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UV effects that come and go: a global comparison of marine benthic community level impacts

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Abstract

Ambient UV radiation has substantially increased during the last decades, but its impact on marine benthic communities is hardly known. The aim of this study was to globally compare and quantify how shallow hard-bottom communities are affected by UV during early succession. Identical field experiments in 10 different coastal regions of both hemispheres produced a consistent but unexpected pattern: (i) UV radiation affected species diversity and community biomass in a very similar manner, (ii) diversity and biomass were reduced to a larger extent by UVA than UVB radiation, (iii) ambient UV levels did not affect the composition of the communities, and (iv) any UV effects disappeared during species succession after 2–3 months. Thus, current levels of UV radiation seem to have small, predictable, and transient effects on shallow marine hard-bottom communities.

Keywords: climate change, community resilience, global assessment, marine benthic diversity, UV radiation

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Introduction

Anthropogenic production of ozone-depleting substances has led to a reduction of stratospheric ozone concentration by up to 5% per decade (Fioletov *et al*., 2002). As a consequence, near-surface UVB radiation increased (i.e. annually + 1.5% at 300 nm and + 0.8% at 305 nm, between 1989 and 1997 (WMO, 1998)). While the emission of ozone-depleting substances is stabilizing, or even decreasing, substantial recovery of the ozone layer is not expected before 2050 (WMO, 1998). In the aquatic environment, the UVB shielding effect of coloured dissolved organic matter (CDOM) is expected to weaken in the forthcoming decades because of warming and acidification (acid rain over lakes, increased CO_2 input in the oceans), and may lead to further increased exposure of aquatic organisms to UV (Schindler *et al*., 1996).

We therefore expect UV to affect community structure and diversity, whenever individual species respond unequally to UV radiation with regard to fitness or survival. These community effects should be most pronounced in systems where some species possess protection against UV while others do not, or where UV protection is metabolically costly. UV effects should also be more intense at shallow depths and with regard to sessile organisms without the capacity on the individual level of spatial (e.g. depth) or temporal (day/night rhythms) escape. UV impact in shallow water and possible avoidance of it have been reported for freshwater zooplankton (Williamson, 1995; Leech & Williamson, 2001). Mechanisms mitigating the impact of UV can be finely tuned to local conditions. For example, Brown *et al*. (1994) demonstrated within-colony effects of higher solar irradiance on corals, which was

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attributed solely to prior experience of each side of the colony (Brown *et al*., 2002). Individual species may also have different responses to UV because recruits may come from deeper water and hence from unstressed and nonadapted populations, or recruits may be preadapted to UV stress because of possession of mycosporine-like amino acids (MAAs) (Adams & Shick, 1996; 2001), or because of conferred tolerance by adaptation to thermal stress (see Brown *et al*., 2002). In addition, higher water temperatures (more pronounced at shallow water depths) may in certain cases enhance UV effects (Williamson *et al*., 2002). It can therefore be hypothesized that early successional coastal marine fouling communities would respond strongly to changes in UV.

Previous research (Leun *et al*., 1995) on UV effects has focussed on organizational levels at, or below, the organism, and also towards micro-organisms, plants, and terrestrial environments (Convey *et al*., 2002; Johnson *et al*., 2002; Paul & Gwynn-Jones, 2003). Studies on the influence of UV on epibenthic communities (i.e. attached to hard substrata) are scarce, and tend to be both regionally focussed and ambiguous in a sense that both presence and absence of negative UV impacts have been demonstrated (Worrest *et al*., 1978; Bothwell *et al*., 1994; Wängberg *et al*., 1996; Kiffney *et al*., 1997; Bischof *et al*., 1998; de Mora *et al*., 2000; Reizopoulou *et al*., 2000; Forster & Schubert, 2001; Davidson & Belbin, 2002; Lotze *et al*., 2002). The inconsistencies in results may stem from the heterogeneity of approaches in relation to their taxonomic focus, to methodology, or to spatiotemporal scale.

In order to search for generalities in the response patterns to UV radiation of poorly studied shallow marine hard-bottom communities, we scaled up from a local to a global approach. This was achieved not by enlarging the experimental area but by replicating across communities. A modular investigation composed of identical experiments in 10 different biogeographic regions of both hemispheres was conducted. At all sites, the impact of UVA and UVB on structure, diversity, and biomass of early successional hard-bottom communities was assessed at very shallow depth (−4 cm). We tested (i) whether and how diversity, biomass, and community structure of shallow marine hard-bottom communities respond to UV radiation during the first 12 weeks of succession and (ii) whether their response varies between radiation spectra (UVB, UVA, total UV), among community types and/or over time.

Material and methods

We standardized the experimental set-up for some potentially confounding factors (season, depth, type of radiation, successional phase) but allowed for variability across others (latitude, water parameters, type of community). Identical experiments were run at 10 sites (Antarctica, Australia, Chile, Namibia, Kenya, China, Israel, Canada, Germany, and Norway) in their respective summer seasons during 2000/2001. Latitude ranged from 66°S to 68°N, local noon UV irradiation from low (6 W m^{-2} UVA, 0.4 W m^{-2} UVB) to high (30 W m^{-2} UVA, 1.3 W m^{-2} UVB, Fig. 1), salinity from 15 to 42, temperature from −2 to 32 °C, productivity from oligo- to eutrophic, and community type (at the end of the experiment) from purely microalgal to functionally diverse. Details of sites are given in Table 1 and their epibenthic assemblages recorded in Table 2.

