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Transient effects of solar ultraviolet radiation on the diversity and structure of a field-grown epibenthic community at Lüderitz, Namibia

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Abstract

While the majority of research on ultraviolet radiation (UVR) has focused on UVR-induced changes in the productivity and abundance of single taxonomic groups, only a few field studies have considered the influence of ambient UVR on complete assemblages, in particular of the macrobenthos. Using cutoff filters, we followed the effects of three radiation treatments, (1) PAR+UVAR+UVBR, (2) PAR+UVAR, (3) PAR, on macrobenthic community structure at Lüderitz, Namibia, SE Atlantic, for 3 months. Species composition, biomass, evenness, and species richness were not significantly affected by UVR, while the diversity H' of PAR+UVAR+UVBR-exposed communities was significantly lower compared to PAR treatments. However, this effect was only observed early in succession. Increased abundance of the red alga *Ceramium* sp. coincided with vanishing UVR effects on the community, suggesting a muted UVR microclimate under the *Ceramium* canopy. Our results demonstrate that UVR could neither decrease diversity persistently, nor affect any of the other tested community parameters. Single UVR-tolerant species may provide protective shading for UVR-sensitive species, thus buffering harmful UVR effects at the community level. Missing UVBR effects suggest a limited influence of ozone depletion on shallow water macrobenthic diversity.

Keywords: Diversity; Macrobenthos; Namibia; Protective shading; UVR stress

1. Introduction

Current ozone-mediated increases in solar ultraviolet B radiation (UVBR) may continue until the middle of this century (WMO, 1998; Tabazadeh et al., 2000).

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Organisms from DOC rich habitats may encounter worldwide strongest increases in UVBR exposure, due to global warming related declines in DOC (Schindler et al., 1996). Differential UVR sensitivities of life stages (Keller et al., 1997; Santas et al., 1998a; Lotze and Worm, 2002) and consumer–prey interactions (Bothwell et al., 1994; Pavia et al., 1997; McNamara and Hill, 1999; Kelly et al., 2001) strongly advocate an implication of present UVR levels on species composition. Surprisingly, only few studies, strongly biased towards primary producers, have tested UVR effects on communities, mainly in a productivity context (Häder et al., 1998). In strong contrast to the many studies at the organismal level, adverse UVR effects on communities were either transient (Bothwell et al., 1993; Kiffney et al., 1997; Santas et al., 1997, 1998a,b), missing (DeNicola and Hoagland, 1996; Hill et al., 1997, but see Rader and Belish, 1997), or contradictory (Bothwell et al., 1994; Kelly et al., 2001).

Two prior studies tested UVR effects on the structure of marine epibenthic communities, both detecting transient adverse UVR effects in Greece (Reizopoulou et al., 2000) and in Canada (Lotze et al., 2002), respectively. In Namibia, UVR and particularly UVBR levels are exceptionally high (Cunningham and Bodeker, 2000), suggesting there may be the strongest possible effects of ambient radiation as found anywhere in the world. The objective of this study was whether (1) UVR decreases diversity in a Namibian epibenthic community, (2) UVR influences species composition of the community, and (3) detrimental effects resulted from UVBR alone or from the entire UV regime.

2. Material and methods

2.1. Study site

A field experiment was conducted in Radford Bay, Lüderitz, Namibia (26°40′ S; 15°09′ E), a wave-sheltered bay on the SE Atlantic coast between 23 November 2000 and 16 February 2001. The seafloor consists of fine (<106 μm) sediments (Molloy, 1992). During the experiment, the water was turbid (Table 1) and relatively cold (14.1±1.1 °C, mean±S.D., K. Noli, personal communication). Minimum water depth in the bay was 2 m at spring low tide. Semi-diurnal tides ranged ±1.5 m (South African Navy Tide Tables, Cape Town) and resulting currents contributed substantially to turbidity. Clouds and fog banks reduced UVAR and PAR equally strong by 19%

