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Impact of solar radiation on the biological removal of dimethylsulfoniopropionate and dimethylsulfide in marine surface waters

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ABSTRACT: The effect of natural surface solar radiation on the biological removal of dimethylsulfoniopropionate (DMSP) and dimethylsulfide (DMS) was determined and compared to the photochemical removal of DMSP and DMS. Natural bacterial assemblages (0.8 µm filtered seawater) from the northern Adriatic Sea and the coastal North Sea were exposed to surface solar radiation and incubated in the dark; the DMSP and DMS concentrations were measured concurrently. Photochemical removal rates were determined in 0.2 µm filtered seawater. Biological removal of DMSP in the light was 62 ± 14% lower than the biological removal rate obtained in the dark. High spatial and temporal variability in the biological removal rates was observed for the dark treatments, as well as for its sensivity to solar radiation, with rates for light treatments varying from 29 to 81% of those in the dark. The DMSP concentration above which no further increase of the biological DMSP removal rate was observed was substantially lower in the light treatments (~30 nM) than in the dark treatments (>80 nM). UV-B radiation only accounted for a minor inhibitory effect (~15% of total inhibition), whereas UV-A and PAR (photosynthetically active radiation) both contributed ~42% of total inhibition. Biological DMS removal under solar radiation was only ~40 ± 14% of the biological DMS removal in the dark. Under surface solar radiation, photochemical removal was always higher than the dark biological removal. Our results indicate therefore, that the DMSP and DMS dynamics in the oceanic surface waters are severely influenced by solar radiation due to the partial inhibition of the microbial consortia responsible for DMSP and DMS turnover.

KEY WORDS: DMSP · DMS · Ultraviolet (UV) radiation · Bacteria · Biological removal · Photochemical alteration

INTRODUCTION

Stratospheric ozone depletion causes an increase in ultraviolet-B (UV-B, 280 to 320 nm) radiation over polar regions during spring when the polar vortex is breaking up (Crutzen 1992, Smith et al. 1992, Kerr & McElroy 1993). This increase in UV-B radiation, however, is not restricted to polar regions but is also detectable in temperate zones (Blumthaler & Ambach 1990). UV-B radiation reaching the earth's surface also penetrates into aquatic systems. Recent studies have shown that UV-B radiation penetrates much deeper into the oceanic water column than previously thought (Gieskes & Kraay 1990, Obernosterer et al. 2001). Therefore, non-motile organisms and dissolved organic matter (DOM) are exposed to high levels of UV-B radiation in the oceanic surface layers due to diurnal stratification of the surface layers down to 40–50 m depth (Obernosterer et al. 2001).

DNA replication and protein synthesis of bacterioplankton are reduced by 40 to 70% under exposure to solar radiation (Herndl et al. 1993, Müller-Niklas et al.

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1995, Sommaruga et al. 1997), and direct DNA damage on a cellular base has been reported (Jeffrey et al. 1996, Lyons et al. 1998). Besides the direct effects of UV radiation on organisms, it also affects organisms indirectly by changing their chemical environment (Palenik et al. 1991). There is increasing evidence, that UV radiation alters DOM in different ways by transforming refractory DOM into more labile forms and vice versa (Benner & Biddanda 1998, Tranvik & Kokalj 1998, Obernosterer et al. 1999, Pausz & Herndl 1999). Additionally, a part of the dissolved organic carbon (DOC) is photo-oxidized into CO_2 and CO (Mopper et al. 1991, Graneli et al. 1995). Moran & Zepp (1997) estimated that photochemical degradation of DOM into low molecular weight organic compounds and dissolved inorganic carbon amounts to 2–3% of the oceanic DOC pool. Moreover, the production of photosensitizers can lead to photochemical alteration of DOM compounds which do not absorb UV radiation (Zafiriou et al. 1984, Cooper & Lean 1989). One example of photosensitizer activity is the photochemical alteration of dimethylsulfide (DMS) (Kieber et al. 1996). It has been shown that the rate of photochemical alteration of DMS strongly depends, among other factors, on the concentration of DOC (Brugger et al. 1998).

The production of DMS in the euphotic zone represents the main source of the biogenic sulfur flux from the oceans to the atmosphere (Barnard et al. 1982, Andreae & Raemdonck 1983, Andreae 1990). In the upper layers of the ocean, DMS is primarily formed via the enzymatic cleavage of dimethylsulfoniopropionate (DMSP) (Cantoni & Anderson 1956, Kiene 1990, Ledyard & Dacey 1994), an organic osmolyte (Vairavamurthy et al. 1985) produced by certain phytoplankton species (Keller et al. 1989a,b). The main pathways of the removal of DMS from the upper oceanic layers are biological consumption by bacteria (Kiene & Bates 1990), biological oxidation (Liss et al. 1997), photochemical transformation (Kieber et al. 1996, Brugger et al. 1998), sedimentation (Lee & Wakeham 1992, Osinga et al. 1996) and evaporation (Andreae & Raemdonck 1983, Nguyen et al. 1983).

