200 cm during high tide.

densities in closed cages were significantly lower (96%) in comparison with open cages (t-test = 6.20, $P < 0.001$).

In March, amphipod density was again higher in half cages than in open cages (t-test = 3.66, $P = 0.011$, Table 2). Their density was significantly higher (about 240%) in closed cages in relation to open cages (t-test = −4.66, $P < 0.001$). For gastropod densities (open and half cages) no significant differences were found (t-test = 1.62, $P > 0.05$); densities in closed cages was 40% lower compared with open cages (t-test = 1.79, $P > 0.05$).

No UV effects on total consumer density were detected (RM ANOVA, radiation effect, $F_{2,18} = 1.69$, $P = 0.213$).

UVR and consumer effects

In general, both experiments (the pilot study in 2004 and the longer experiment in 2005) gave very similar

Table 1 Mean irradiance (±SD) above the water surface, at 10 and 200 cm water depth and the percentage of the irradiance relative to surface values (100%)

	PAR ($\mu mol\, m^{-2}\, s^{-1}$)		UVA ($W\, m^{-2}$)		UVB ($W\, m^{-2}$)	
	Mean	SD	Mean	SD	Mean	SD
Above surface	1136	327	24.1	12.6	1.4	0.7
% irradiance in 10 cm	64	14.4	55	15.4	60	7.3
10 cm	734	291	13.7	8.4	0.8	0.4
% irradiance in 200 cm	30	11.4	13	9.8	7	5.7
200 cm	314	150	2.9	2.7	0.1	0.1

All measurements ±1 h around local noon for three solar wavebands: (1) PAR (400–700 nm, $n = 7$); (2) UVA (320–400 nm, $n = 12$); (3) UVB (280–320 nm, $n = 12$); measured with a broad-band sensor from December 2004 until February 2005.
PAR, photosynthetically active radiation; UV, ultraviolet radiation.

Table 2 Consumer density (number of individuals) in cages from different consumer treatments

	Closed cage ($n = 12$)		Open cage ($n = 12$)		Half cage ($n = 4$)	
	Mean	SE	Mean	SE	Mean	SE
January						
Nacella concinna	0	0	3.00	0.82	2.25	0.95
Other Gastropods	0.58	0.43	13.33	2.24	28.80	8.61
Amphipods	28.75	3.15	14.58	2.92	22.50	4.79
March						
Nacella concinna	0	0	1.67	0.47	3.25	1.03
Other Gastropods	2.58	0.74	2.67	0.58	3.50	1.89
Amphipods	25.42	3.61	7.50	1.31	22.50	4.79

outcomes. Table 3 gives an overview of the significant results of the two seasons. The following sections refer to the second, longer experiment.

In general, neither significant differences between open and half cages, nor between PAB and full sunlight treatments were detected for all tested parameters (*t*-test, $P > 0.05$), showing that there were no cage or filter artefacts.

UVR and consumer effects on biomass and abundance

Overall, both consumers and the interaction of UV radiation and consumers had a significant effect on biomass over the whole time span. These effects did not change over the duration of the experiment, shown by a nonsignificant time × treatment interaction (RM ANOVA, Table 4). For single sampling dates, no significant treatment effects on biomass were observed for either UV radiation or the interaction of UVR and consumers (Table 3). Consumers significantly reduced biomass on all sampling events (ANOVA or Kruskal–Wallis, January, $F_{1,18} = 70.31$, $P < 0.001$; early February, $H_{1,24} = 16.80$, $P < 0.001$; late February, $F_{1,18} = 298.03$, $P < 0.001$; March, $H_{1,24} = 17.29$, $P < 0.001$, correspondingly, Fig. 4).

The most abundant colonizer throughout the experiment was the green alga *Monostroma hariotii* Gain, reaching a total of 92–99% of all germlings on the tiles. Green algal recruitment was suppressed by UV radiation after 43 (ANOVA, $F_{2,18} = 14.58$, $P < 0.001$) and 71 days (ANOVA, $F_{2,18} = 7.69$, $P = 0.004$, Table 3, Fig. 5), but not at later samplings. During the last three sampling events, the density of green algal recruits was significantly reduced when consumers were present (day 71: ANOVA, $F_{1,18} = 23.69$, $P = 0.004$, day 88: $F_{1,18} = 31.51$, $P < 0.001$, day 106: ANOVA, $F_{1,18} = 41.50$, $P < 0.001$, Table 3, Fig. 5).