Table 1
Irradiance (W m^{-2}) above the water surface, in 4 and 100 cm water depth ±15 min around local noon and diffuse vertical attenuation coefficients of downward irradiance (K_d) for three solar wavebands: PAR (400–700 nm), UVAR (315–400 nm) and UVBR (280–315 nm)

	n	Above surface		4 cm		100 cm		K_d	
		Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
PAR	7	730.9	164.1	455.6	157.7	211.7	92.9	0.81	0.27
UVAR	9	38.1	3.6	19.4	5.1	3.7	2.1	1.89	0.67
UVBR	2	2.8	0.2	0.8	0.3	0.03	0.0	4.41	1.01

See text for details of radiation measurements. *n*=number of days when measurements were done.

(personal measurements) and prevailed for less than 2% during the experiment (personal observation). Colonization pressure, especially by algae seems to be intense, covering new substratum within a few weeks (D. Harvey, personal communication). According to Molloy (1992), *Gracilaria gracilis* is the dominant alga at Radford Bay. *Ceramium* sp. is substantially lower in abundance and biomass, followed by *Ulva capensis*. The subtidal sessile fauna consists of only few species (<25) with albeit high biomass (personal observation). Two isopod species *Paridotea* sp. and *Idotea metallica* Bosc were the only consumers encountered. An oyster farm was the only observed human activity in the bay but it did not affect the experiment, since oysters were not fed and no biocidal antifoulants were used (D. Harvey, personal communication). Moreover, filtering by oysters should not have decreased settler density substantially, because our experiment was conducted at a distance >100 m from the active area of the farm.

2.2. Experimental design and setup

Six rafts (=blocks) were fixed equidistantly to a mooring 100 m off shore, in a single 33 m long row. Each raft consisted of a Perspex plate (1100×500×5 mm). To lift rafts approximately 1 cm above sea surface, a 20-mm-thick Styrofoam panel was glued to the underside using silicone. On each raft, eight openings (100×100 mm) were arranged in two rows of four, separated equidistantly by 200 mm. Four openings were randomly chosen for the experiment described here, the remaining four openings were used for additional experiments described elsewhere. Beneath each opening a cubic, transparent polycarbonate

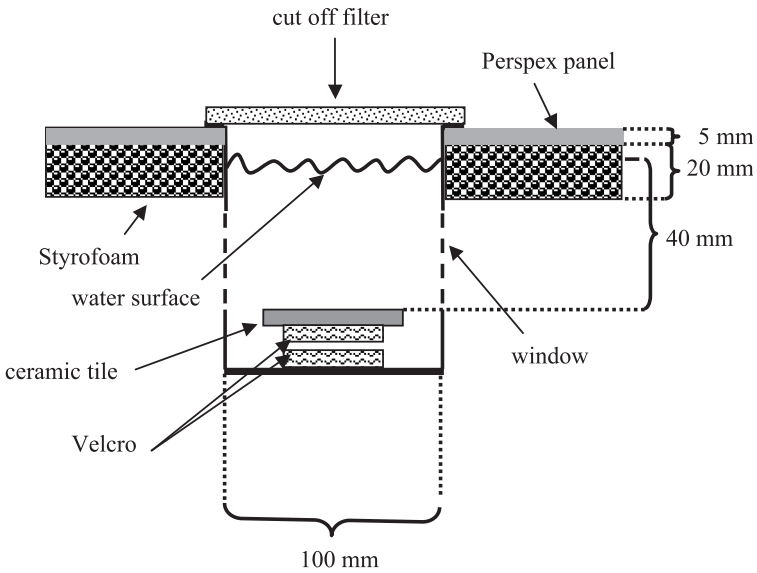

Fig. 1. Cross section of a single experimental unit from one block. For clarity, stippled lines indicate positions of fully cut out windows. Material of filter was treatment dependent. Note: Drawing not to scale.

container (1 l volume) positioned a grey ceramic tile, representing an artificial settlement substratum, horizontally in 40 mm water depth (Fig. 1). Using Velcro, the tile was fixed centrally underneath an opening. A 75×75 mm window was cut in each container wall. Cutoff filters (for specifications, see next section) above the openings could be unlatched and flipped open for cleaning and sampling purposes. To minimise a reduction in transmission due to salt spray or fouling, filters were cleaned with a soft sponge every other day. In addition, landing of sea birds on the rafts was effectively prevented by a tent-like construction of crisscrossed fishing line, without reducing solar radiation levels significantly (personal measurements).