Experimental units were transparent plastic containers carrying horizontally a ceramic settlement tile (75 mm × 75 mm) at a depth of 40 mm below water surface (Fig. 2). The length and width of the container were varied between locations to ensure that the settlement tile would receive direct irradiance for a minimum of 2 h either side of noon. Containers were suspended in a floating array (polystyrene or wood), which was painted black to avoid reflection of radiation. UVA and UVB were measured at each site during the experiment at the same deployment depth of 40 mm using submersible broadband sensors (280–315 nm (UVB), 315–400 nm (UVA)) at noon on cloudless days. Measurements lasted for 5 min and the average irradiance dose-rate per second was calculated as W m^{-2} (Fig. 1). In addition, total ozone mapping spectrometry (TOMS) erythemal UV exposure data were obtained from NASA (http://toms.gsfc.nasa.gov/ery_uv/euv.html). The side-walls of the containers were cut open to allow flow-through of ambient seawater. Solar radiation was manipulated by cutoff filters above the experimental units on four levels: (a) Perspex (3 mm GS 2648 Röhm, Darmstadt, Germany) permitted penetration of the full spectrum (treatment Photosynthetically active radiation (PAR) + UVA + UVB), (b) Perspex covered by a 0.1 mm polyester transparency film (LTF Copy Nashua), cutting off UVB (treatment PAR + UVA, 50% cutoff at 323 nm), (c) Makrolon (4 mm LongLifePlus 293, Röhm) cutting off UVA and UVB (treatment PAR, 50% cutting off at 412 nm), (d) no filter as treatment control. Full spectral characteristics for all three filters are given in Molis & Wahl (2004). Six replicates per treatment combination were exposed in a random block design. Because the optical filters were positioned several centimetres above the water surface, fouling was not an issue and only occasional sea spray and bird droppings had to be wiped off every other day. Regular spectral measurements revealed no change in filter performance over the duration of the experiment, except for the polyester transparency film, which consequently was replaced monthly.

Fouling communities developed over up to 12 weeks on the upper surface of the tiles. At biweekly to

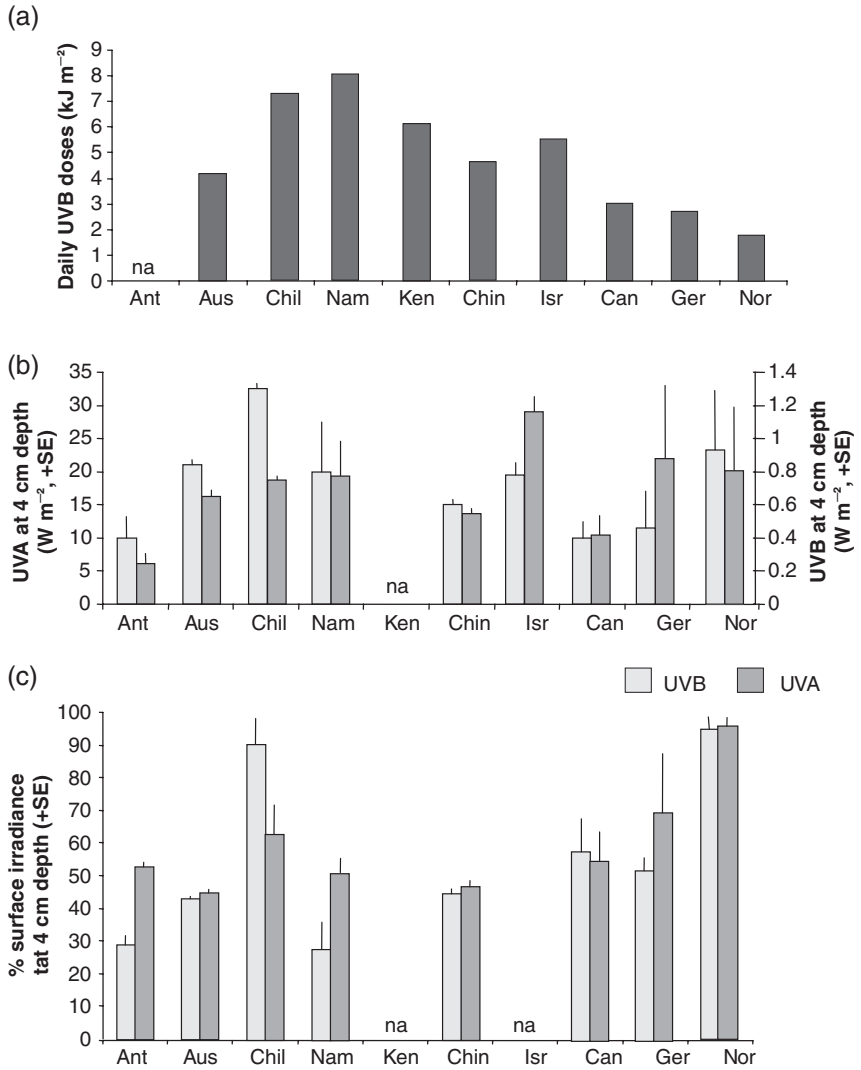

Fig. 1 UV regime averaged over the experimental phase at each site. (a) Total ozone mapping spectrometry data for daily UVB doses. (b) UVA and UVB irradiance around solar noon at 4 cm depth (immersion depth of the experimental units). (c) Percentage of incident UVA and UVB reaching the depth at which the settlement panels were deployed (−40 mm). na, not assessed; Ant, Antarctica; Aus, Australia; Chil, Chile; Nam, Namibia; Ken, Kenya; Chin, China; Isr, Israel; Can, Canada; Ger, Germany; Nor, Norway.

