Vol. 19: 269–278, 1999 | AQUATIC MICROBIAL ECOLOGY
Aquat Microb Ecol | Published October 27

UV radiation effects on microbenthos—a four month field experiment

Angela Wulff[1,*], Claes Nilsson[1], Kristina Sundbäck[1], Sten-Åke Wängberg[2] Svante Odmark[1]

[1]Department of Marine Botany and [2]Department of Plant Physiology, Göteborg University, PO Box 461, 405 30 Göteborg, Sweden

ABSTRACT: A 4 mo field experiment, covering the period May to September, was carried out in a shallow microtidal sandy bay on the Swedish west coast. To test whether the ambient UV radiation (UVR) had any effect on a marine microbenthic community, screens of Plexiglas, Plexiglas + Mylar-D film and polycarbonate were used. This gave 3 different treatments: Ambient (PAR+UVAR+UVBR), NoUVB (PAR+UVAR) and NoUV (PAR) plus Control (areas without screens to test the 'frame effect'). The response of the community was studied on 2 occasions (June, September) by measuring primary productivity (^{14}C), carbon allocation (^{14}C) and bacterial productivity (^{3}H-thymidine) (rate variables), as well as biomass and composition of microalgae and meiofauna, pigment composition (HPLC), content of mycosporine-like amino acids (MAA, HPLC) and composition of fatty acids (GC). The UVR maximum penetration depth (1%) in the sediment, measured by microsensors, was 800 µm for UVAR and 600 µm for UVB. No UVR effects were found for any structural variables but ostracodal biomass, which doubled when exposed to UVR compared with the UVR excluding treatments. Significant treatment effects were found for the rate variables primary productivity and carbon allocation. The effects on primary productivity and ostracods were observed in September only. All the treatment effects were found between exclusion of and exposure to UVR. Primary productivity increased in treatments shielded from UVR. For carbon allocation, significant effects on all fractions were found, however, with a partly different outcome in June and September. We conclude that the UVBR part of the spectrum exerted some stress on the microbenthic community, but this was almost exclusively found for rate variables in September, and that the ambient UVAR did not have any harmful effects. It is also concluded that the choice of time scales and experimental approach (laboratory vs field experiments) is crucial for the outcome and interpretation of UVBR experiments.

KEY WORDS: Microalgae · Production · Bacteria · Meiofauna · Carbon allocation · Pigments · Mycosporine-like amino acids · Sediment

INTRODUCTION

Even under a 'normal' ozone column (350 to 400 Dobson units), the ultraviolet-B part (UVBR; 280 to 315 nm) of the solar spectrum has detrimental effects on marine organisms (Holm-Hansen et al. 1993a, Wängberg et al. 1996 and references therein). The exclusion of ambient UVBR has been shown to increase the photosynthesis of natural phytoplankton communities (Lorenzen 1979, Holm-Hansen et al. 1993b) as well as in natural marine microphytobenthic communities (Odmark et al. 1998).

Organisms have different ways to avoid damage from harmful effects of UV radiation (UVR). Such strategies include avoidance, extracellular or intracellular UVR screening, quenching reactions for phototoxic products and repair of UVR damage (Karentz 1994). Although we are beginning to understand some of the molecular and cellular mechanisms of UVR damage on individual organisms, surprisingly little is known about responses at the community or ecosystem level (for reviews see Siebeck et al. 1994, Häder et al. 1995). Large variabilities in UVR tolerance have been shown to affect interactions between organisms at different trophic levels and this emphasizes the importance of simultaneously studying several trophic levels in order to predict UVR effects at the ecosystem level (Bothwell et al. 1993,

*E-mail: angela.wulff@marbot.gu.se

1994, Bergeron & Vincent 1997, Cabrera et al. 1997, Vinebrook & Leavitt 1999). Very few studies, however, have tackled long-term (weeks, months) UVR effects on natural marine communities (e.g. Helbling et al. 1992, Santas et al. 1997, Wängberg & Selmer 1997) and even fewer have dealt with sediment-inhabiting microbenthic systems (Bebout & Garcia-Pichel 1995, Sundbäck et al. 1996a, Odmark et al. 1998, Vinebrook & Leavitt 1999).

In shallow estuaries, the autotrophic part of the microbenthic communities serves a crucial ecological function. The microphytobenthic communities can account for one third or more of the total primary productivity (Pinckney & Zingmark 1993) and they constitute the basis of the food web in shallow bays, which are important feeding and nursing areas for fish and their prey (Pihl 1989, Mallin et al. 1992). Since the water depth in these bays is very shallow, UVR may well reach detrimental levels at the sediment surface. Moreover, the potential for UVR to penetrate down into the sediment, and through scattering even exceed the incoming radiation (especially at the sediment-water interface), has been shown by Garcia-Pichel & Bebout (1996). Due to the high photosynthetic oxygen production in the photic zone, there is also a high potential for photochemical production of harmful free radicals (Garcia-Pichel & Castenholz 1994, Abele-Oeschger et al. 1997).

Earlier experiments, where the UVBR exposure of intact sediment cores was manipulated in outdoor experimental set-ups, have been limited by the short time (weeks) that they could be run before stagnant conditions started to create experimental artefacts, e.g. flaking of the sediment surface (Sundbäck et al. 1996a, 1997, Odmark et al. 1998). Therefore, to overcome these incubation effects, a field experiment was set up.