2.3. Treatments

In a randomised block design (n=6), we tested for UVR effects on macrobenthic community structure. Using cutoff filters (see Fig. 2 for optical properties), three radiation treatments were generated: (1) PAR+UVAR+UVBR (=PAB), 3-mm-thick Perspex, GS 2648 Röhm, Germany; (2) PAR+UVAR (=PA), 3-mm-thick Perspex, covered by a 0.1-mm-thick clear polyester transparency, LTF NashuaCopy; and (3) PAR (=P), 4-mm-thick Makrolon, long life plus 293, Röhm, Germany). As a fourth treatment, unfiltered plots (=procedural controls) controlled for filter artifacts, e.g. reflection of sunlight, short-term obscuration due to salt spray or fouling. At no time did filtered PAB-exposed plots

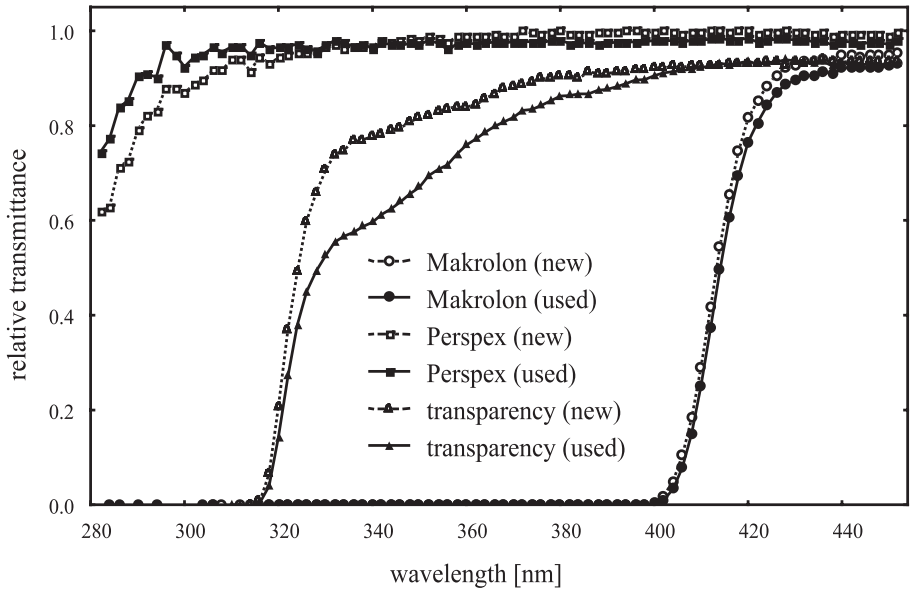

Fig. 2. Transmittance of new and used filter materials in relation to 100% transparent quartz glass. See Treatments for details. No data beyond 450 nm are presented since relative transmittance of all tested filter materials were constantly 90% or higher.

significantly differ from unfiltered PAB-exposed plots. Thus the presence of filters did not affect radiation effects on any tested response variable.

Transparencies were exchanged once a month. All filter materials were measured before and after the experiment to test for changes in their filtering abilities. Transmittance of used filters was significantly reduced but reduction rarely exceeded 5%, except for the waveband 320–350 nm with transmittance reduced by almost 20% compared to unused filters (Fig. 2). All optical properties of filters and quartz glass (type Herasil-1, Heraeus, Germany) were measured with a spectroradiometer (DM 150 double monochromator in Czerny–Turner arrangement, Bentham Instruments, England), using a Bentham DH3 as the selective photo-multiplier and a 1000-W, 8-A quartz-halogen lamp (General Electrics, United States) as a light source.

