

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

MARTIN WAHL\*, MARKUS MOLIS\*, ANDREW DAVIS†, SERGEY DOBRETSOV‡, SIMONE T. DÜRR†, JOSEFIN JOHANSSON§, JEFF KINLEY†, DAVID KIRUGARA¶, MATTHIAS LANGER||, HEIKE K. LOTZE\*\*, MARTIN THIEL||, JEREMY C. THOMASON††, BORIS WORM\*\*, DAFNA ZEEVI BEN-YOSEF‡‡

\*Marine Ecology Section, Leibniz Institute of Marine Science, Kiel University, Duesternbrookerweg 20, 24105 Kiel, Germany, †Department of Biological Sciences, University of Wollongong, Wollongong, Australia, ‡Department of Biology, Hong Kong University of Science and Technology, Hong Kong, China, §Department of Aquatic BioSciences, University of Tromsø, Tromsø, Norway, ¶Kenya Marine Fisheries Research Institute, Mombasa, Kenya, ||Fac. Cienc. Mar., Univ. Catolica del Norte, Coquimbo, Chile, \*\*Biology Department, Dalhousie University, Halifax, NS, Canada B3H 4J1, ††School of Biology, University of Newcastle, Newcastle upon Tyne, UK, ‡‡Department of Zoology, Tel Aviv University Tel Aviv, Israel

## 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

Received 10 February 2004; revised version received 28 May 2004 and accepted 4 June 2004

## 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<sub>2</sub> 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

Correspondence: Martin Wahl, tel. +49 431 600 4577, fax +49 431 600 1671, e-mail: mwahl@ifm-geomar.de

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.