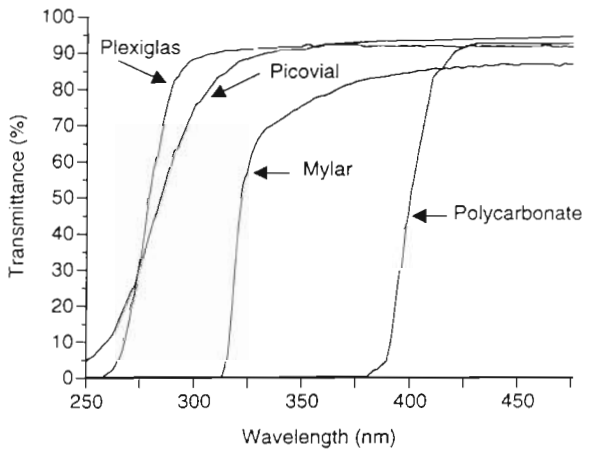

Fig. 1. Spectral transmission characteristics for the filter materials employed in the experiment and for the vials used for bacterial incubations

The aim of our field study was to examine the response of a natural marine microbenthic community to ambient UVR (through exclusion of UVAR+UVBR or UVBR only) over a time period long enough to allow changes due to long-term mechanisms. Variables studied were biomass and composition of microalgae and meiofauna, microalgal pigments (HPLC), content of mycosporine-like amino acids (MAA, HPLC), fatty acid composition (GC), primary productivity, bacterial productivity and allocation of photosynthetic products. The present study is, to our knowledge, the first long-term field experiment studying the UVR responses over more than 1 trophic level in a microbenthic community of a *marine* sediment.

MATERIAL AND METHODS

Study site and experimental set-up. The study was carried out in a brackish (salinity 20 to 23) microtidal bay, Vallda-Sandö, on the west coast of Sweden (57° 29' N, 11° 56' E) that had sediment consisting of silty sand (grain size >90% <63 µm). The tidal amplitude in the area is only 7 to 20 cm (Swedish Meterological and Hydrological Institute, SMHI), but water level fluctuations can be higher due to changing weather conditions. The study location is a typical bay in this area. It is sheltered from wind and water movement, changes in water level being generally small, with low water prevailing during spring and early summer (SMHI). The experiment lasted for ca 4 mo, from April 25 to September 5, 1996. During this period, the UVR is expected to reach its seasonal peak (Nunez & Chen 1998). The experimental period was relatively calm, dry and sunny.

Eighteen wooden frames (80 × 80 cm) on wooden poles were pressed 10 to 20 cm down into the sediment, leaving the frames ca 50 cm above the sediment surface. The frames were placed randomly in the bay, ca 4 m apart, within an area of approximately 100 m^2. To screen out UVBR, 6 randomly chosen frames were covered with Mylar film (Dupont, Mylar-D) supported by UVBR-transparent Plexiglas (Altuglas Plexi GS OF 2458 UV, 3 mm). Six other frames were covered with polycarbonate (LEXAN 9030 PC) to screen out both UVBR and UVAR (for the transmittance of all screens see Fig. 1). The remaining 6 frames were covered with Plexiglas only. This gave us 3 different treatments: NoUVB, NoUV and Ambient (treatment control). Six areas without frames (Control) served as frame controls. Since the water depth was expected to vary from a few centimeters to about 40 cm during the experiment, the height of the screens was adjusted to prevent them from getting flooded. To check for differences in light reaching the sediment surface below each screen,

PAR (400 to 700 nm), UVA (315 to 400 nm) and UVB (280 to 315 nm), respectively, were measured once at 12 different spots under and close to each screen/frame (IL 1400A photometer with cosine corrected sensors; detector types SUL 033 and SUL 240). The screens were cleaned regularly. Sediment movement was checked visually and appeared negligible, since footprints from April remained visible in late June.

Sampling. Initial samples were taken on April 25 (prior to the screens being put in position) and thereafter samples were taken on 2 occasions (June 24 and September 5). On each sampling day, 3 replicate screen areas were sampled. To avoid repeated (i.e. dependent) sampling, samples were only taken on 1 occasion from below each replicate screen, and thereafter the screen was discarded. Due to seasonal differences (sun angle and sun height on Nordic latitudes) care was taken to choose sampling sites that had been shaded by the screen during the experimental period as a whole. Two types of tubes were used for sampling. For primary productivity and carbon allocation, 1 intact sediment core (i.d. = 69 mm) was taken from below each replicate screen plus control using a percolation tube (see below). For sampling of other variables, 2 sediment cores below each replicate screen (plus control) were taken using simple tubes (i.d. = 90 mm), subsamples being randomly distributed between these 2 cores. From all tubes, subsamples of the upper 2 mm sediment were taken using cut-off plastic syringes (i.d. = 4.6 or 8.7 mm).

Light measurements. UVB irradiance was measured every tenth minute by a UV Biometer model 501 (Nunez & Chen 1998), located at 57.7° N, close to the study area. All UV data (erythemal weighted) were received from Dr Deliang Chen, Earth Sciences Centre, Göteborg University. The average daily dose of global radiation (Wh m^{-2}) was 3481, 5245, 5831, and 4582 for May, June, July and August, respectively (SMHI) and for UVBR the average daily dose (kJ m^{-2}) was 1.8, 3.5, 3.0 and 2.3. For light measurements during the incubation periods (primary productivity and carbon allocation), see Table 1. Potential light penetration depths (1%) in dry sediment were 1100–1200 µm for PAR (650 nm), 500–800 µm for UVA (365 nm) and 400–600 µm for UVB (310 nm), measured with spherical fiberoptic microsensors connected to an IL1783 spectroradiometer system (for PAR sensor, see Lassen et al. 1992; for UV sensors, see Garcia-Pichel 1995).

Table 1. Light doses and light intensities during the incubation periods for primary productivity and carbon allocation

	UVBR (J m^{-2})	Global radiation (Wh m^{-2})	UVBR (W m^{-2})	Global radiation (W m^{-2})
Apr	303	745	0.041	372
Jun	292	458	0.065	229
Sep	450	911	0.067	456

Microalgae. Seven subsamples (i.d. = 4.6 mm) from the sediment cores were pooled, diluted and live cells were counted in an epifluorescence microscope in 2 fractions: one before ('epipelic' fraction) and one after ultrasonication ('epipsammic' fraction). Average cell volumes were calculated using geometric formulae and converted to carbon (for details see Sundbäck et al. 1996b).

Algal pigments. Eight subsamples (i.d. = 4.6 mm) from the sediment cores were pooled into 2 vials (4 subsamples per vial), and immediately frozen in liquid nitrogen (–196°C). Pigments were analysed by high performance liquid chromatography (HPLC) according to Wright et al. (1991) with a modification of the solvent protocol (Kraay et al. 1992). Chlorophyll *a* (chl *a*) was quantified according to Wright et al. (1991) and converted to mg m^{-2}.