At the beginning of the experiment, very few red algal recruits settled but the density increased towards the end of the study (Fig. 5). UV radiation significantly reduced the red algal density at the end of the experiment (Kruskal–Wallis, $H_{2,24} = 15.14$, $P = 0.001$, Table 3) mostly due to UVA rather than UVB (Newman–Keuls, P : PAB and P : PA, $P < 0.05$; PAB : PA, $P > 0.05$). The density of red algal recruits was not affected by consumers.

UVR and consumer effects on species composition and diversity

Eight macroalgal species were found on the experimental tiles throughout the experiment (see Fig. 6). Three belonged to Chlorophyta (*M. hariotii* Gain, *Urospora penicilliformis* (Roth) Areschoug, and *Ulothrix* sp.) and

Table 3 Two-factorial ANOVA or nonparametric Kruskal–Wallis test on ultraviolet radiation (UV) and consumer (C) effects on biomass, density of Chlorophyta and Rhodophyta, species richness d and diversity H' for the sampling dates (numbers one to four in the table) of both studies 2004 and 2005 (− not significant, + significant), P-values Bonferroni corrected (significance level $P < 0.0125$)

		Biomass		Density Chlorophyta		Density Rhodophyta		Species richness		Diversity	
		2004	2005	2004	2005	2004	2005	2004	2005	2004	2005
1	UV	−	−	−	+	−	−	−	−	−	−
	C	+	+	−	−	−	−	−	−	−	−
	UV:C	−	−	−	−	−	−	−	−	−	−
2	UV	−	−	−	+	−	−	−	−	−	−
	C	+	+	+	+	−	−	−	−	−	+
	UV:C	−	−	−	−	−	−	−	−	−	−
3	UV	−	−	+	−	−	−	−	−	−	−
	C	+	+	+	+	−	−	−	−	−	−
	UV:C	−	−	−	−	−	−	−	−	−	−
4	UV	−	−	−	−	+	+	−	+	+	+
	C	+	+	+	+	+	−	−	+	−	−
	UV:C	−	−	−	−	−	−	−	−	−	−

Note that samplings one to four did not take place in the same time interval in 2004 and 2005 (see 'Materials and methods').

Table 4 RM ANOVA on UV radiation and consumer (C) effects on biomass, species richness d and diversity H' (four sampling events between January and March 2005, $n = 4$)

	Biomass			Species richness		Diversity	
Source	df	F	P	F	P	F	P
UV	2	2.84	0.085	0.77	0.480	1.99	0.165
C	1	33.95	**<0.001**	0.17	0.681	0.56	0.464
UV:C	2	39.96	**<0.001**	1.52	0.246	1.27	0.305
Residuals	18						
Time	3	2.36	0.081	4.35	**0.008**	10.87	**<0.001**
Time:UV	6	1.50	0.197	0.34	0.915	1.78	0.120
Time:C	3	2.19	0.010	2.19	0.099	3.28	**0.028**
Time:UV:C	6	1.66	0.148	4.53	**<0.001**	6.94	**<0.001**
Residuals	54						

Bold numbers indicate significant results.
UV, ultraviolet radiation; RM, repeated measures.

the remaining five belonged to Rhodophyta (*Iridaea cordata* Turner (Bory), *Palmaria decipiens* (Reinsch) Ricker plus three unidentified Gigartinales). During postcultivation in the laboratory, four Heterokontophyta were encountered (*Petalonia fascia* (Müller) Kuntze, *Adenocystis utricularis* (Bory) Skottsberg, *Geminocarpus geminatus* (Hooker *et* Harvey) Skottsberg, and one unidentified microthallus). Their young germlings were not detectable under the dissection microscope in Antarctica and could only be seen after being held in culture for an additional period of time. In sum, after cultivation 12 different macroalgal species were identified.

Overall, UV × consumer interactions on species richness were dependent on sampling dates (Table 4). Only at the final sampling, species richness was significantly increased by consumers (ANOVA, $F_{1,18} = 11.48$, $P = 0.003$) and decreased by UV (ANOVA, $F_{2,18} = 6.51$, $P = 0.007$; Table 3, Fig. 7). This was an effect of UVA rather than UVB (Newman–Keuls, P:PAB and P:PA, $P < 0.05$; PAB:PA, $P > 0.05$, Fig. 7).