monthly monitoring intervals, the tiles were removed from the experimental units, carefully rinsed in filtered seawater, and inspected nondestructively under a microscope or stereo-microscope, as appropriate. Assemblage biomass (dripped-off tile wet weight minus the wet weight of the preweighed empty tile) and per cent cover of each species were quantified. Care was taken to enumerate both overlying and understorey organisms. In Chile, green algae grew so fast during the weeks 4–12, that they had to be cut back biweekly to a height of 1 cm in order to allow water flow through the containers; biomass of the removed algae was added to the total biomass developed over a given period. After quantification, tiles were returned to the containers.

Since the treatment controls (no filter) did not differ from fully transparent filter treatments in more than 95% of all comparisons, a filter artefact could be ruled out. Consequently, the treatment control data were considered redundant and excluded from analysis. Community diversity (Shannon Index H') computed from species cover (both animals and algae), and community biomass (assemblage wet weight) were used as response variables. To analyse the relative magnitude of treatment effects between sites, a recently developed factorial meta-analysis technique was used (Gurevitch *et al*., 2000). This approach allowed us to compare in an objective manner structurally different communities, which had been assessed by a number of different researchers. Data were standardized using the

Table 1 Details of sites where experiments were conducted

Country	Antarctica	Australia	Chile	Namibia	Kenya	China	Israel	Canada	Germany	Norway
Investigators	J. K. & A. D.	S. T. D.	M. L. & M. T.	M. M. & M. W.	D. K.	S. D.	D. Z. B.-Y.	H. L. & B. W.	M. M.	J. J.
Longitude	110°E	150°E	71°W	15°E	39°E	114°E	35°E	63°W	11°E	13°E
Latitude	66°S	34°S	30°S	23°S	4°S	22°N	30°N	44°N	54°N	68°N
Start of experiment (d.m.y)	07.01.2001	06.01.2001	12.12.2000	25.11.2000	20.02.2001	23.05.2001	01.08.2001	25.05.2001	19.06.2001	13.05.2001
End of experiment (d.m.y)	24.02.2001	03.03.2001	05.03.2001	16.02.2001	10.03.2001	11.09.2001	17.10.2001	15.10.2001	04.10.2001	15.08.2001
TOMS UV data [J m^{-2}, (SE)]	na	4922 (251)	7246 (176)	8036 (111)	6170 (217)	4603 (156)	5324 (114)	2997 (105)	2700 (107)	1864 (63)
Smallest noon sun angle (date)	33.4 (24.2.)	62.8 (3.3.)	65.8 (5.3.)	79.2 (16.2.)	83.2 (20.2.)	72.5 (11.9.)	50.7 (17.10.)	37.3 (15.10.)	31.5 (4.10.)	35.6 (15.8.)
Largest noon sun angle (date)	46.4 (7.1.)	78.5 (6.1.)	83.1 (12.12.)	87.8 (25.11)	89.9 (10.3.)	88.6 (23.5.)	77.9 (1.8.)	67.0 (25.5.)	59.4 (19.6.)	40.5 (13.5.)
Daylight hours (SD)	18.5 (3.5)	13.6 (0.7)	13.7 (0.3)	13.3 (0.3)	12.0 (0)	12.8 (2.9)	12.5 (1)	13.5 (2.2)	14.3 (3.1)	19.8 (3.6)
Salinity range	34–35	37	34–35	30–37	33–36	23–35	42	31–32	15–20	30–33
Sea surface temperature range (°C)	−2 to 2	18–22	13–20	12–24	24–32	30	21–26	10–18	15–22	3.5–12
Tidal amplitude (m)	2	1.6	2	0	1.5	1.5	1.5	2.1	0.2	1.8
Richness (number of species with >1% cover)	30	6	12	8	4	12	6	4	8	7
Type of community	Diatom dominated	Macroalga dominated	Macroalga dominated	Macroalga dominated	Diatom dominated	Macroalga dominated	Mixed	Diatom dominated	Macroalga and mussel dominated	Diatom dominated
Structurally dominant macroforms	None	*Ulva, Ceramium*	*Ulva*	*Ceramium*	None	*Ulva, Ectocarpus Cladophora*	*Ulva*	*Chordaria*	*Ulvopsis, Mytilus*	*Chorda*

Data (means, errors, extrema) valid for the experimental duration at each site.
na, not accessed.

Table 2 Species list for the communities that developed on the panels at the different sites.