Mycosporine-like amino acids (MAA). Four subsamples (i.d. = 4.6 mm) from the sediment cores were pooled and frozen in liquid nitrogen (–196°C). For extraction, 25% aqueous methanol (v/v) was added and the samples were stored at 4°C overnight. UV-absorbing compounds (MAA) were analysed by isocratic reversed phase HPLC (Linear 206 detector, 336 nm) mainly according to Nakamura & Kobayashi (1982), using a Sphaerisorb C_8 column (5 µm, 250 × 4.6 mm i.d.). The mobile phase was 25% aqueous methanol (v/v) plus 0.1% acetic acid (v/v) and the flow rate was set to 0.7 ml min^{-1}. For peak identification, only the retention time was used, since no more than one peak was found, and this made further peak identification unnecessary in the present study.

Fatty acids. Four subsamples (i.d. = 4.6 mm) from the sediment cores were pooled and frozen on dry ice in ethanol (–76°C). The lipids were extracted with a chloroform:methanol:water solution, washed and dried under nitrogen gas as described earlier (Carlsson et al. 1994, Sundbäck et al. 1997). Fatty acids were transmethylated in the presence of nanodecanoic acid (19:0) as an internal standard. Before methylation, the lipids were fractionated into neutral and polar lipids as described earlier (Sundbäck et al. 1997). Fatty acid methyl ester composition was analysed by capillary gas chromatography using splitless injection (Carlsson et al. 1994).

Meiofauna. Four subsamples (i.d. = 4.6 mm) from the sediment cores were pooled and preserved in 5% borax buffered formalin containing Rose Bengal. Meiofauna were defined as metazoa and foraminifera passing through a mesh size of 500 µm and retained by a mesh size of 40 µm. The samples were extracted, sieved, sorted and counted as previously described in

Sundbäck et al. (1990). Meiofauna numbers were converted to carbon per taxonomic group (Widbom 1984). Meiofauna were originally classified to 10 groups but, since no treatment effects were found for the first 6 groups, they were combined in the group 'others' in the graphs.

Primary productivity. One intact sediment core from below each screen was taken with a Plexiglas tube (i.d. 69 mm) that enables percolation of radiolabeled carbon into undisturbed sediment (Jönsson 1991). To each core, 8–9 µCi ^{14}C-bicarbonate was added, and the overlying water was gently stirred and allowed to percolate into the sediment. For further details see Jönsson (1991). The cores were incubated for 1 to 2.5 h under small screens corresponding to their different treatments. The cores were placed on an inclined plane facing the sun in order to illuminate the whole sediment surface in the tube and thus avoiding light penetration through the tube walls. After incubation, 2 subsamples (i.d. = 8.7 mm) were taken from each core, transferred to scintillation vials and processed as described by Nilsson et al. (1991). According to P/I curves from the area (Degerstedt unpubl.) no light saturation was expected and the carbon values were converted to daily production using insolation values from SMHI. Light doses during the incubation periods are shown in Table 1. Due to technical problems in September, only 1 core from the NoUV treatment could be analysed. Therefore, this treatment was excluded from the graph (see Fig. 4) and the statistical analyses in September.

Carbon allocation. One sample (i.d. = 8.7 mm) was taken from each percolation tube, frozen on dry ice in ethanol (–76°C) and stored at –20°C until analysis. Fractionation of the organic carbon into polysaccharides, proteins, low molecular weight compounds (LMW) and lipids was done using the method of Li et al. (1980). Lipids were further separated into polar and neutral lipids as described in Sundbäck et al. (1997).

Bacterial productivity. Bacterial productivity was measured by incorporation of ^{3}H-thymidine in a sediment slurry (Moriarty 1990). Two subsamples (i.d. = 4.6 mm) from the sediment cores were pooled. Each sample was placed in a UV-transparent picovial (Packard, for transmittance see Fig. 1) and to each vial 40–50 µCi [methyl-^{3}H]-thymidine (TRA 120, Amersham) was added (final concentration = 8 to 10 nmol sample^{-1}). The samples were incubated under each treatment and formalin inactivated samples were used as background controls. For further details see Sundbäck et al. (1996b).

Statistical analyses. The data were analysed by 1-factor ANOVA for each sampling date. The HPLC pigment data were analysed by nested ANOVA, with cores nested in treatment. We have not included time as a factor in the ANOVA since sampling was done only once in each season (no replication in time). Cochran's test (Winter et al. 1991) was used to check for heterogeneous variances. Data with heterogeneous variances were transformed according to Underwood (1997). Post-hoc analyses were made by the Student-Newman-Keul test (SNK). p-values <0.05 were accepted for significant differences. All p-values shown originate from the ANOVA.

RESULTS

The community studied

Total microalgal biomass (live cells) varied between 226 and 1142 mg C m^{-2} (individual samples, including all single measurements) (Fig. 2) and was dominated

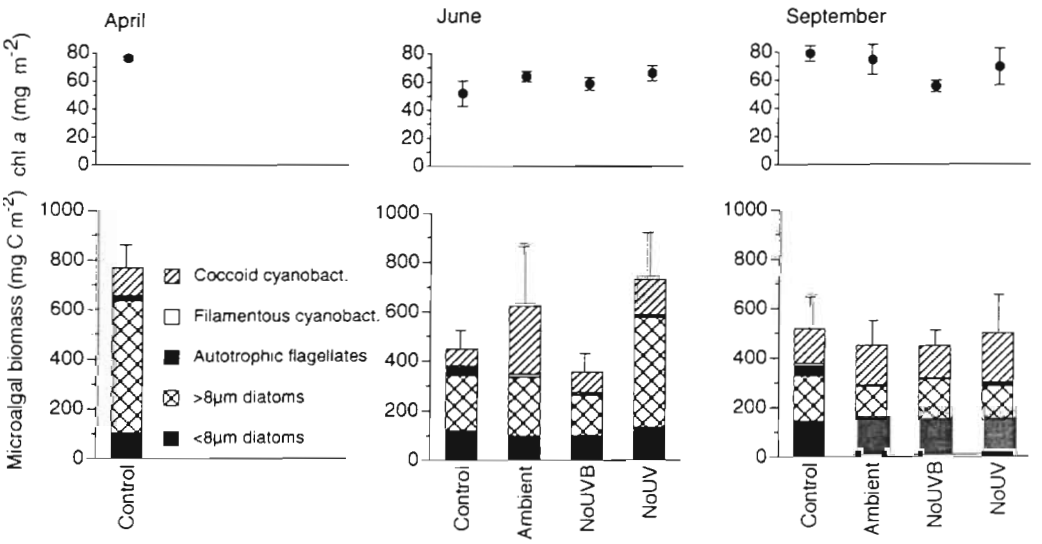

Fig. 2. Composition of living (autofluorescing) microalgal biomass and content of chl *a* (HPLC; ●) in sediment cores from the 3 experimental treatments (Ambient, NoUVB and NoUV) and Control. Bars show mean values for n replicate cores +SE; n = 12 for April, and n = 3 for June and September