2.4. Radiation measurements

All field measurements were performed with broadband sensors (Gröbel, Germany). Due to technical problems, solar irradiance was only recorded on the first 2 days of the experiment (23 and 24 November 2000) and on 7 days between the 29 January and 10 February 2001. November readings were done with the UVBR (280–315 nm) and UVAR (315–400 nm) sensors. The remaining measurements were done with the UVAR and the PAR (400–700 nm) sensors. Prior to the experiment, irradiance was measured with all sensors at local noon on a cloudless day above water as well as with the sensor submersed in 1 mm of distilled water to adjust for a submersion effect. Readings in the field were taken within 30 min around local noon above the water surface, at 4 and 100 cm depth. At each depth, measurements with all available sensors were done simultaneously over a 5-min period.

Diffuse vertical attenuation was determined from 4 and 100 cm readings for each waveband using the formula $K_d=\ln(E_{(100\ cm)}/E_{(4\ cm)})\times(4\ cm-100\ cm)^{-1}$, where K_d is the diffuse vertical attenuation coefficient and E is the energy of irradiance measured in 4 and 100 cm water depth.

2.5. Community sampling

Samples were taken nondestructively 21, 42, 63, 77 and 84 days after initiation of the experiment. To avoid edge effects, no data were taken from a 10-mm-wide margin of the 75×75 mm tiles, leaving $\cong 30\ cm^2$ of substrate to be sampled. From this area, three 1-cm^2 fields were randomly chosen and percent cover of each species encountered was estimated, using a stereo microscope with 12× magnification. The arithmetic mean of the three estimates for each species was determined. Only species ≥1% mean cover per tile were used for computation of the Shannon index H' (=diversity H') and Evenness J and the cumulative species richness R was recorded. In addition, we measured wet weight of assemblages after tiles rested vertically for 1 min to allow water to drain. The same panels were repeatedly sampled, using a new randomisation for each sampling date. After the experiment, accumulated material was scraped off the tiles, dried to constant weight at 60 °C and weighed.

2.6. Statistical analysis

Using repeated-measures ANOVA, we tested for irradiance effects on diversity H', evenness, species richness and wet weight with "radiation" (four levels, fixed) and "time" (five levels, repeated) as factors. Mauchley's test for sphericity was only performed where significant radiation effects were detected (Quinn and Keough, 2002). Data of single sampling dates were analysed with mixed-model ANOVA to examine irradiance effects on diversity H', evenness, species richness, total abundance, and wet and dry weight with "radiation" as fixed factor (four levels). "Block" (six levels) was treated as a random factor for which sums of squares were calculated, but not variance ratios. Because there was no within block replication, we could not test for block interactions. In order to lower the probability of making a type I error, the level of significance was corrected with the Bonferroni method to α=0.01 (Sokal and Rohlf, 1995). Arcsine square root transformation was performed for all species cover data which were directly analysed in the ANOVA (Sokal and Rohlf, 1995). Prior to all analyses, homoscedasticity of data was confirmed with Cochran's test and where necessary data were log-transformed. Adjusted post hoc tests were done with the Tukeys honest significant difference test (Tukeys HSD), comparing multiple means at the α=0.05 significance level. All calculations and graphics for ANOVA were performed with the Statistica™ software package.

A Spearman rank correlation was performed between the mean of TOMS satellite data of erythemal weighted daily UVBR exposure between two sampling dates and diversity H', evenness, and species richness.

Based on multi-species abundance data, Bray–Curtis similarity indices were calculated with PRIMER™ software package and used for an analysis of similarity (ANOSIM) to evaluate differences in species composition among treatments.