Antarctica	
Actinocyclus actinochilus	Bacillariophyceae
Achnanthes brevips	Bacillariophyceae
Achnanthes delicatula var.	Bacillariophyceae
Achnanthes c.f. lanceolata	Bacillariophyceae
Asteromphalus hookeri	Bacillariophyceae
Azpeitia tabularis	Bacillariophyceae
Amphora sp. A	Bacillariophyceae
Amphora sp. B	Bacillariophyceae
Catacombas camtschatica var. *antarctica*	Bacillariophyceae
Chaetoceras dicheata	Bacillariophyceae
Chaetoceros socialis	Bacillariophyceae
Cocconeis costata v. costata	Bacillariophyceae
C. costata v. pennata	Bacillariophyceae
Cocconeis fasciolata	Bacillariophyceae
Cocconeis schuetti	Bacillariophyceae
Coscinodiscus oculus iridus	Bacillariophyceae
Diploneis sp. A	Bacillariophyceae
Diploneis sp. B	Bacillariophyceae
Eucampia antarctica	Bacillariophyceae
Fragilaria striatula	Bacillariophyceae
Fragilariopsis curta	Bacillariophyceae
Fragilariopsis cylindrus	Bacillariophyceae
Fragilariopsis linearis	Bacillariophyceae
Fragilariopsis obliquecostata	Bacillariophyceae
Fragilariopsis pseudonana	Bacillariophyceae
Fragilariopsis kerguelensis	Bacillariophyceae
Fragilariopsis rhombica	Bacillariophyceae
Fragilariopsis ritscheri	Bacillariophyceae
Fragilariopsis sublinearis	Bacillariophyceae
Fragilariopsis vanheurckii	Bacillariophyceae
Gomphomematrophis sp.	Bacillariophyceae
Licomorphora sp. A	Bacillariophyceae
Licomorphora sp. B	Bacillariophyceae
Licomorphora sp. C	Bacillariophyceae
Licomorphor decora	Bacillariophyceae
Odentella litigenosa	Bacillariophyceae
Odentella wiesfloggii	Bacillariophyceae
Ophiphora pacifica	Bacillariophyceae
Melosira monoliformis	Bacillariophyceae
Navicula glaciei	Bacillariophyceae
Navicula cancellata	Bacillariophyceae
Navicula directa	Bacillariophyceae
Navicula perminuta	Bacillariophyceae
Navicula sp. A	Bacillariophyceae
Navicula sp. B	Bacillariophyceae
Navicula sp. C	Bacillariophyceae
Nitzschia closterium	Bacillariophyceae
Nitzschia c.f. hybrida	Bacillariophyceae
Nitzschia lecointei	Bacillariophyceae
Nitzschia prolongatoides	Bacillariophyceae
Nitzschia stellata	Bacillariophyceae
Nitzschia subcurvata	Bacillariophyceae
Nitzschia taeniiformis	Bacillariophyceae
Nitzschia sp. A	Bacillariophyceae
Nitzschia sp. B	Bacillariophyceae
Paralia sol	Bacillariophyceae
Paralia c.f. sulcata	Bacillariophyceae
Pinnularia quadratarea	Bacillariophyceae
Pleurosigma spp.	Bacillariophyceae
Porosira glacialis	Bacillariophyceae
Pseudogomphonema kamtschaticum	Bacillariophyceae
Psudonitzschia lineola	Bacillariophyceae
Psudonitzschia prolongatoides	Bacillariophyceae
Psudonitzschia turgiduloides	Bacillariophyceae
Rhysosolenia sp.	Bacillariophyceae
Stauroneis type species	Bacillariophyceae
Synedropsis fragilis	Bacillariophyceae
Synedropsis c.f. fragilis var A	Bacillariophyceae
Synedropsis hyperborea	Bacillariophyceae
Synedra sp. B *c.f fragilis*	Bacillariophyceae
Synedropsis c.f. hyperboreoides	Bacillariophyceae
Synedropsis recta	Bacillariophyceae
Synedra sp. A	Bacillariophyceae
Synedra sp. C	Bacillariophyceae
Thalassiosira dichotomica	Bacillariophyceae
Thalassiosira gracilis	Bacillariophyceae
Trachyneis aspera	Bacillariophyceae
China	
Perna viridis	Bivalvia
Modiolus comptus	Bivalvia
Anomia chinense	Bivalvia
Ulva sp.	Chlorophyta
Cladophora	Chlorophyta
Balanus trigonus	Crustacea
Hydroides elegans	Polychaeta
Ceramium sp.	Rhodophyta
Norway	
Mytilus edulis	Bivalvia
Hiatella arctica	Bivalvia
Spongomorpha aeruginosa	Chlorophyta
Cladophora rupestris	Chlorophyta
Balanus balanoides	Crustacea
Licmophora gracilis	Bacillariophyceae
Bougainvillia ramose	Hydrozoa
Obelia geniculata	Hydrozoa
Ectocarpus siliculosus	Phaeophyta
Elachista sp.	Phaeophyta
Pilayella littoralis	Phaeophyta
Spongonema tomentosum	Phaeophyta
Fucus sp.	Phaeophyta
Chorda filum	Phaeophyta
Spirorbis spirorbis	Polychaeta
Israel	
Bivalvia indet.	Bivalvia
Ceracodictyon variabilis	Chlorophyta
Boodlea composita	Chlorophyta

Continued

Table 2 (Contd.)