UV × consumer interactions and consumer effects on diversity significantly changed over time (Table 4). At day 71, the presence of consumers increased diversity significantly (ANOVA, $F_{1,18} = 11.41$, $P = 0.003$, Table 3, Fig. 7). At day 106, UV radiation suppressed diversity

Table 5 Results of ANOSIM (pairwise test and Global *R*, *P*) on species composition for all sampling events, and results of SIMPER for significant results, indicating the contribution of single species to total dissimilarity in species composition due to treatment effects

	UV PAB : P	Consumer
After 43 days	$R = 0.286$, $P = 0.018$	$R = 0.015$, $P = 0.300$
After 71 days	**$R = 0.323$, $P = 0.006$**	**$R = 0.406$, $P < 0.001$**
Monostroma hariotii	41.5% −	35.0% −
Palmaria decipiens	18.8% −	23.8% +
Red 1	27.1% −	24.1% −
Iridaea cordata	12.6% −	10.9% −
After 88 days	$R = 0.073$, $P = 0.261$	**$R = 0.291$, $P = 0.001$**
M. hariotii	nt	39.0% −
P. decipiens	nt	19.2% ±
Ulothrix sp.	nt	19.2% +
I. cordata	nt	14.7% −
After 106 days	**$R = 0.792$, $P = 0.001$**	**$R = 0.331$, $P = 0.001$**
M. hariotii	17.7% −	27.2% −
Red 2	40.3% −	25.6% −
P. decipiens	11.5% −	15.2% +
I. cordata	15.0% −	17.4% +

Data were fourth root transformed, *P*-values Bonferronie corrected (significance level $P < 0.0125$), PAB = PAR + UVA + UVB, P = PAR; nt, not tested. The direction of the effect is given as +, positive UV or consumer effect; −, negative UV or consumer effect; ±, inconsistent.

Bold numbers indicate significant results.

PAR, photosynthetically active radiation; UV, ultraviolet radiation.

significantly (Kruskal–Wallis, $H_{2,24} = 11.96$, $P = 0.003$, Table 3). Diversity under the PAB treatment was significantly lower than under P treatment, with PA regimes resulting in intermediate levels of diversity (Newman–Keuls, P : PAB, $P < 0.05$; PAB : PA and P : PA, $P > 0.05$, Fig. 7).

UV radiation affected species composition at later stages of succession (Fig. 8 for sampling 4). At day 71, species composition was significantly different between PAB and P treatments. This difference was mainly due to the strong decline in the density of recruits of the green alga *M. hariotii* and one unidentified Gigartinales recruit (Red 1) under the PAB treatments, which explained together 70% of the dissimilarity between the treatments (Table 5). Again, at day 106, species composition was significantly different between PAB and P treatments. This difference was mostly due to the negative UV impact on the density of one unidentified Gigartinales recruit (Red 2) and *M. hariotii* under the PAB treatment, which explained together 60% of the dissimilarity between the treatments (Table 5). The PA treatments took an intermediate position between the P and the PAB treatments (Fig. 8).

Consumer affected species composition significantly during the last three samplings (e.g. Fig. 8 for sampling 4). SIMPER analysis showed that *M. hariotii* and *P. decipiens* recruits together explained 60%, 60% and 40% of the dissimilarities between the open and closed cages at the three samplings, respectively. Thereby, consumers decreased *M. hariotii* density, whereas *P. decipiens* density was favored by consumer presence (or inconsistent at sampling 3, Table 5).

Discussion

Overall, the experiments revealed significantly negative effects of ambient levels of UV radiation and consumers on the intertidal Antarctic macroalgal assemblage. The treatment effects were more pronounced at the end of the study. In general, consumer effects (mainly on biomass and recruit density) were more often observed than UV effects (affecting mainly diversity and species composition).

The pilot study showed the importance of choosing an adequate experimental period due to the slow growth of the recruits. Therefore, in the second year a maximal experimental exposure time was chosen (from sea ice break up until the end of summer). However, the general outcome of the two experiments was similar.

Consumer effects

Consumers reduced biomass of macroalgal assemblages throughout the experiment. Herbivores preferred green algae over red seaweeds, decreasing the density of green algal recruits in open and half cages