In the troposphere, DMS is oxidized to sulfate and methane sulfonate, both contributing to the pool of sub-µm aerosols and cloud condensation nuclei which are involved in cloud albedo and backscatter of incoming solar radiation hence affecting the global climate (Charlson et al. 1987, Ayers et al. 1991, Prospero et al. 1991, Berresheim 1993). The flux of DMS to the atmosphere is strongly dependent on the concentration of DMS in the surface layer of the ocean (Liss 1973).

As pointed out by Zepp et al. (1995), increased solar UV radiation might influence the oceanic sulfur cycle due to altered dynamics of production and turnover of DMSP and DMS. There are only a few studies on the photochemical transformation of DMS (Brimblecombe & Shooter 1986, Kieber et al. 1996, Brugger et al. 1998) and on the role of microorganisms on these dynamics as influenced by UV radiation (Hefu & Kirst 1997, Sakka et al. 1997). Hefu & Kirst (1997) found that artificial radiation including UV-B caused an increase in the conversion rate of DMSP to DMS compared to treatments without UV-B, suggesting a photochemical cleavage of DMSP.

The aim of this study was to determine the role of surface solar radiation levels on the degradation of DMSP and DMS mediated by bacteria. Furthermore, biological removal was compared to photochemical alteration of DMSP and DMS in order to assess the relative importance of these 2 processes in the upper layers of coastal waters.

MATERIAL AND METHODS

Sampling sites. Surface water was collected in acid-rinsed carboys or buckets from the coastal northern Adriatic Sea about 5 km off the coast of Ancona (43° 33′ N, 13° 9′ E, Italy) and from the coastal North Sea (52° 59′ N, 4° 50′ E, The Netherlands). Water from the coastal North Sea was collected at high tide from the NIOZ pier in the North Sea and from a boat in the Adriatic Sea. In most experiments, samples were processed immediately. However, in the case of the coastal North Sea when water was collected in the evening, Whatman GF/C filtered samples were stored at *in situ* temperature overnight before starting the experiments the next morning. Storage effects are considered to be low, since almost all the phytoplankton were retained by the GF/C filter. The composition of the bacterial community might, however, experience some storage-induced changes.

Experimental setup. In order to determine the bacterial removal of DMSP and/or DMS, natural water samples were filtered through 0.8 µm polycarbonate filters (Millipore) to remove most of the non-bacterial organisms. For the determination of free DMSP lyase activity and the photochemical alteration of DMSP and DMS, 0.2 µm filtered samples (polycarbonate filters, Millipore) served as a control. Experiments were performed either with natural DMSP and DMS concentrations or with elevated concentrations by adding DMSP or DMS up to a final concentration of ~50 nM and gently inverting the samples several times before taking subsamples to determine the initial concentrations. The unamended and DMSP- and DMS-amended samples were filled gently into quartz Erlenmeyer flasks (100 ml) and sealed with glass stoppers without headspace. For sampling over time, 1 to 2 flasks were sacrificed at each time point to avoid the

formation of headspace via subsampling. Half of the bottles were wrapped with aluminum foil to serve as dark controls. The quartz Erlenmeyer flasks were incubated outdoors under natural surface solar radiation during cloudless days at *in situ* temperature in a water bath. As an example, on 10 July 1997 radiation intensity for the incubation period was 54 and 785 kJ m^{-2} for UV-B and UV-A and 48 E m^{-2} for PAR (photosynthetically active radiation), respectively (measured with a biospherical PUV-510 radiometer, see also Obernosterer & Herndl 2000).

Effect of solar radiation on the kinetics of bacterial DMSP removal. Time course experiments were conducted at *in situ* DMSP concentrations to study the kinetics of the biological DMSP removal in the presence of surface levels of natural solar radiation. To determine the potential removal rate, experiments were performed after adding DMSP (~50 nM final concentration) to 0.8 µm filtered seawater (Kiene 1996b). Incubations started between 09:30 and 10:30 h and lasted for 6 to 7 h to cover almost the entire period of UV radiation. In 30 to 120 min intervals, Erlenmeyer flasks incubated in the dark or exposed to solar radiation were brought to the lab and processed for further analysis as described below. Incubations were made in duplicate (time interval >1 h) or in single bottles (time interval = 30 to 60 min). In 4 out of 11 experiments conducted to determine the kinetics of biological DMSP removal, the DMS concentrations were also measured. The bacterial DMS removal in the dark and the DMS removal under solar radiation were compared with the photochemical removal of DMS under solar radiation. Seawater filtered through 0.2 µm filters and incubated in the dark served as controls for free DMSP lyase activity.

Effect of different DMSP concentrations on the inhibition of DMSP removal by solar radiation. In order to test whether the inhibitory effects of UV radiation on DMSP removal are dependent on the initial DMSP concentration, experiments were performed with different DMSP additions. After filtering the water through 0.8 or 0.2 µm polycarbonate filters, 250 ml glass bottles were filled and DMSP was added to the different flasks at 5 different concentrations ranging from 3 to 93 nM final concentration. After gently mixing, the flasks were subsampled for t_0 measurements and transferred into quartz Erlenmeyer flasks and incubated outdoors under surface solar radiation for 6 h. Incubations were always made in duplicate; the 0.2 µm filtered samples served as a control.