Ulva ramulosa	Chlorophyta
Barnacle indet.	Crustacea
Obelia sp.	Hydrozoa
Steochospermum marginatum	Phaeophyta
Spirorbis sp.	Polychaeta
Ceramium strictum	Rhodophyta
Didemnum sp.	Tunicata
Kenya	
Amphora sp.	Bacillariophyceae
Asterionella sp.	Bacillariophyceae
Biddulphia sp.	Bacillariophyceae
Cocconeis sp.	Bacillariophyceae
Coscinodiscus sp.	Bacillariophyceae
Epithemia sp.	Bacillariophyceae
Fragilaria sp.	Bacillariophyceae
Grammatophora sp.	Bacillariophyceae
Licmophora sp.	Bacillariophyceae
Navicula sp.	Bacillariophyceae
Nitzschia sp.	Bacillariophyceae
Pleurosigma sp.	Bacillariophyceae
Schizothrix sp.	Bacillariophyceae
Striatella sp.	Bacillariophyceae
Synedra sp.	Bacillariophyceae
Tabellaria sp.	Bacillariophyceae
Cyanophyte sp.	Cyanobacteria
Oscillatoria sp.	Cyanobacteria
Spirrulina sp.	Cyanobacteria
Dinoflagellate sp.	Dinophyceae
Germany	
Diatoms spp.	Bacillariophyceae
Melosira sp.	Bacillariophyceae
Mytilus edulis	Bivalvia
Ulvopsis grevellei	Chlorophyta
Balanus improvisus	Crustacea
Laomedea flexuosa	Hydrozoa
Clava multicornis	Hydrozoa
Pilayella littoralis	Phaeophyta
Polydora sp.	Polychaeta
Ceramium strictum	Rhodophyta
Callithamnium sp.	Rhodophyta
Australia	
Watersipora cucullata	Bryozoa
Bryopsis australis	Chlorophyta
Cladophora sp.	Chlorophyta
Ulva sp.	Chlorophyta
Padina	Chlorophyta
Foraminiferan indet.	Foraminifera
Campanulariidae	Hydrozoa
Colpomenia	Phaeophyta
Ectocarpus sp.	Phaeophyta
Hydroides elegans	Polychaeta
Pileolaria lateralis	Polychaeta
Pomatostegus sp.	Polychaeta
Branched red alga	Rhodophyta
Ceramium sp.	Rhodophyta
Crustose coralline algae	Rhodophyta
Halocynthia sp.	Tunicata
Pyura stolonifera	Tunicata
Chile	
Diatoms (lawn)	Bacillariophyceae
Diatoms (erect)	Bacillariophyceae
Ulva sp.	Chlorophyta
Cladophora sp.	Chlorophyta
Lepas	Crustacea
Bugula neritina	Hydrozoa
Tubularia sp.	Hydrozoa
Capitella sp.	Polychaeta
Polysiphonia mollis	Rhodophyta
Ciona intestinalis	Tunicata
Namibia	
Bivalvia indet.	Bivalvia
Bugula neritina	Bryozoa
Ulva intestinalis	Chlorophyta
Codium fragile	Chlorophyta
Cladophora flagelliformis	Chlorophyta
Notomegabalanus algicola	Crustacea
Chylocaldia capensis	Rhodophyta
Ceramium sp.	Rhodophyta
Centroceras clavulatum	Rhodophyta
Grateloupia filicina	Rhodophyta
Canada	
Mytilus edulis	Bivalvia
Acrosiphonia arcta	Chlorophyta
Ulva intestinalis	Chlorophyta
Ulva lactuca	Chlorophyta
Cladophora rupestris	Chlorophyta
Cladophora albida	Chlorophyta
Chaetomorpha linum	Chlorophyta
Ulothrix flacca	Chlorophyta
Obelia sp.	Hydrozoa
Chordaria flagelliformis	Phaeophyta
Petalonia fascia	Phaeophyta
Pilayella littoralis	Phaeophyta
Ectocarpus fasciculatus	Phaeophyta
Fucus vesiculosus	Phaeophyta
Ceramium nodosum	Rhodophyta
Polysiphonia harveyi	Rhodophyta
Callithamnion tetragonum	Rhodophyta
Bonnemaisonia hamifera	Rhodophyta
Cystoclonium purpureum	Rhodophyta
Dumontia contorta	Rhodophyta

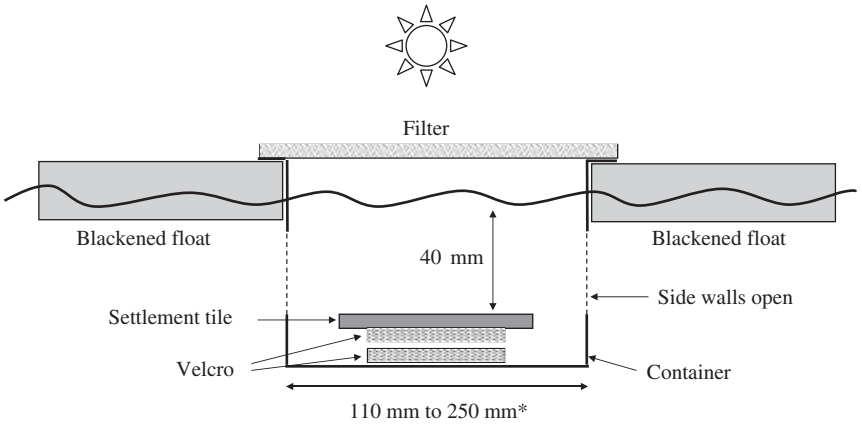

Fig. 2 Experimental set-up. Cross-section of one experimental unit. The distance between water surface and settlement tile was 40 mm. *, Length of unit depended upon latitude, and was such that the entire settlement tile was exposed to sun radiation for at least 2 h either side of noon.