by diatoms and cyanobacteria on all 3 sampling occasions. The lowest biomass values were found in June and coincided with the lowest chl *a* values measured. The chl *a* values were within the range 30 to 106 mg m^{-2} (individual samples, including all single measurements) (Fig. 2). Flagellates showed a very patchy distribution, comprising 0.2 to 8% of the total biomass. In general, the pigment ratios agreed with the microalgal counts, showing a high abundance of the diatom pigments fucoxanthin, diadinoxanthin, and chl c_1+c_2. Basically, no MAA were present, but occasionally a single peak was seen in the chromatogram. This UV-absorbing compound most likely originated from benthic dinoflagellates, since it corresponded to the single peak found in a culture of *Amphidinium carterae* (*Amphidinium* is a common dinoflagellate genus found in shallow-water sediment).

The total meiofaunal biomass ranged from 77 to 794 mg C m^{-2} (individual samples, including all single measurements), with nematodes dominating together with ostracods (Fig. 3). The lowest values for meiofaunal biomass (April) coincided with the highest found for microalgae; in April, the meiofaunal biomass was approximately 20% of the sum of microalgal and meiofaunal biomass, but in both June and September the proportion of meiofauna increased, ranging from 43 to 55%. Among macrofauna (not quantified), mud snails (*Hydrobia* spp.) appeared in great numbers, especially in June.

Treatment effects

Significant UVR effects (Table 2) were found for primary productivity, carbon allocation and biomass of ostracods (meiofauna), but only in September. The significant differences were found between the exclusion of and the exposure to UVR. No significant differences were found between the NoUVB and NoUV treatments, nor between the Control and Ambient treatments. Some tendencies, however, were observed for bacterial productivity and meiofaunal biomass.

Table 2. UVR effects for all variables studied. +: significant effects ($p < 0.05$, $n = 3$), –: non-significant effects

	Jun	Sep
Microalgal biomass	–	–
Microalgal composition	–	–
Photosynthetic pigments	–	–
Mycosporine-like amino acids	–	–
Fatty acids	–	–
Meiofaunal biomass	–	–
Meiofaunal composition (ostracodal biomass)	–	+
Primary productivity	–	+
Carbon allocation	+	+
Bacterial productivity	–	–

In September, the primary productivity was significantly higher when the community was shielded from UVR ($p = 0.0115$) (Fig. 4). In June, no significant differences between treatments were found, although there seemed to be a tendency for increased primary productivity when exposed to UVR.

For carbon allocation, significant effects were found, but with a partly different outcome in June and September (Fig. 5). The fraction allocated to total (sum of neutral and polar) lipids was not affected by UVBR. However, when separated into neutral and polar lipids, the ratio neutral lipids/polar lipids was in the UVR exclusion treatments significantly higher in June ($p = 0.014$) and lower in September ($p < 0.001$) (Fig. 5, pie charts). Allocation to proteins was significantly higher in June ($p = 0.009$) when UVR was excluded, but not in September. In September, microalgae shielded from UVR allocated less carbon to LMW ($p = 0.008$) and more into polysaccharides ($p = 0.0499$), when compared with microalgae exposed to UVR.

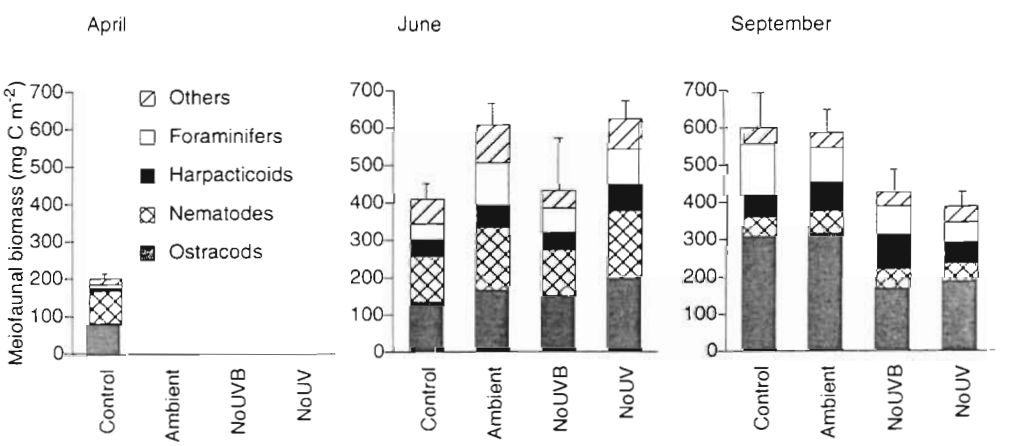

Fig. 3. Composition of meiofaunal biomass in sediment cores from the 3 experimental treatments (Ambient, NoUVB and NoUV) and Control. Bars show mean values for n replicate cores +SE; n = 12 for April, and n = 3 for June and September