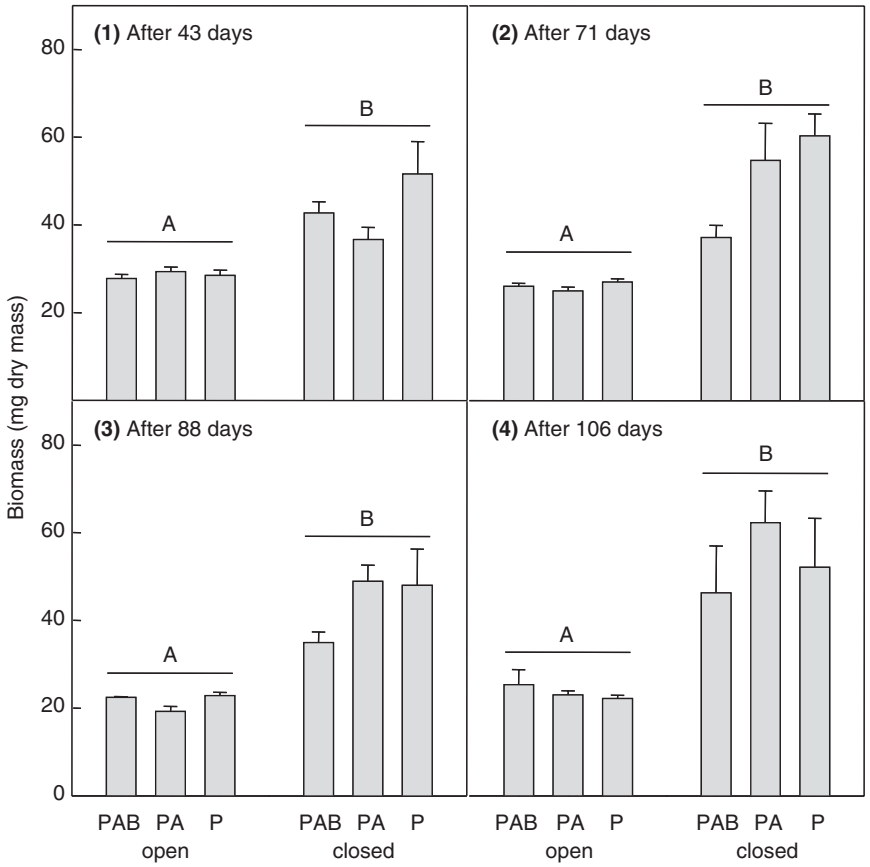

Fig. 4 Effects of ultraviolet radiation: (UV) (PAB = PAR + UVA + UVB, PA = PAR + UVA, P = PAR) and consumers (open and closed cages) on the biomass at the four samplings (mean of total biomass of each tile = 100 cm^2 ± 1 SE, $n = 4$). Capitals indicate significant differences between consumer treatments, i.e. A is significant different from B (as mean of the UV treatments). PAR, photosynthetically active radiation.

compared with closed cages. This effect on biomass was not caused by the small-sized amphipods, as they were not excluded by cages. Antarctic amphipods (e.g. *G. antarctica*) feed on some macroalgae, such as *I. cordata* and *P. decipiens* (Huang *et al*., 2006), but are apparently not able to graze on macroalgae during early succession were recruits are very small and well attached to the ground. Similar results were found in laboratory experiments with the green alga *Enteromorpha intestinalis* where snails had strong negative effects on macroalgal recruitment, whereas amphipods did not feed on *Enteromorpha* recruits but consumed adult *Enteromorpha* pieces (Lotze & Worm, 2002). The firm attachment of recruits made it difficult to detach them, even with a brush. Thus, the impact of amphipods on early successional stages of the macroalgal species growing on our experimental tiles seems to be negligible. Other species might have been grazed by amphipods from the start and therefore do not grow in the field but later in culture (e.g. *Geminocarpus*). Consequently, biomass effects in our set-up were mainly caused by larger limpets, (e.g. *Nacella concinna*, which were successfully excluded by cages). In contrast to amphipods, *N. cocinna* is clearly the largest (length $\leq$46 mm) and most important grazer at our study site and can reach densities from 28 to 131 ind. m^{-2} in the Antarctic intertidal (Brêthes *et al*., 1994). *N. concinna* mostly feeds on macroalgal propagules and benthic microalgae (Iken, 1996; Kim, 2001), whereas the smaller snail *L. antarctica* was shown to feed on *M. hariotii*, the most dominant green alga on our tiles (Iken, 1999). At the experimental site (Peñón Uno), a negative correlation between the density of *N. concinna* and macroalgae was also detected by Kim (2001), indicating effective grazing of this species. This further demonstrates the importance of gastropods, especially *N. concinna* as drivers on community structure in the intertidal during early macroalgal succession. For example, *N. concinna* and *L. antarctica* contributed up to 47% of the biomass of macroalgae-associated herbivores at the study site (Iken, 1996). Grazers can also influence the diversity by e.g. increasing or decreasing the spatial heterogeneity of the system