3. Results

3.1. Radiation measurements

Daily erythemal weighted UVR exposure (http://toms.gsfc.nasa.gov/ery_uv/euv.html) was 8.15±0.67 kJ m^{-2} (mean±S.D.), indicating relatively high and constant UVBR flux at Namibia throughout the experiment when compared to other regions. The penetration depth of radiation was strongly waveband dependent. On average, 62.3±14.0% (mean±S.D.) of surface PAR, 50.1±10.5% of UVAR and 28.8±11.8% of UVBR reached our plots in 4 cm water depth, depending on radiation flux and water turbidity. Measured attenuation coefficients indicated relatively high water turbidity at the study site (Table 1).

3.2. Biomass and total abundance

Overall, wet weight was not significantly affected by radiation treatments throughout the study period (Table 2). Moreover, measurements of dry weight as the final biomass of the community were not significantly affected by radiation treatments (one-factorial ANOVA, $F_{(3,15)}$=0.99, p=0.424).

Table 2
Repeated-measures ANOVA

Source	*df*	Diversity		Evenness		Species richness		Wet weight	
		F	*p*	F	*p*	F	*p*	F	*p*
Radiation *R*	3	3.35	0.040	2.13	0.129	2.38	0.100	1.79	0.182
Residual	20								
Time	4	6.86	<0.001	9.14	<0.001	1.35	0.260	6.83	<0.001
T×*R*	12	0.95	0.504	0.918	0.538	0.84	0.606	0.54	0.886
Residual	80								

Effects of radiation over the entire study period (0–84 days) on diversity *H*′, evenness, species richness, and wet weight.

3.3. Biodiversity

A total of 10 species with a minimum mean cover ≥1% on single tiles was encountered (Table 3). Diversity *H*′ levels under the ambient irradiance regime were initially high (21 days: 0.69±0.37, mean±S.D.), dropped as succession proceeded (42 days: 0.32±0.25), followed by a strong increase (63 days: 0.68±0.30), remaining thereafter with almost no change (77 days: 0.71±0.18) until the end of the experiment (84 days: 0.69±0.31). Averaged over the entire study period, diversity *H*′ was significantly different among radiation treatments and also among sampling dates (Table 2). Test of sphericity revealed that diversity *H*′ data met the assumptions for repeated measures (Huynh–Feldt ε=1.0, Mauchley *W*=0.498, *p*=0.170). Among radiation treatments, diversity *H*′ was significantly higher under P compared to PAB when analysed over the entire study period (Table 2). A nonsignificant time×radiation interaction indicated constancy of this pattern over time (Table 2; Fig. 3). Analysis of radiation effects at separate sampling dates revealed significantly higher diversity *H*′ under P

Table 3
List of species recruiting on panels

Species name	Day	PAB	PA	P
Enteromorpha intestinalis L. (Link)	21	●	●	●
Codium fragile (Suringar) Hariot	21	●	●	●
Unidentified green algal film	21	●	●	●
Ceramium sp.	42	●	●	●
Chylocladia capensis Harvey	42	○	●	●
Notomegabalanus algicola (Pilsbury)	42	○	●	○
Cladophora flagelliformis (Suhr) Kützing	42	○	●	●
Grateloupia filicina (J.V. Lamouroux) C. Agardh	77	●	●	●
Bugula neritina L.	77	○	○	●
Centroceras clavulatum (C. Agardh) Montagne	84	●	○	○

Numbers in column "day" indicate sampling date of first appearance of the respective species. PAB (>280 nm), PA (>320 nm) and P (>400 nm). ●=species present, ○=species absent. Species were regarded as present when coverage was ≥1% on plots.