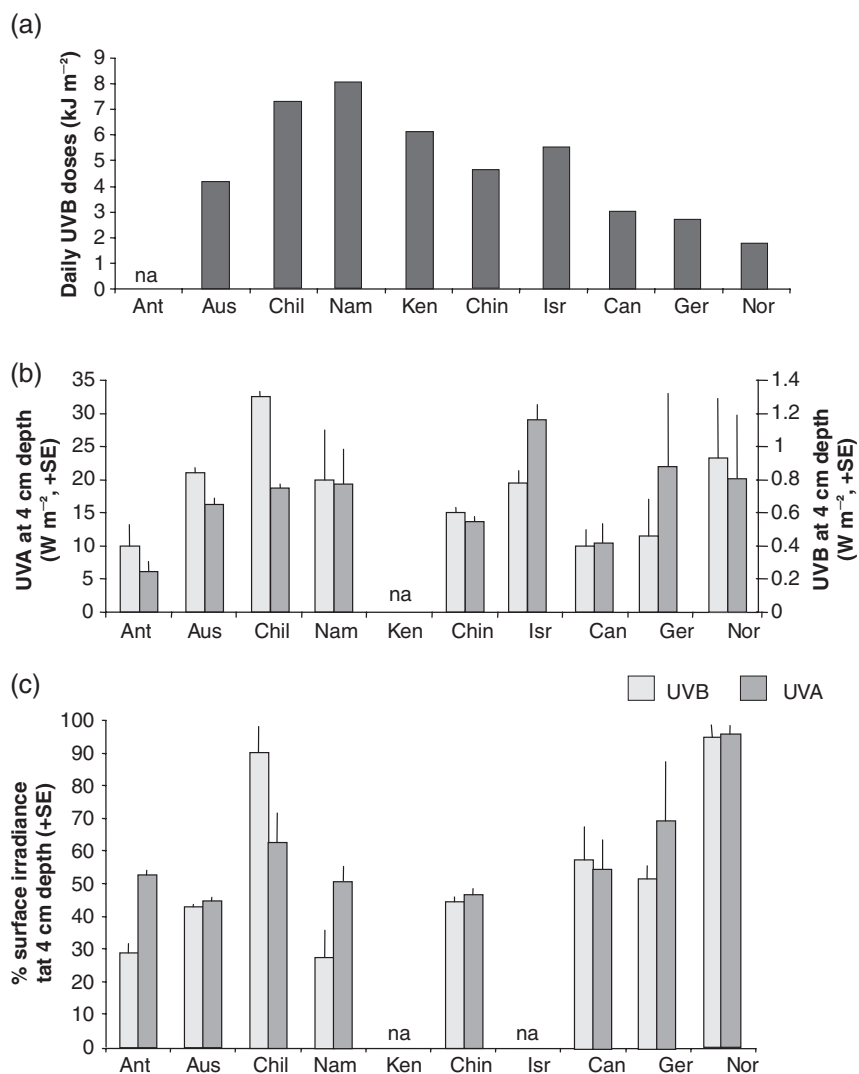
## Material and methods

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 ( $6 \text{ W m}^{-2}$  UVA,  $0.4 \text{ W m}^{-2}$  UVB) to high ( $30 \text{ W m}^{-2}$  UVA,  $1.3 \text{ W m}^{-2}$  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 ( $75 \text{ mm} \times 75 \text{ mm}$ ) 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  $\text{W m}^{-2}$  (Fig. 1). In addition, total ozone mapping spectrometry (TOMS) erythral UV exposure data were obtained from NASA ([http://toms.gsfc.nasa.gov/ery\\_uv/euv.html](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 <sup>-2</sup> , (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             | <i>Ulva</i> , <i>Ceramium</i> | <i>Ulva</i>         | <i>Ceramium</i>     | None             | <i>Ulva</i> , <i>Ectocarpus</i> , <i>Cladophora</i> | <i>Ulva</i>   | <i>Chordaria</i> | <i>Ulvaopsis</i> , <i>Mytilus</i> | <i>Chorda</i>    |

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

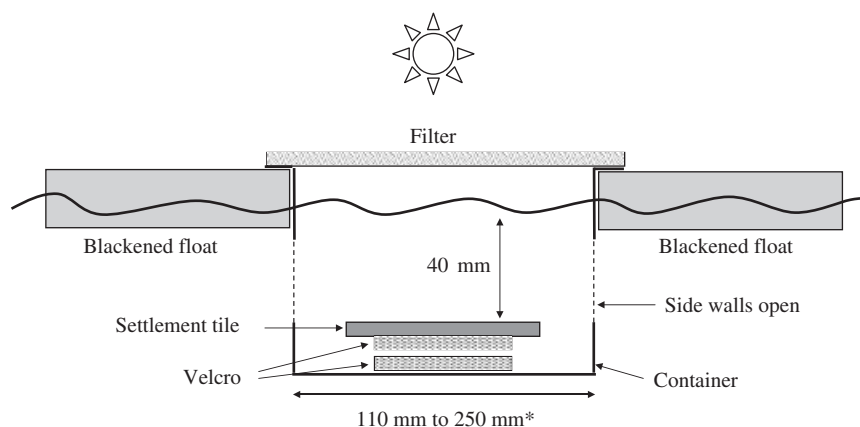
**Table 2** Species list for the communities that developed on the panels at the different sites.

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

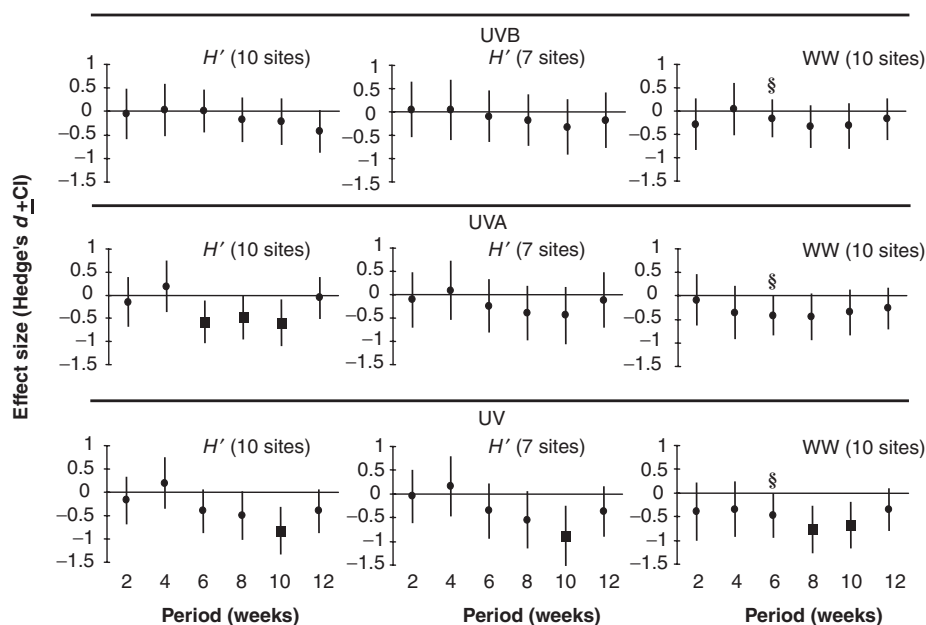
Continued

Table 2 (Contd.)

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



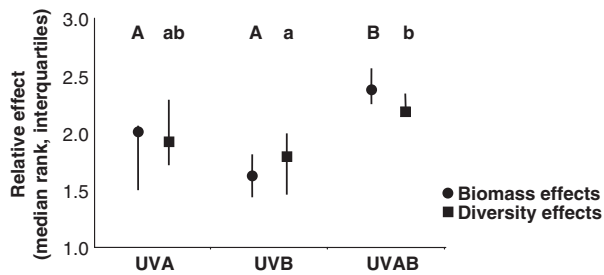


Fig. 4 Relative strength of negative effects of UVA, UVB, and total UV on species diversity (squares) and community biomass (dots). Median ranks and interquartile ranges are plotted. UVA tends to reduce diversity and biomass more strongly than UVB (Kruskal–Wallis test,  $P < 0.02$ ). Treatments sharing 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 *Ulvoopsis 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 understory 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.