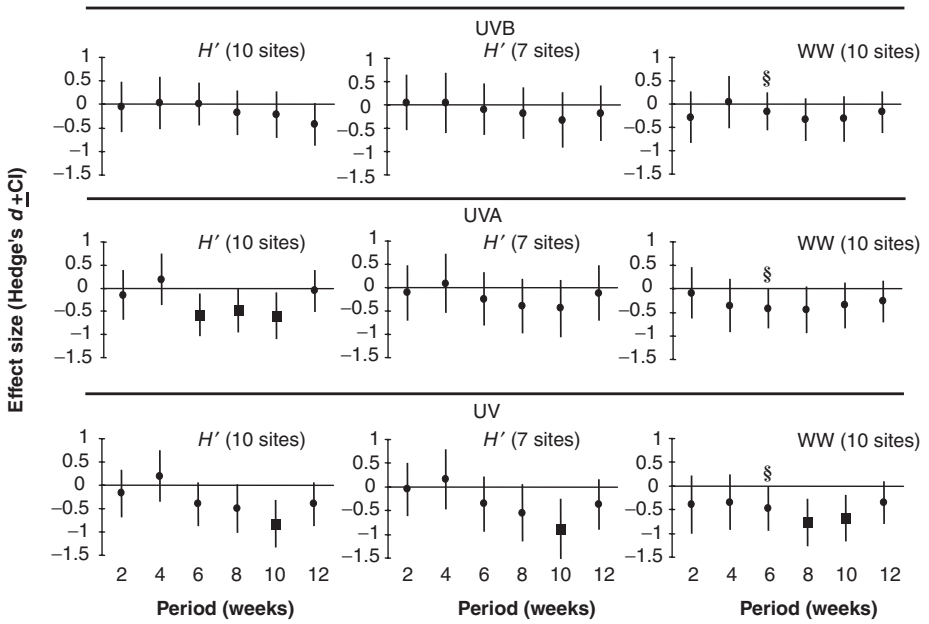

Fig. 3 Impacts of different spectral ranges of UV radiation on species diversity H' and biomass. Shown are the mean effect sizes (Hedges's d, ± 95% confidence interval (CI)) as obtained by factorial meta-analysis of UV on the diversity and biomass of benthic communities in the course of a 12 week successional period. For instance, a $d = -1$ corresponds to a treatment-driven decrease in diversity H' by 27.5% and a decrease in biomass WW by 60%, respectively. Nonoverlapping CIs indicate significant differences ($P < 0.05$). Significant effects are highlighted by squares, instead of dots. §, heterogeneous d values during period 6 were excluded from meta-analysis.

meta-analysis metric of standardized effect size, Hedges's d (Gurevitch *et al*., 2000). This is a measure of the difference between treatment and control means, divided by a pooled standard deviation, and multiplied by a correction factor to account for small sample sizes. UVB effects were assessed as the difference in diversity or biomass between PAR + UVA + UVB and PAR + UVA treatments, UVA effects as the difference between PAR + UVA and PAR treatments, and effects of total UV as the difference between PAR + UVA + UVB and PAR treatments. The graphical representation uses mean effect size ± 95% confidence intervals (CI). Non-overlap between CI and zero-line indicates a significant effect, nonoverlap between CIs indicates significantly different effect sizes in different periods. Homogeneity of effect sizes was tested using the Q-statistic (Gurevitch *et al*., 2000). Heterogeneity of effect sizes was caused by the three most pole ward sites (Antarctica,

Norway, Germany). Their exclusion did not change the overall pattern (Fig. 3), but meta-analysis was run with the remaining seven sites only. To compare the relative effects of the different light spectra over the entire experiment, the effects were ranked within sampling periods and sites. The ranks for each treatment effect were then averaged over periods within sites. Finally, the average ranks of the three treatments for each site were used in a Kruskal–Wallis test, with sites representing the replicates. Differences in community structure between treatments within sites were calculated as Bray–Curtis dissimilarities and subsequently analysed using ANOSIM (Primer® software, Plymouth, UK (Clarke & Warwick, 1994)).

Results

In Antarctica and Kenya, the fouling communities consisted of microalgae, mostly diatoms (Table 2), because of slow succession and shorter exposure time, respectively. At all other sites, the panels accumulated biomass-rich and diverse assemblages of micro-organisms (not assessed), macroalgae, and sessile animals. As typical for horizontal shallow-water substrata, most assemblages became dominated by canopy-forming macroalgae within 2–3 months. With 2 exceptions (substrata exposed to full UV in Norway and China), community structure was not persistently altered by the treatments applied (all ANOSIM R at the end of the experiment <0.12 and $P>0.05$) although occasionally single species were absent under full UV radiation. Thus, when not stated otherwise, the following description of the regional communities at the end of the experiments applies similarly to all light regimes.