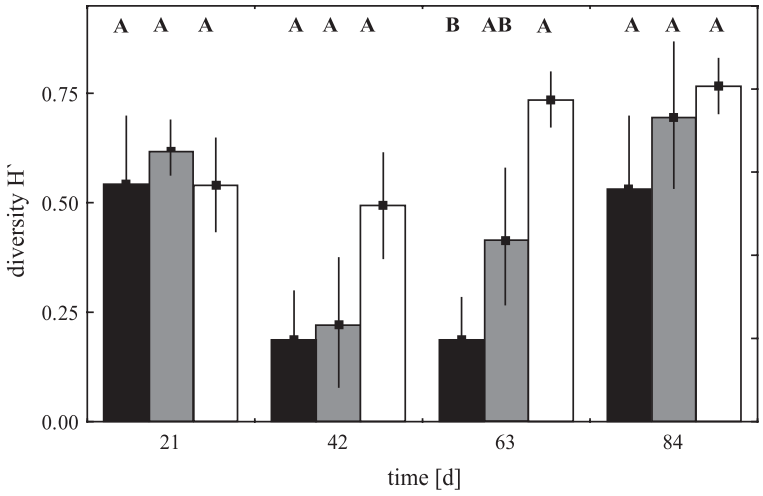

Fig. 3. Mean (±S.E.) diversity H' of fouling assemblage after 21, 42, 63 and 84 days among three radiation treatments. PAB (>290 nm, black), PA (>320 nm, hatched) and P (>400 nm, white). Treatments sharing a letter are not significantly different.

compared to PAB at an intermediate stage of succession (one-factorial ANOVA, 63 days: $F_{(3,15)}$=5.31, p=0.01; Fig. 3). Evenness of communities exposed to ambient light levels was high at an early stage of succession (21 days: 0.52±0.25), declined (42 days: 0.25±0.20) and subsequently increased to an almost constant level (63 days: 0.50±0.18 and 77 days: 0.59±0.11) until the end of the experiment (84 days: 0.58±0.28). An analysis over the complete study period displayed no significant radiation effects on evenness, but a significant change in evenness over time (Table 2). An analysis of radiation effects on evenness for separate sampling dates did not reveal significant differences among treatments.

Species richness was nearly constant under ambient irradiance conditions. Mean number of species was 3.67±0.52 (S.D.) after 21 days, 3.50±1.05 after 42 days, 4.00±1.10 after 63 days, 3.83±1.60 after 77 days, and 3.50±1.05 at the end of the experiment. We detected neither significant treatment effects on overall species richness (Table 2), nor at single sampling dates.

Erythemal weighted above ground UVBR was neither correlated (all Spearman rank) with diversity H' (r=−0.1, p=0.87), nor with evenness (r=0.4, p=0.51) and species richness (r=−0.8, p=0.10).

3.4. Species composition

Despite fluctuations in the abundance of species among treatments and through succession (Table 3), no significant differences in species composition were found among assemblages exposed to the three radiation regimes at any sampling date (all global R values of ANOSIM between −0.07 and 0.11).

4. Discussion

Overall, ambient irradiance affected the macrobenthic community very little. Only the combined impact of UVAR and UVBR had a transient detrimental effect on diversity H' while other community parameters were left unaffected. Significant shifts in species composition were absent, although 50% of the species recruited differentially among treatments, of which all but one species avoided UVBR-exposed panels.

Both *Ceramium* and the green alga film accounted for >90% of total abundance and were unaffected by radiation treatments. As the <1-mm-thin green algal film contributed negligibly to biomass, *Ceramium* cover almost exclusively determined biomass on the panels. Consequently, UVR effects on biomass were missing. In other studies, UVR either enhanced biomass accrual of communities (Bothwell et al., 1993, 1994; Kelly et al., 2001), was without effect (DeNicola and Hoagland, 1996; Hill et al., 1997) or only detrimental during an early successional phase (Santas et al., 1998a,b; Reizopoulou et al., 2000; Lotze et al., 2002, but see Kiffney et al., 1997). A lack of adverse UVR effects on community biomass contrasts strongly with the vast number of deleterious UVR effects on growth and photosynthetic efficiency of single plant species (reviewed in Franklin and Forster, 1997; Häder et al., 1998). Thus studying the effects of UVR on single species may overestimate the radiation impact for ecologically more realistic situations, i.e. in the context of communities. Communities seem to have buffering capacities which result for instance from (1) a differential sensitivity to UVBR between grazers and their prey that contributes to increases in algal biomass in UVBR-exposed habitats (Bothwell et al., 1994) or (2) the compensation potential of UVR-tolerant species, i.e. *Ceramium* in this study, to offset a reduction in productivity of UVR intolerant species (Santas et al., 1998a).