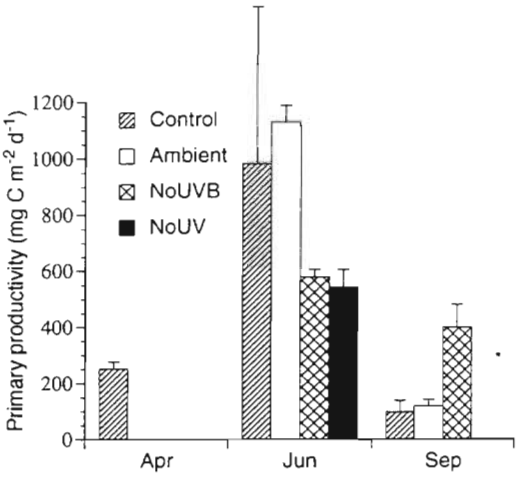

Fig. 4. Primary productivity of intact sediment cores from the 3 experimental treatments (Ambient, NoUVB, NoUV) and Control incubated under their different treatment conditions. *No values shown for the NoUV treatment in September, since 2 replicates were lost. Bars show mean values for n replicate cores +SE; n = 12 for April, n = 3 for June and September

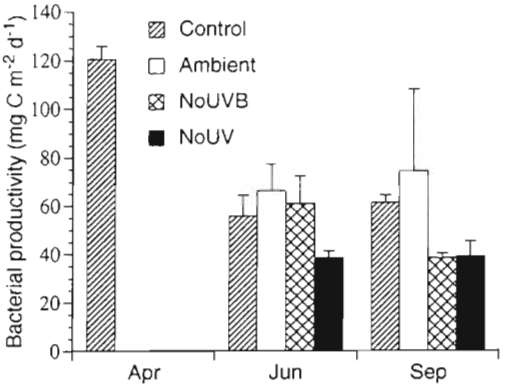

Fig. 6. Bacterial productivity of sediment from the 3 experimental treatments (Ambient, NoUVB, NoUV) and Control incubated under their different treatment conditions. Bars show mean values for n replicate cores +SE; n = 12 for April, and n = 3 for June and September

Among meiofauna, the biomass of ostracods was significantly higher in September in both the Control and Ambient treatments ($p = 0.015$). The total biomass, or numbers, of meiofauna was not significantly affected, although there was a tendency in September for higher biomass in communities exposed to UVR. This was caused by the higher biomass of ostracods and foraminifera. Simultaneously, a tendency for higher bacterial productivity in UVR-exposed treatments occurred, though this was not significant because of a high standard error in the Ambient treatment (Fig. 6).

DISCUSSION

Methodology and progress from previous studies

Screening off UVR *in situ*, instead of using sediment cores in flow-through systems, made it possible to extend the experimental period for a time period (4 mo) long enough to allow changes through natural selection in all organism groups studied. It could be argued, however, that a long-term effect would still not have been possible to detect in our field set-up because of sediment transport into and out from the screened areas. There was, however, no sign of any major sediment movement (footprints were visible for

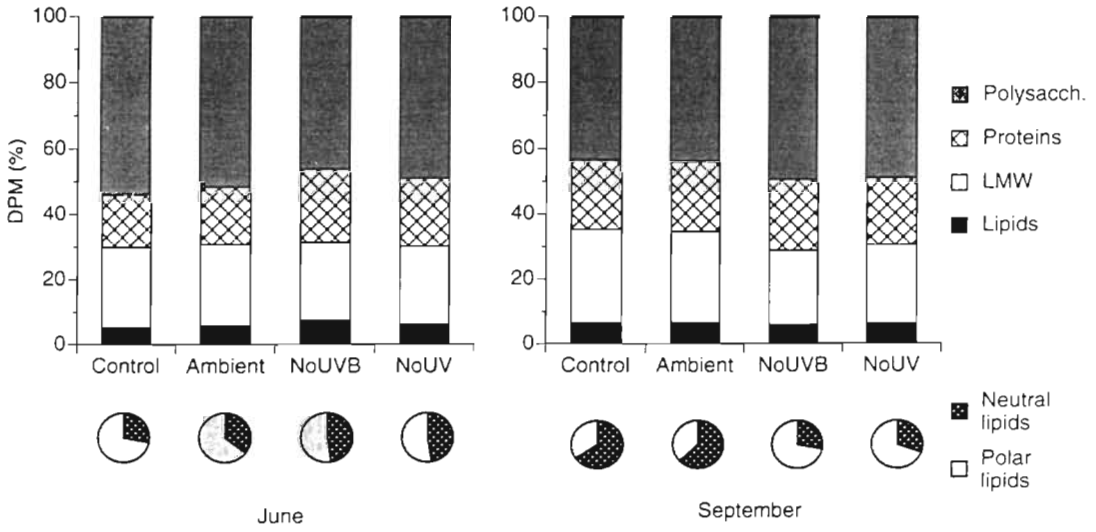

Fig. 5. Allocation of incorporated carbon of intact sediment cores from the 3 experimental treatments (Ambient, NoUVB, NoUV) and Control incubated under their different treatment conditions, respectively. Bar and pie graphs show mean values for 3 replicate cores. DPM: disintegrations per minute

several months) and bioturbation by macroscopic infauna, such as polychaetes, appeared minimal. Naturally some migration of organisms occurred. In this context, we also want to point out that, although the experiment lasted for several months, it should not be considered a seasonal study, as there was no replication in time for each season, and therefore, time effects were not tested.

Both UVAR and UVBR were studied simultaneously, thereby allowing for distinction between these different UV parts of the spectrum. Moreover, by measuring the potential penetration of UV and PAR into the sediment, we were able to estimate the depth to which the organisms could be exposed to UVR. The subsampling depth was restricted to the upper 2 mm (a normal sampling depth is 5 mm), the shallowest possible depth to sample using cut-off syringes. The sample depth corresponded well to the photosynthetic zone. Also, the incubation technique was improved by labeling intact sediment cores instead of 'slurries'. This is a better approach since only the cells that are exposed to enough light *in situ* will incorporate the radiolabeled carbon, while using a slurry causes an overestimation of the primary productivity (for discussion see Jönsson 1991).

Treatment effects

The results are contradictory. On the one hand, no UVR effects were found for any structural variables but ostracodal biomass. On the other hand, significant treatment effects were found for rate variables such as primary productivity and carbon allocation. The third rate variable, bacterial productivity, was not affected. Furthermore, the effects on primary productivity and ostracods were observed in September only. A possible explanation for this is the occurrence of a decreased ozone column in the area during autumn 1996 (Chen & Nunez 1998).