## Acknowledgements

We gratefully acknowledge financial support by GTZ Proklima, Namibia & Germany. The University of Namibia and BENEFT, Namibia, generously provided submersible UV meters. Additional support was provided by the Australian Antarctic Division

(AD), Dr P.-Y. Qian (SD), DAAD (STD, MM), DFG (HL, BW, MM), FONDECYT (ML, MT), and the Royal Society (JT).

## References

- Adams NL, Shick JM (1996) Mycosporine-like amino acids provide protection against ultraviolet radiation in eggs of the green sea urchin *Strongylocentrotus droebachiensis*. *Photochemistry and Photobiology*, **64**, 149–158.
- Adams NL, Shick JM (2001) Mycosporine-like amino acids prevent UVB-induced abnormalities during early development of the green sea urchin *Strongylocentrotus droebachiensis*. *Marine Biology*, **138**, 267–280.
- Bischof K, Hanelt D, Wiencke C (1998) UV-radiation can affect depth-zonation of Antarctic macroalgae. *Marine Biology*, **131**, 597–605.
- Bothwell M, Sherbot D, Roberge A *et al.* (1993) Influence of natural ultraviolet radiation on lotic periphytic diatom community growth, biomass accrual, and species composition: short-term versus long-term effects. *Journal of Phycology*, **29**, 24–35.
- Bothwell ML, Sherbot DMJ, Pollock CM (1994) Ecosystem response to solar ultraviolet-B radiation: influence of trophic-level interactions. *Science*, **265**, 97–100.
- Brown BE, Downs CA, Dunne RP *et al.* (2002) Exploring the basis of thermotolerance in the reef coral *Goniastrea aspera*. *Marine Ecology Progress Series*, **242**, 119–129.
- Brown BE, Dunne RP, Scoffin TP *et al.* (1994) Solar damage in intertidal corals. *Marine Ecology Progress Series*, **105**, 219–230.
- Clarke KR, Warwick RM (1994) *Change in marine communities: an approach to statistical analysis and interpretation*. Natural Environment Research Council, UK.
- Convey P, Pugh PJA, Jackson C *et al.* (2002) Response of Antarctic terrestrial microarthropods to long-term climate manipulations. *Ecology*, **83**, 3130–3140.
- Cullen J, Neale P (1994) Ultraviolet radiation, ozone depletion, and marine photosynthesis. *Photosynthesis Research*, **39**, 303–320.
- Davidson A, Belbin L (2002) Exposure of natural Antarctic marine microbial assemblages to ambient UV radiation: Effects on the marine microbial community. *Aquatic Microbial Ecology*, **27**, 159–174.
- de Mora S, Demers S, Vernet M (2000) *The effects of UV radiation in the marine environment*. Cambridge University Press, Cambridge.
- Fioletov VE, Bodeker GE, Miller AJ *et al.* (2002) Global and zonal total ozone variations estimated from ground-based and satellite measurements: 1964–2000. *Journal of Geophysical Research – Atmospheres*, **107**: (D22), 4647, doi:10.1029/2001JD001350.
- Forster RM, Schubert H (2001) The effects of ultraviolet radiation on the planktonic community of a shallow eutrophic estuary: results of mesocosm experiments. *Helgolander Marine Research*, **55**, 23–34.
- Gleason DF, Wellington FM (1995) Variation in UVB sensitivity of planula larvae of the coral *Agaricia agaricites* along a depth gradient. *Marine Biology*, **123**, 693–703.
- Gurevitch J, Morrison JA, Hedges LV (2000) The interaction between competition and predation: a meta-analysis of field experiments. *American Naturalist*, **155**, 435–453.