In the Tasman Sea (Australia), the panels were covered to about 45%, and communities were dominated by macroalgae (*Ulva* sp., *Ceramium* sp., *Ectocarpus* sp., *Cladophora* sp.) and tube-building polychaetes (*Hydroides elegans, Pileolaria lateralis* and *Pomatostegus* sp.). The SE-Pacific panels (Chile) were covered to 200–220% mostly because of a lush growth of *Ulva intestinalis*, intermingled with *Bugula neritina* (bryozoan), *Capitella* sp. (polychaete), and *Tubularia* sp. (hydrozoan). *Polysiphonia mollis* (red alga) was only found in the absence of UV radiation. In the South Chinese Sea (China), coverage was between 90% and 100%, and the communities were dominated by the green algae, *Cladophora* sp. and *Ulva* sp., followed in abundance by the red alga *Ceramium* sp., the mussels *Perna viridis* and *Modiolus comptus* and the barnacle *Balanus trigonus*. The Red Sea communities (Israel) exhibited an average coverage of 50% and were dominated by the algae *Steochospermum marginatum* (brown), *Ulva ramulosa,* and *Ceracodictyon variabilis* (greens), accompanied by some bivalves, polychaetes, and tunicates. In the NW Atlantic (Canada), panel coverage was slightly above 80%, and clearly dominated by the algae *Polysiphonia harveyi* and *Spongomorpha arcta* (greens), *Chordaria filiformis* (brown) and *Ceramium rubrum* (red), followed in abundance by the blue mussel *Mytilus edulis*. *Ectocarpus fasciculatus* (brown alga) was absent under full UV radiation. In the Western Baltic Sea (Germany), the dominant species was the blue mussel *Mytilus edulis*, followed in abundance by the tube building polychaete *Polydora* sp., the algae *Ulvopsis grevellei* (green) and *Ceramium strictum* (red), and the barnacle *Balanus improvisus*. Coverage was around 120%. The SE Atlantic panels (Namibia) featured as dominant community components the algae *Ceramium* sp., *Centroceras clavulatum,* and *Nemastoma lancelatus* (reds). The bryozoan *Bugula neritina* was absent under full UV radiation – in contrast to its distribution in Chile. Coverage was between 120% and 130%. At the NE Atlantic site (Norway) total UV radiation (but not the separate effects of UVA and UVB) impacted community structure until the end of the experiment (ANOSIM $R=0.6$, $P<0.05$). Total coverage and diversity of the panels were reduced under full UV radiation relative to UV-sheltered panels (coverage of 81% vs. 45%, t-test $P=0.009$; H' of 1.3 vs. 0.7, t-test $P=0.003$). When UV, especially UVB, was excluded the community, as usually, was alga-dominated with *Ectocarpus siliculosus* being the canopy species. In the presence of full UV radiation, *E. siliculosus* was suppressed as was its congeneric *E. fasciculatus* in Canada. Besides *Ectocarpus*, abundant colonizers under all light regimes were the hydrozoans *Bougainvillea ramosa* and *Obelia geniculata*, the brown alga *Chorda filum*, and the blue mussel *Mytilus edulis*.

Across this wide range of systems studied, meta-analysis revealed a surprisingly uniform pattern of UV effects over time both for diversity and for biomass (Fig. 3). Whenever UV effects were significant, they depressed diversity and total biomass. A strong and significant effect, however, appears to be the exception and occurred predominantly during the mid phase of the 12 week succession. Effects were absent during the first and – Norway and China excepted – last phase of the experiment.

The community responses varied between treatments. At no stage during the investigation, did UVB affect diversity or biomass at the global level. In a transitory manner, UVA significantly reduced diversity, and total UV reduced both diversity and biomass during the midphase of the experiment.

UVB tended to affect diversity less than UVA, but as they both generally acted in the same direction (reducing diversity) their combined action was strongest (Kruskal–Wallis test, $P<0.02$, Fig. 4).

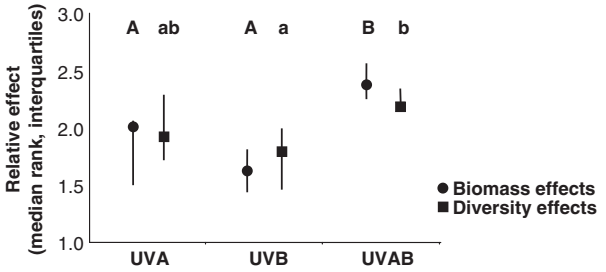

Fig. 4 Relative strength of negative effects of UVA, UVB, and total UV on species diversity (squares) and community biomass (dots). Median ranks and interquartile ranges are plotted. UVA tends to reduce diversity and biomass more strongly than UVB (Kruskal–Wallis test, $P < 0.02$). Treatments sharing a letter in the top row do not differ significantly (uppercase letters for biomass, lower case letters for diversity).

Discussion

We anticipated early successional shallow-water epibenthic communities to be sensitive to UV radiation because of (i) little attenuation of UV at this depth, (ii) possible differential sensitivity to UV between species, and (iii) because of the presence of juveniles. Juveniles may be particularly sensitive to UV because they tend to have higher metabolism, are often less pigmented or thinner-shelled than adults, and they may recruit from deeper-water populations unaffected by UV (Wiencke *et al*., 2000). Even when species have evolved morphological or chemical defences against UV damage or are able to repair these, their competitiveness may be reduced by the costs of these adaptations and non-defended species might be favoured under reduced UV radiation. In addition, in the course of intense (competitive) interactions, which are typical for early stages in species succession, UV-stressed species should be more readily excluded from the assemblage. So if there were any UV effects at the organizational level of benthic hard-bottom communities they should be demonstrable in the successional phase and at the water depth examined in this study.