Why were the UVR effects found for primary productivity and carbon allocation not reflected in any structural variables? There could be methodological as well as biological reasons. One possible explanation for finding treatment effects in primary productivity, but not in microalgal biomass, may be that there was still a 'dilution effect' despite the fact that we sampled only the top 2 mm. This 'dilution effect' also applies to pigment ratios and fatty acid composition. The vertical resolution should perhaps be hundreds of microns instead of millimetres and in particular this should apply to sandy sediment with a high proportion of small epipsammic (i.e. attached) diatoms. There is a technique available that involves freezing of intact sediment in liquid nitrogen and then slicing the sediment using a cryomicrotome (Wiltshire et al. 1997). However, this is very time consuming and not feasible for living material. We cannot exclude the possibility that our instruments are still too crude to detect UVR effects on sediment microbenthic communities and the answer might be found on a taxonomic level lower than investigated here.

Another explanation is simply that there are no detrimental long-term UVR effects on sediment communities from ambient UVR at these latitudes. On a daily scale, due to a variable sun angle, these communities are not exposed to high levels of UVR for more than a few hours a day. Moreover, on a seasonal scale, this is even more pronounced. The UVR effects found for rate variables could then be explained by an 'acute effect' due to the light dose received during the hours of incubation and do not reflect a long-term effect. This is supported by the higher UVBR dose received during the incubation periods in September (0.45 kJ) compared with in June (0.29 kJ). Furthermore, the epipelic part of the microalgal community may be able to avoid the UVR through vertical migration (Underwood et al. 1999). Migration to a less deleterious light climate might temporarily decrease primary productivity but need not necessarily be reflected in a decreased total biomass.

If the increased primary productivity in the UVR-protected treatments did result from the long-term treatment, then we can only speculate about the fate of the increased amount of carbon produced in the UVR-shielded treatments in September. If not grazed, the carbon was apparently not incorporated into microalgal biomass. This is supported by the increased amount of carbon allocated into polysaccharides (e.g. exudates) instead of structural components (e.g. polar lipids). Furthermore, if the microalgal part of the community was nitrogen limited, growth was not likely to occur. Nitrogen limitation of microphytobenthos has previously been shown for sandy sediment (Flothman & Werner 1992 and references therein).

UVAR versus UVBR

All the UVR effects were found between exposure to and exclusion from UVR, whereas no difference was found between the 2 different UVR exclusion treatments. This implies that it was the UVBR part of the solar spectrum that constituted a stress factor to the microbenthic community of the sediment and that ambient levels of UVAR had no (detrimental) effects.

How do our results relate to previous findings?

The UVR effects on primary productivity and carbon allocation agree with the results from a previous 3 wk

experiment (Odmark et al. 1998), as well as with an experiment on effects of enhanced UVB (Sundbäck et al. 1997). However, in contrast to the 3 wk experiment, neither microalgal composition, chl *a* nor fatty acid composition were affected in our field experiment. On the other hand, in the present experiment, a UV effect was found among the meiofauna (ostracodal biomass), which was not observed in the previous experiments.

Although the UVR effect was only significant for 1 group of meiofauna, there was also a tendency for higher total biomass in treatments exposed to UVR in September. It is difficult to discuss UVR effects on meiofauna simply because they have not been investigated by others and we can therefore only speculate on the basis of our own results. One possible scenario for the higher meiofaunal biomass is that the tendency for increased bacterial productivity with UVR exposure favoured the bacterial grazers among the meiofauna. Ostracods do graze on bacteria and their generation time (years) is long enough to allow the individuals to increase their biomass. Furthermore, this group could have had a competitive advantage over e.g. nematodes and harpacticoids (also potential bacterial grazers), benefiting due to the protection from UVR exposure afforded by their shells (cf. Hill et al. 1997).

The tendency for increased bacterial productivity with exposure to UVR is consistent with our earlier findings (Odmark et al. 1998). Most studies regarding UVBR and bacteria concern pelagic populations but there are no reasons why these effects should not apply to benthic bacterial populations as well. The results reported in the literature are, however, somewhat contradictory; bacterial productivity has been found to benefit from UVBR (through the breakdown of DOM to more bioavailable molecules; Lindell et al. 1995), but the opposite has also been shown (Herndl et al. 1993, Naganuma et al. 1996).

Essentially no MAA were found in our experiment. This agrees with the fact that virtually all benthic diatoms are pennate, and pennate diatoms have been shown to have very low concentrations of MAA (Helbing et al. 1996). Since benthic diatoms can be very tolerant to UVBR (Peletier et al. 1996), they must apparently rely on mechanisms other than UV-absorbing compounds to avoid UVR damage. Bebout & Garcia-Pichel (1995) found that UVBR can induce vertical migration in cyanobacteria but up to now this has not been shown for diatoms.

Time scales

To date, we have studied the effects of UVR (both ambient and enhanced) on sediment microbenthic communities on time scales ranging from a few days to over 4 mo, and, although not very strong, we have found some significant UVR effects. It is important to note that different time scales of UVR-exclusion experiments lead to different interpretations of the influence of UVR. For example, Cabrera et al. (1997) found that chl *a* values were negatively affected by UVBR in a short-term exposure (6 to 12 d), while the opposite was found after 26 to 33 d. Furthermore, Santas et al. (1997) found that an initial change in diatom community structure did not persist at later successional stages. The different outcome for different time scales is valid even over shorter time spans, i.e. hours (Hazzard et al. 1997) or days (for example see Sundbäck et al. 1997). In a 3 wk experiment (Odmark et al. 1998), different conclusions could have been drawn if the experiment had been completed after 12 instead of 19 d. Also, Bothwell et al. (1993, 1994) found that an initial inhibitory effect of UVR on microalgae was reversed after 3 to 4 wk through trophic interactions.