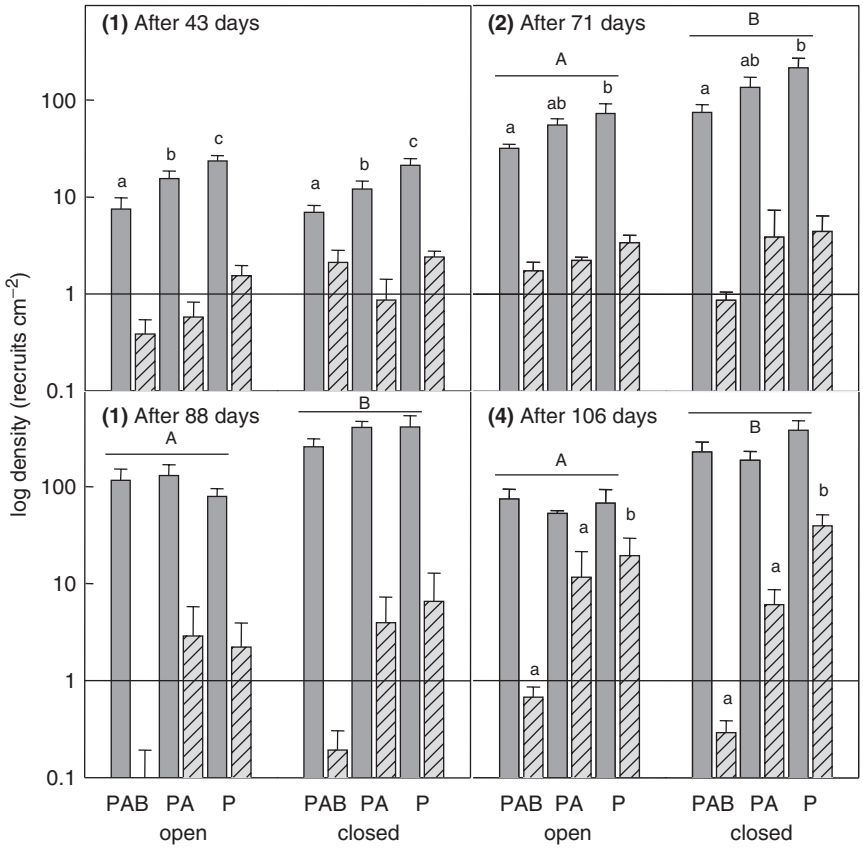

Fig. 5 Effects of ultraviolet (UV) (PAB = PAR + UVA + UVB, PA = PAR + UVA, P = PAR) and consumers (open and closed cages) on density of red (diagonal hatched) and green algal (gray) recruits at the four samplings (mean ± 1 SE, $n = 4$). Note logarithmic scale. Lower case letters indicate significant differences between different UV treatments (as mean of closed and open treatments, respectively) and capitals significant differences between consumer treatments (as mean of the UV treatments, here only for green algal density, different letters demonstrate significant differences). If no letters were used no significant difference was found. PAR, photosynthetically active radiation.

(Sommer, 2000). Gastropods, like *Littorina littorea* were shown to increase the diversity by creating a diverse mosaic of microhabitats (Sommer, 2000). In our study, feeding tracks alternate with untouched biofilm (due to snail grazing) and species richness and diversity were generally higher in cages where gastropods were present.

UV radiation effects

UV effects changed over time showing species-specific differences. Strongest impacts on the community structure were observed at the end of the experiment (after 3.5 months) in contrast to other studies (Santas *et al*., 1998; Lotze *et al*., 2002; Molis & Wahl, 2004; Wahl *et al*., 2004 but see also Wulff *et al*., 1999 and Dobretsov *et al*., 2005). UVA radiation was mainly responsible for a decrease in recruit density and species richness whereas additional UVB had a significant negative influence on species composition and diversity. The different effects of UVB and UVA (with UVA exceeding UVB by a factor around 20 on a daily dose) demonstrated that UVB radiation was more damaging per unit irradiance, but that UVA is more damaging at the actual daily doses received (Cullen & Neale, 1994; Wahl *et al*., 2004; Wiencke *et al*., 2006).