In this study, 40% of all species did not recruit under PAB conditions, indicating that species were not living in their optimal UVR environment and thus were not adapted to the natural UV regime. Although such species-specific UVR sensitivities are expected to result in changes in species composition (Cullen and Neale, 1994), we were unable to detect them. In contrast to microbial communities, UVR effects on diversity, species composition and structure of macrobial communities were clearly missing in other studies (Santas et al., 1998a; de Lange et al., 1999; Reizopoulou et al., 2000; Lotze et al., 2002), corroborating our results. The absence of shifts towards more UVR-tolerant species may result from an unavailability of such recruits. Nevertheless, this seems unlikely to be the case in our study because the UVR-tolerant green alga *Enteromorpha intestinalis* (Santas et al., 1998a), recruited initially on UVR-exposed plots. Several explanations for the transient nature of UV effects in our study are conceivable. First, strongest UV effects on diversity may match with seasonal radiation fluxes. Yet a missing correlation between UVBR levels and diversity H' rejects this possibility, at least for this part of the spectrum. Second, communities on our panels perhaps experienced variable UVR exposure as a result of temporal variation in turbidity. Unfortunately, we were not able to monitor turbidity in order to determine whether or not is was negatively correlated to detrimental UVR effects. Compared to other parts of the ocean (Wängberg et al., 1996; Franklin and Forster, 1997), UVBR transparency of the water was low at our study site, suggesting that the water body may functioned as an irradiance shield. Even though activation of adverse UVR effects as a result of relaxed turbidity levels was found (Kiffney et al., 1997),

turbidity-mediated activation and deactivation of detrimental UVR effects on community diversity within <3 weeks seems improbable. Third, screening pigments and/or repair mechanisms may have been induced upon UVR exposure as has been demonstrated for marine invertebrates (Gleason and Wellington, 1995), and autotrophs (e.g. Karsten et al., 1998). However, missing UVR effects would require a simultaneous induction of such adaptations in all community members. This seems unlikely. Accompanying the experiment, measurements of the screening and repair compound levels of all species would be most revealing in this context but were not performed in this study. Finally, and perhaps most convincing, protective shading of canopy-dwelling *Ceramium* may have muted the UVR climate across all treatments and allowed colonization of UVR-sensitive species, e.g. *Chylocaldia capensis*. Although, these UVR relaxing effects of spore migration were only short term in the study of Underwood et al. (1999), a few days might be sufficiently long for the spores of UV-sensitive species of macroalgae to pass through their bottleneck of relatively high UVR susceptibility. For instance, micro- and macroscale shading of substrate enabled macroalgae to develop under sublethal irradiance conditions to later stages that were no longer adversely affected by high irradiance regimes (Wood, 1987; Graham, 1996).

5. Conclusions

At this stage, it might be to early to conclude that UVR effects are negligible at the community level. Missing UVBR effects on macrobenthic communities (Lotze et al., 2002, this study) suggest that present ozone depletion may not ultimately cause structural changes in shallow water benthic assemblages through an increase in UVBR. In order to improve predictions of UVR impacts on macrobenthic communities, more information about the UVR susceptibility of larvae and spores is required. In addition, multifactorial experiments including other ecological factors are required to assess the relative ecological relevance of UVR effects.

In sum, besides a transient effect on diversity, UVR did not further affect the structure of the species-poor macrobenthic community at Radford Bay, Namibia. The importance of a buffering capacity in assemblages, i.e. protective shading by canopy-building UVR-tolerant species, in muting detrimental UVR effects was stressed.

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