Laboratory versus field experiments

Some of the most clear-cut UVBR effects have been found in laboratory experiments, using cultures or simplified communities. On the other hand, a lack of UV effects on natural communities has lately been reported in an increasing number of papers (Halac et al. 1997, Hill et al. 1997, Laurion et al. 1997). This proves once again that laboratory results cannot simply be extrapolated to complex natural communities. Therefore, despite contradictory results, we must put more effort into designing field experiments and persist in trying to figure out what is really going on in natural systems. However, it is not only the complexity of the community that makes UVR experiments in the field difficult. Changes in light and weather conditions make it hard to repeat a field experiment. In future experiments we should try to find a way to standardize the light climate during incubation periods. As a concluding remark we would like to point out that the lack of UVR effects in this field study does not necessarily mean that there are no such effects to be found and we would like to encourage more studies on long-term UVR effects in natural communities.

Acknowledgements. We thank Dr Ferran Garcia-Pichel for the microsensor measurements, Dr Deliang Chen for the UV data, Dr Lars Hellgren for analysis of fatty acids, and Eva Göransson, Elisabeth Thysell and Ingrid Winterlind for help during the field work. Financial support was provided by research grants from the Swedish Environmental Protection Agency, the Swedish Natural Science Research Council, the Futura Foundation, and the Marine Research Centre at Göteborg University. Additional support was given by the funds of

Wilhelm and Martina Lundgren, Captain Carl Stenholm, Hierta-Retzius, Anna Ahrenberg and Helge Ax:son Johnsson.

LITERATURE CITED

Abele-Oeschger D, Tüg H, Röttgers R (1997) Dynamics of UV-driven hydrogen peroxide formation on an intertidal sandflat. Limnol Oceanogr 42:1406–1415

Bebout BM, Garcia-Pichel F (1995) UV B-induced vertical migrations of cyanobacteria in a microbial mat. Appl Environ Microbiol 61:4215–4222

Bergeron M, Vincent WF (1997) Microbial food web responses to phosphorus supply and solar UV radiation in a subartctic lake. Aquat Microb Ecol 12:239–249

Bothwell ML, Sherbot D, Roberge AC, Daley RJ (1993) Influence of natural ultraviolet radiation on lotic periphytic diatom community growth, biomass accrual, and species composition: short-term versus long-term effects. J Phycol 29:24–35

Bothwell ML, Sherbot D, Pollock CM (1994) Ecosystem response to solar ultraviolet-B radiation: influence of trophic-level interactions. Science 265:97–100

Cabrera S, Lopez M, Tartarotti B (1997) Phytoplankton and zooplankton response to ultraviolet radiation in a high-altitude Andean lake: short- versus long-term effects. J Plankton Res 19:1565–1582

Carlsson AS, Hellgren LI, Selldén G, Sandelius AS (1994) Effects of moderately enhanced levels of ozone on acyl lipid composition of leaves of garden pea *Pisum sativum*. Physiol Plant 91:754–762

Chen D, Nunez M (1998) Temporal and spatial variability of total ozone in southwest Sweden revealed by two ground-based instruments. Int J Climatol 18:1237–1246

Flothman S, Werner J (1992) Experimental eutrophication on an intertidal sandflat: effects on microphytobenthos, meio- and macrofauna. In: Colombo G, Ferrari IJ, Ceccherelli VU, Rossi R (eds) Marine eutrophication and population dynamics. Olsen & Olsen, Fredensborg, p 93–100

Garcia-Pichel F (1995) A scalar irradiance fiber-optic microprobe for the measurement of ultraviolet radiation at high spatial resolution. Photochem Photobiol 61:249–254

Garcia-Pichel F, Bebout BM (1996) Penetration of ultraviolet radiation into shallow water sediments: high exposure for photosynthetic communities. Mar Ecol Prog Ser 131: 257–262

Garcia-Pichel F, Castenholz RW (1994) On the significance of solar ultraviolet radiation for the ecology of microbial mats. In: Stal LJ, Caumette P (eds) Microbial mats. Springer-Verlag, Berlin, p 77–84

Häder DP, Worrest RC, Kumar HD, Smith RC (1995) Effects of increased solar ultraviolet radiation on aquatic ecosystems. Ambio 24:174–180

Halac S, Felip M, Camarero L, Sommaruga-Wögrath S, Psenner R, Catalan J, Sommaruga R (1997) An *in situ* enclosure experiment to test the solar UVB impact on plankton in a high-altitude mountain lake. I. Lack of effect on phytoplankton species composition and growth. J Plankton Res 19:1672–1686

Hazzard C, Lesser MP, Kinzie RA III (1997) Effects of ultraviolet radiation on photosynthesis in the subtropical marine diatom, *Chaetoceros gracilis* (Bacillariophyceae). J Phycol 33:960–968

Helbling EW, Villafañe V, Ferrario M, Holm-Hansen O (1992) Impact of natural ultraviolet radiation on rates of photosynthesis and on specific marine phytoplankton species. Mar Ecol Prog Ser 80:89–100

Helbling EW, Chalker BE, Dunlap WC, Holm-Hansen O, Villafañe VE (1996) Photoacclimation of Antarctic marine diatoms to solar ultraviolet radiation. J Exp Mar Biol Ecol 204:85–101

Herndl GJ, Müller-Niklas NG, Frick J (1993) Major role of ultraviolet-B in controlling bacterioplankton growth in the surface layer of the ocean. Nature 361:717–719

Hill W, Dimick SM, McNamara A, Branson CA (1997) No effects of ambient UV radiation detected in periphyton and grazers. Limnol Oceanogr 42:769–774

Holm-Hansen O, Lubin D, Helbling EW (1993a) Ultraviolet radiation and its effects on organisms in aquatic environments. In: Young AR, Björn LO, Moan J, Nultsch W (eds) Environmental UV photobiology. Plenum Press, New York, p 379–425

Holm-Hansen O, Helbling EW, Lubin D (1993b) Ultraviolet radiation in Antarctica: inhibition of primary production. Photochem Photobiol 58:567–570

Jönsson B (1991) A ^{14}C-incubation technique for measuring microphytobenthic primary productivity in intact sediment cores. Limnol Oceanogr 36:1485–1492

Karentz D (1994) Ultraviolet tolerance mechanisms in Antarctic marine organisms. Antarct Res Ser 62:93–110