Green algal recruit density was decreased by UV radiation at the start of the experiment whereas red algal recruit density was most affected at the end with impacts on diversity, species richness and species composition. Several explanations for the changing nature of UV effects on the assemblage level are conceivable: (i) UV effects may match with changing radiation fluxes during the experiments, (ii) shading effects, where less UV-sensitive canopy species allow colonization of more UV-sensitive species as understorey algal and (iii) different adaptation strategies (e.g. morphology, protective substances like MAAs or phlorotannins, DNA repair mechanisms) leading to species-specific

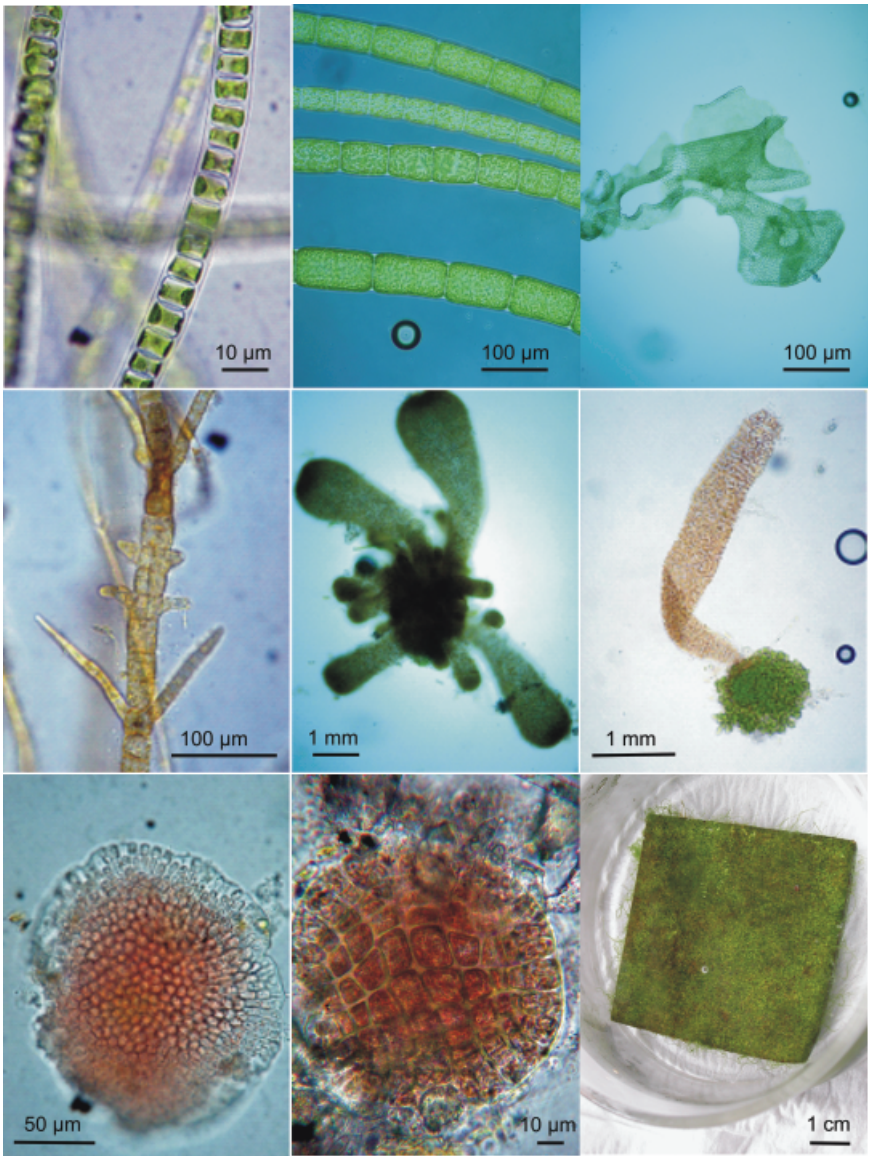

Fig. 6 Macroalgal germlings on postcultivated tiles. (first row: left *Ulothrix* sp., middle *Urospora peniciliiformis*, right *Monostroma hariotii*; second row: left *Geminocarpus geminatus*, middle *Adenocystis utricularis*, right *Petalonia fascia*; third row: left *Iridaea cordata*, middle *Palmaria decipiens*, right postcultured tile).

response to UV radiation (Lotze *et al.*, 2002; Molis & Wahl, 2004).

In our study, a correlation between diminishing UV effects and a decrease in UV doses over time (model i) was shown for the density of green algal recruits (i.e. its most dominant representative *M. hariotii*). An adaptation to UV radiation over time together with decreasing UV doses are possible explanations. The macrothallus of *M. hariotii* occurs in high abundance in the Antarctic intertidal. Early life stages, however, are shown to be more sensitive to UV stress compared with adults of the same species (reviewed by Coelho *et al.*, 2000), but have the capacity to acclimate as they mature (Lotze *et al.*, 2002).