- Hannach G, Sigleo A (1998) Photoinduction of UV-absorbing compounds in six species of marine phytoplankton. *Marine Ecology Progress Series*, **174**, 207–222.
- Johnson D, Campbell CD, Lee JA *et al.* (2002) Arctic micro-organisms respond more to elevated UV-B radiation than CO<sub>2</sub>. *Nature*, **416**, 82–83.
- Karsten U, Sawall T, Hanelt D *et al.* (1998) An inventory of UV-absorbing mycosporine-like amino acids in macroalgae from polar to warm-temperate regions. *Botanica Marina*, **41**, 443–453.
- Kiffney P, Clements W, Cady T (1997) Influence of ultraviolet radiation on the colonization dynamics of a Rocky Mountain stream benthic community. *Journal of the North American Benthological Society*, **18**, 520–530.
- Kim DS, Watanabe Y (1994) Inhibition of growth and photosynthesis of fresh-water phytoplankton by ultraviolet-a (UVA) radiation and subsequent recovery from stress. *Journal of Plankton Research*, **16**, 1645–1654.
- Leech DM, Williamson CE (2001) In situ exposure to ultraviolet radiation alters the depth distribution of *Daphnia*. *Limnology and Oceanography*, **46**, 416–420.
- Leun JCvd, Tang X, Tevini M (1995) Environmental effects of ozone depletion: 1994 assessment. *Ambio*, **24**, 138–142.
- Ley RD, Fourtanier A (1997) Sunscreen protection against ultraviolet radiation-induced pyrimidine dimers in mouse epidermal DNA. *Journal of Photochemistry and Photobiology B: Biology*, **65**, 1007–1011.
- Lotze HK, Worm B, Molis M *et al.* (2002) Effects of UV radiation and consumers on recruitment and succession of a marine macrobenthic community. *Marine Ecology Progress Series*, **243**, 57–66.
- Masi A, Melis A (1997) Morphological and molecular changes in the unicellular green alga *Dunaliella salina* grown under supplemental UV-B radiation: cell characteristics and Photosystem II damage and repair properties. *Biochimica and Biophysica Acta: Bioenergetics*, **1321**, 183–193.
- Molis M, Lenz M, Wahl M (2003) Radiation effects along an UVB gradient on diversity and species composition of a shallow-water macrobenthic community in the Western Baltic. *Marine Ecology Progress Series*, **263**, 113–125.
- Molis M, Wahl M (2004) Transient effects of solar ultraviolet radiation on the diversity and structure of a field-grown epibenthic community at Lüderitz, Namibia. *Journal of Experimental Marine Biology and Ecology*, **302**, 51–62.
- Paul ND, Gwynn-Jones D (2003) Ecological roles of solar UV radiation: towards an integrated approach. *Trends in Ecology and Evolution*, **18**, 48–55.
- Reizopoulou S, Santas P, Danielidis D *et al.* (2000) UV-effects on invertebrate and diatom assemblages of Greece. *Journal of Photochemistry and Photobiology B: Biology*, **56**, 172–180.
- Rozema J, Björn LO, Bornman JF *et al.* (2002) The role of UV-B radiation in aquatic and terrestrial ecosystems: an experimental and functional analysis of the evolution of UV-absorbing compounds. *Journal of Photochemistry and Photobiology B: Biology*, **66**, 2–12.
- Santas R, Korda A, Lianou C *et al.* (1998a) Community responses to UV radiation: I. Enhanced UVB effects on biomass and community structure of filamentous algal assemblages growing in a coral reef mesocosm. *Marine Biology*, **131**, 153–162.
- Santas R, Santas P, Lianou C *et al.* (1998b) Community responses to UV radiation: II. Effects of solar UVB on field-grown diatom assemblages of the Caribbean. *Marine Biology*, **131**, 163–171.
- Schindler DW, Curtis PJ, Parker BR *et al.* (1996) Consequences of climate warming and lake acidification for UVB penetration in North American boreal lakes. *Nature*, **379**, 705–708.
- Swanson A, Druehl L (2000) Differential meiospore size and tolerance of ultraviolet light stress within and among kelp species along a depth gradient. *Marine Biology*, **136**, 657–664.
- Wahl M, Hay ME (1995) Associational resistance and shared doom: effects of epibiosis on herbivory. *Oecologia*, **102**, 329–340.
- Wängberg SA, Selmer JS, Ekelund NGA *et al.* (1996) UV-B Effects on Nordic Marine Ecosystems: a literature review. Nordic Council of Ministers, Copenhagen.
- Wiencke C, Gomez I, Pakker H *et al.* (2000) Impact of UV-radiation on viability, photosynthetic characteristics and DNA of brown algal zoospores: implication for depth zonation. *Marine Ecology Progress Series*, **197**, 217–229.
- Williamson C (1995) What role does UV-B radiation play in freshwater ecosystems? *Limnology and Oceanography*, **40**, 386–392.
- Williamson CE, Grad G, De Lange HJ *et al.* (2002) Temperature-dependent ultraviolet responses in zooplankton: Implications of climate change. *Limnology and Oceanography*, **47**, 1844–1848.
- WMO (1998) *Scientific assessment of ozone depletion*. World Meteorological Organization, Geneva.
- Worrest RC, van Dyke H, Thomson BE (1978) Impact of enhanced simulated solar ultraviolet radiation upon a marine community. *Journal of Photochemistry and Photobiology B: Biology*, **27**, 471–478.
- Xenopoulos M, Schindler D (2003) Differential responses to UVR by bacterioplankton and phytoplankton from the surface and the base of the mixed layer. *Freshwater Biology*, **48**, 108–122.