Kraay GW, Zapata M, Veldhuis MJW (1992) Separation of chlorophylls c_1, c_2 and c_3 of marine phytoplankton by reversed-phase-C18-high-performance liquid chromatography. J Phycol 28:708–712

Lassen C, Ploug H, Jørgensen BB (1992) A fibre-optic scalar irradiance microsensor: application for spectral light measurements in sediments. FEMS Microbiol Ecol 86: 247–254

Laurion I, Vincent WF, Lean DRS (1997) UV effects on the growth of planktonic microbial organisms in lake enclosures. ASLO Aquatic Sciences Meeting, Santa Fe New Mexico, Program and Abstracts

Li WKW, Glover HE, Morris I (1980) Physiology of carbon photoassimilation by *Oscillatoria thiebautii* in the Caribbean Sea. Limnol Oceanogr 25:447–456

Lindell MJ, Granéli W, Tranvik LJ (1995) Enhanced bacterial growth in response to photochemical transformation of dissolved organic matter. Limnol Oceanogr 40:195–199

Lorenzen CJ (1979) Ultraviolet radiation and phytoplankton photosynthesis. Limnol Oceanogr 24:1117–1120

Mallin MA, Burkholder JM, Sullivan MJ (1992) Contributions of benthic microalgae to coastal fishery yield. Trans Am Fish Soc 121:691–693

Moriarty DJW (1990) Bacterial productivity in sediment. Arch Hydrobiol Beih Ergebn Limnol 34:183–189

Naganuma T, Konishi S, Inoue T, Nakane T, Sukizaki S (1996) Photodegradation or photoalteration? Microbial assay of the effect of UV-B on dissolved organic matter. Mar Ecol Prog Ser 135:309–310

Nakamura H, Kobayashi J (1982) Separation of mycosporine-like amino acids in marine organisms using reversed-phase high-performance liquid chromatography. J Chromatogr 250:113–118

Nilsson P, Jönsson B, Lindström Swanberg I, Sundbäck K (1991) Response of a marine shallow-water sediment system to an increased load of inorganic nutrients. Mar Ecol Prog Ser 71:275–290

Nunez M, Chen D (1998) A comparison of cloudless sky erythermal ultraviolet radiation at two sites in southwest Sweden. Int J Climatol 18:915–930

Odmark S, Wulff A, Wängberg SÅ, Nilsson C, Sundbäck K (1998) Effects of UVB radiation in a microbenthic community of a marine shallow-water sandy sediment. Mar Biol 132:335–345

Peletier H, Gieskes WWC, Buma AGJ (1996) Ultraviolet-B radiation resistance of benthic diatoms isolated from tidal flats in the Dutch Wadden Sea. Mar Ecol Prog Ser 135: 163–168

Pihl L (1989) Abundance, biomass and production of juvenile flatfish in southeastern Kattegat. Neth J Sea Res 24:69–81

Pinckney J, Zingmark RG (1993) Biomass and production of benthic microalgal communities in estuarine habitats. Estuaries 16:887–897

Santas R, Lianou C, Danielidis D (1997) UVB radiation and depth interaction during primary succession of marine diatom assemblages of Greece. Limnol Oceanogr 42: 986–991

Siebeck O, Vail TL, Williamson CE, Vetter R, Hessen D, Zagarese H, Little E, Balseiro E, Modenutti B, Seva J, Shumate A (1994) Impact of UV-B radiation on zooplankton and fish in pelagic freshwater ecosystems. Arch Hydrobiol Beih Ergebn Limnol 43:101–114

Sundbäck K, Jönsson B, Nilsson P, Lindström I (1990) Impact of accumulating drifting macroalgae on a shallow-water sediment system: an experimental study. Mar Ecol Prog Ser 58:261–274

Sundbäck K, Nilsson C, Odmark S, Wulff A (1996a) Does ambient UV-B radiation influence marine diatom-dominated microbial mats? A case study. Aquat Microb Ecol 11: 151–159

Sundbäck K, Nilsson P, Nilsson C, Jönsson B (1996b) Balance between autotrophic and heterotrophic components and processes in microbenthic communities of sandy sediments: a field study. Estuar Coast Shelf Sci 43:689–706

Sundbäck K, Odmark S, Wulff A, Nilsson C, Wängberg SÅ (1997) Effects of enhanced UVB radiation on a marine benthic diatom mat. Mar Biol 128:171–179

Underwood AJ (1997) Experiments in ecology. Cambridge University Press, Cambridge

Underwood GJC, Nilsson C, Sundbäck K, Wulff A (1999) Short-term effects of UVB radiation on chlorophyll fluorescense, biomass, pigments and carbohydrate fractions in a benthic diatom mat. J Phycol 35:656–666

Vinebrook R, Leavitt P (1999) Differential responses of littoral communities to ultraviolet radiation in an alpine lake. Ecology 80:223–237

Wängberg SÅ, Selmer JS (1997) Studies of effects of UV-B radiation on aquatic model ecosystems. In: Häder DP (ed) The effects of ozone depletion on aquatic ecosystems. RG Landes Company, Austin, p 199–213

Wängberg SÅ, Selmer JS, Ekelund N, Gustavson K (1996) Effects of increased UV-B radiation on the Nordic marine ecosystem—a literature review. Nordic Council of Ministers TemaNord 1996:515–560

Widbom B (1984) Determination of average dry weights and ash-free dry weights in different sieve fractions of marine meiofauna. Mar Biol 75:101–109

Wiltshire KH, Blackburn J, Paterson DM (1997) The cryolander: a new method for *in situ* sampling of intertidal surface sediments minimizing distortion of sediment structure. J Sediment Res 67:980–984

Winer BJ, Brown DR, Michels KM (1991) Statistical principles in experimental design. McGraw-Hill Inc, New York

Wright SW, Jeffrey SW, Mantoura RFC, Llewellyn CA, Bjørnland T, Repeta D, Welschmeyer N (1991) Improved HPLC method for the analysis of chlorophylls and carotenoids from marine phytoplankton. Mar Ecol Prog Ser 77: 183–196

Editorial responsibility: William Li, Dartmouth, Nova Scotia, Canada

Submitted: December 3, 1998; Accepted: March 29, 1999
Proofs received from author(s): October 18, 1999