In contrast to the green algal recruits, red algal recruits were more sensible to UV radiation during later stages of succession but early negative UV effects on red algal germlings might have been masked by low densities at the beginning of the experiment (few individuals and species settled in the first weeks and the variance between replicates was high; Dobretsov *et al.*, 2005). Most red algae are fertile in late summer whereas green algae like *M. hariotii* release spores earlier in the season (Wiencke & Clayton, 2002). Especially, one unidentified Gigartinales recruit (red2), occurring only at the end of the experiment was highly UV susceptible and mainly responsible for the strong UV effects on red

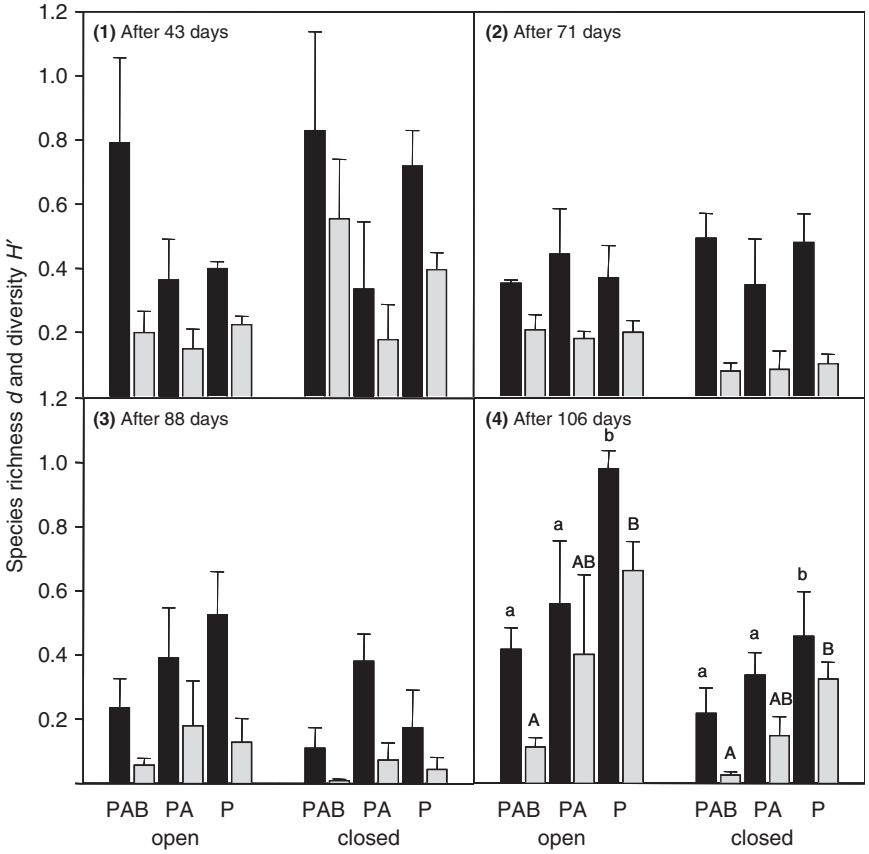

Fig. 7 Effects of ultraviolet radiation: (UV) (PAB = PAR + UVA + UVB, PA = PAR + UVA, P = PAR) and consumers (open and closed cages) on species richness *d* (black) and diversity *H′* (grey) of red and green algal recruits at the four samplings (mean ± 1 SE, $n = 4$). Letters indicate significant differences between different UV treatments, a (A) is significant different from b (B), AB is not significantly different from A or B (as mean of closed and open treatments, respectively). Consumer effects on diversity were found on day 71 and for species richness for day 106 with the open cages having higher values than the closed ones. PAR, photosynthetically active radiation.

algal recruits. Macrothalli of some Antarctic red algal species (e.g. *P. decipiens* and *I. cordata*) produce MAAs which enable them to grow in the intertidal (Hoyer *et al*., 2001). However, little is known about MAA production in spores and germlings. In temperate and tropical regions, some UV-tolerant species provide protective shading and allow colonization of more UV-sensitive species (model ii, Lotze *et al*., 2002; Molis & Wahl, 2004; Wahl *et al*., 2004). In our experiment, however, these shading effects were lacking because propagules were still very small at the end of the experimental period. The macrothalli of many species develop in the winter period or in early spring of the following season. The UV radiation could, therefore, directly inhibit growth and influence negatively species richness and diversity.