Both UVA and full UV reduced diversity and full UV additionally reduced biomass in midsuccession. These effects disappeared as succession proceeded. The transitory negative impacts illustrate that not all species settling in these habitats are preadapted to tolerate UV radiation. The UV effects (direct or indirect) on some species persisted until the end of the experiment. Thus, the brown algae *E. fasciculatus* in Canada and *E. siliculosus* in Norway and the red alga *Polysiphonia mollis* in Chile (but not its congeneric *P. harveyi* in Canada) only occurred in the absence of natural UV radiation. The bryozoan *B. neritina* was suppressed by UV in Namibia but not so in Chile, where it may have been better protected by the copious growth of *Ulva intestinalis*. These occasional absences, however, usually did not lead to persistent significant structural differences between UV-exposed and UV-sheltered communities.

When effects were measurable, UVA impacted communities stronger than UVB. As UVA on a daily dose basis exceeded UVB by a factor of 10 or larger, the just slightly smaller effect of UVB demonstrated that UVB is more damaging per unit irradiance, but that UVA is more damaging at the actual daily doses received (see also Cullen & Neale, 1994). Differential UV effects were reported for freshwater microalgal communities by Bothwell *et al*. (1994). In their study, the difference between UVB and UVA effects was explained by UVB suppressing the chironomid grazers, which otherwise (under UVA and PAR) heavily reduced periphyton biomass. Strong UVA effects have also been shown for diatoms in freshwater phytoplankton (Kim & Watanabe, 1994). Interestingly, shallow-water *Laminaria saccharina* are more sensitive to UVA while individuals from greater depth are more sensitive to UVB, and UVA damage is more easily reversible than UVB damage (Bischof *et al*., 1998).

The fact that any UV effects during midphase generally declined after a few weeks could be because of (i) seasonal changes in UV irradiance, (ii) an acclimatization response of organisms to UV, or (iii) a successional or UV-driven shift in community structure to a less sensitive status. If the decline of solar irradiance in late summer (model (i)) contributed to the results it did so in an inconsistent way. Maximum effects generally did not nearly coincide with the seasonal maximum of irradiance and at at least half of the sites (Antarctica, Namibia, Kenya, China, Canada) no substantial decline of seasonal irradiance occurred during the experimental period. In Norway, on the other hand, irradiance did decline substantially during the course of the experiment, nevertheless UV effects persisted.

The induction or activation of morphological or chemical UV protection shields (model (ii)) within individuals has been reported for several species of microalgae (e.g. Masi & Melis, 1997; Hannach & Sigleo, 1998), macroalgae and terrestrial plants (e.g. Rozema *et al*., 2002), coral larvae (e.g. Gleason & Wellington, 1995) and vertebrates (e.g. Ley & Fourtanier, 1997). If the observed absence of sustained UV effects were only due to the induction of protection, then the absence of any shift in community structure between irradiance regimes would indicate that all species present were equally capable of this kind of adaptation. This seems unlikely.

Alternatively, the temporary UV effects may have disappeared because of the proliferation of UV-resistant species (model iii), which after having formed a

shading canopy permitted a recovery of the remaining components of the community. Indeed, canopy formation was observed at most sites and comprised pure or mixed stands of the green algae *Ulva* spp. (Australia, China, Chile, Israel) and *Ulvopsis grevillei* (Germany), the red filamentous algae *Ceramium* spp. (Australia, China, Namibia), the brown alga *Chordaria flagelliformis* (Canada) and the blue mussel *Mytilus edulis* (Germany). This proliferation of canopy-forming organisms was, however, not UV driven as it occurred on UV-sheltered panels as well, and it did not lead to a significant shift in community structure for the same reason. Thus, some components of the local shallow-water communities seem to be adapted to UV while others are not, as demonstrated by the UV effects on diversity and biomass earlier in succession. Notably, at the site with most persistent UV effects, Norway, the potentially canopy forming brown alga *E. siliculosus* formed dense bushy stands under PAR but was partially inhibited by UVA and completely excluded by UVB. For a closely related tropical alga, settlement inhibition through adverse UV effects on propagules have been described (Santas *et al*., 1998a), and protection of understorey growth from UV by canopy-forming organisms has been observed before (Karsten *et al*., 1998; Swanson & Druehl, 2000).

Transitory local UV effects on the community level have been reported previously for a filamentous algal assemblage (Santas *et al*., 1998a), diatom assemblages (Bothwell *et al*., 1993; Santas *et al*., 1998b), a diatom-invertebrate assemblage (Reizopoulou *et al*., 2000), freshwater bacterial and phytoplankton communities (Kim & Watanabe, 1994; Xenopoulos & Schindler, 2003) and one brackish epibenthic community (Molis *et al*., 2003). The ecological buffering found in the extremely different communities in these studies and the present investigation could be a general feature at this organizational level: single resistant species may provide protection to others against directional stresses (e.g. UV, currents, sedimentation, abrasion), or more diffuse pressures (e.g. consumption by macrograzers, (Wahl & Hay, 1995)).

Thus, deleterious UV effects seem to be smaller in epibenthic communities than described on the species level. The majority of shallow water fouling communities investigated were impacted by current levels of UV only in a moderate and generally transient manner.

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