UVB doses in Antarctica have increased for more than two decades. No long-term studies exist for this area but Karentz (2003) speculated that subtle shifts in community structure to more UV resistant species have already occurred and are continuing as a result of increased UV exposure. Species encountered in the intertidal nowadays should, therefore, be well adapted to UV radiation. However, our results show that this is only partly true for macroalgal recruits, which are species-specifically inhibited by UV radiation.

Interactive UV and consumers effects

Overall interactive effects of UV × consumer were found on biomass but not for single sampling dates. Interactions between UV radiation and consumers can occur when UV induces changes in the chemical composition of algae thereby altering consumption patterns (Lotze *et al*., 2002). On the other hand, UV radiation can have a direct negative effect on consumers, resulting in an enhanced algal productivity (Bothwell *et al*., 1994). From the second to the last sampling date, the biomass was lower in the PAB treatment when consumers were

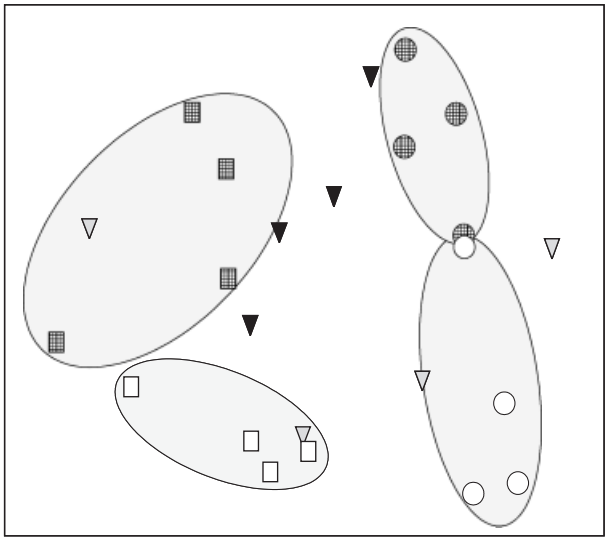

Fig. 8 MDS plot of macroalgal assemblages after 106 days (sampling 4). The species composition is different from P to PAB but also differs between grazed and nongrazed plots. The PA treatment does not show a clear pattern. Key: white circle, open PAB treatments; hatched circle, closed PAB treatments; gray triangle, open PA treatments; black triangle, closed PA treatments; white square, open P treatments; hatched square, closed P treatments; $n = 4$; Stress = 0.17. PAB = PAR + UVA + UVB; PA = PAR + UVA; P = PAR; PAR, photosynthetically active radiation.

absent, but this effect was not significant for the single sampling dates. As there was no UV effect on biomass and no UV effect on consumers, we assume this to be a spurious effect.

Species composition was significantly affected by both UV and consumers due to different species and group-specific responses to radiation and consumer treatments, especially at the last sampling dates. Whereas UV radiation suppressed recruit density after 106 days, consumers favored the density of some leathery red algal recruits (*P. decipiens* and *I. cordata*). Therefore, at least in some cases consumers have the potential to counteract negative UV effects. On the other hand, UV and consumer effects on *M. hariotii* and one unidentified red alga worked in the same direction further decreasing their density. In general, changes in UV radiation and consumer pressures might cause seasonal and/or spatial shifts in species composition and community structure (see also Lotze *et al*., 2002; Dobretsov *et al*., 2005).

In conclusion, our results show that Antarctic macroalgal recruits are particularly sensitive to UV radiation and consumer pressure. Consumers, especially snails, can compensate for negative effects of ambient UV on richness and diversity up to a certain level, but never reach the same level as without UV radiation. While UVB radiation had a significant negative influence on macroalgal composition and diversity a further increase, due to stratospheric ozone depletion, would influence these variables most, whereas species richness and biomass would be less affected. Therefore, we hypothesise that UVB radiation in general, and an increase of these wavelengths in particular has the potential to affect the zonation, composition and diversity of Antarctic intertidal seaweeds altering trophic interactions in this system. Whether the significant negative impact of ambient UV radiation at the end of the experiments is persistent when recruits develop into macrothalli in the next spring requires further studies. Therefore, we suggest that future research in the Antarctic region should include long-term monitoring studies considering the community development during the Antarctic winter and early spring. Combining ecological and abiotic factors would further increase our understanding of the integrated response of Antarctic species, communities and ecosystems to their changing environment (Karentz, 2003; Molis & Wahl, 2004; Bischof *et al*., 2006). However, these types of experiments are, due to the extreme climatic situation in this region, difficult to perform and would require logistically difficult maintenance throughout the entire year.

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