Influence of different solar radiation regimes on the DMSP removal. To investigate the effects of various ranges of the solar radiation spectrum, samples in quartz Erlenmeyer flasks were exposed to 4 different radiation regimes: PAR (400 to 700 nm; wavelengths <400 nm were cut off by acrylic glass; XT 20013, 3 mm, Röhm, Germany), PAR+UV-A (wavelengths <320 nm were cut off with Mylar D-foil), full radiation (PAR+UV-A+UV-B) and darkness. After subsampling for t_0 measurements, samples were incubated under surface solar radiation at *in situ* temperature for 6 h. Incubations were made in duplicate; 0.2 µm filtered samples served as control. Experiments were performed 4 times with DMSP additions of up to 50 nM (final conc.).

Analysis of DMSP and DMS. Total DMS and DMSP concentrations were determined by putting 20 ml samples into glass vials and adding 2 ml of 5 N NaOH (non-degassed sample). For complete alkaline DMSP cleavage to DMS, samples were kept at 4°C for 24 h. DMSP concentrations were determined by transferring the samples into glass columns with a glass frit at the lower end and sparging them with nitrogen gas for 20 min. Subsequently the samples were treated as described above. DMS concentrations were calculated as the difference between degassed and non-degassed samples.

DMS analysis was performed using a modified purge and trap system as described elsewhere (Andreae & Barnard 1983, Kiene & Service 1991). Volatile sulfur compounds were stripped from the water samples by a stream of nitrogen gas, cryo-trapped in liquid nitrogen and analyzed by gas chromatography (Hewlett Packard Model 5890 Series II, equipped with a flame photometric detector and a Chromosil 330 teflon column, Supelco). Ethylmethylsulfide (EMS, 99% Aldrich Chemical) served as an internal standard for the analytical system; it was injected in appropriate amounts (50 ± 5 pmol) directly into the bubble chamber and stripped together with the sample. The gas chromatograph was operated isothermally at 70°C and at a carrier gas flow rate of 50 ml min^{-1}. Retention times of DMS and EMS were 1.2 and 2.1 min, respectively. Calibration was carried out by injecting various amounts of DMS together with 50 ± 5 pmol EMS and then relating the ratio of the peak areas of DMS and EMS to the absolute amount of DMS. Standards for DMS and EMS were prepared gravimetrically. Under these conditions the analytical precision was always >95%.

Rate calculations. The DMSP and DMS removal rate was calculated by taking the linear fit of the time courses of the DMS(P) disappearance according to (Ledyard & Dacey 1996a) based on at least 4 to 5 measurements beginning at t_0 (initial removal rate). The initial removal rate in the 0.8 µm filtered samples was corrected for the decline in the 0.2 µm filtered controls. In one of the experiments, DMSP removal showed hardly any linear decrease; therefore, the first-order rate constant was determined and multiplied with the initial DMSP concentration to calculate the initial DMSP removal rate (see Fig. 1A) (Kiene 1996b). DMS

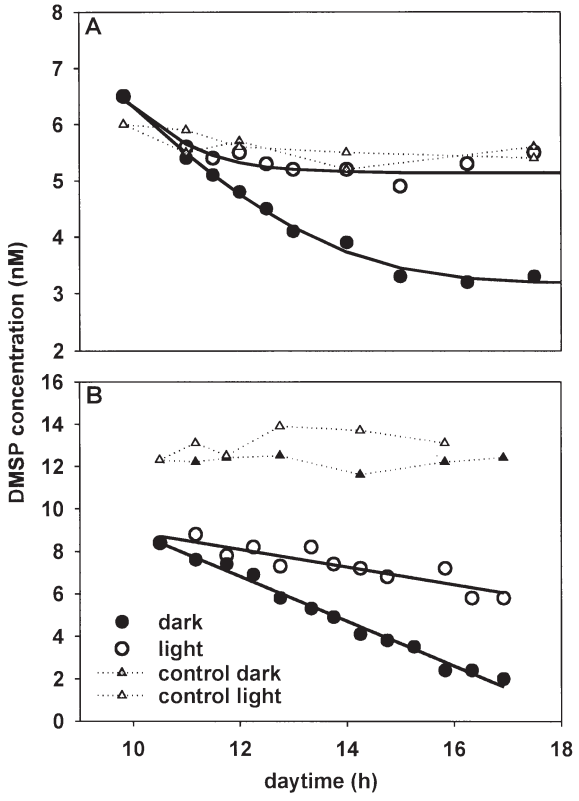

Fig. 1. Effects of surface solar radiation on the kinetic of the biological removal of DMSP in 2 experiments. (A) 17 August 1997, (B) 18 June 1997. Time course of the decline of DMSP in 0.8 µm filtered natural seawater in the dark (dark) compared to treatments exposed to the full range of natural solar radiation (light); 0.2 µm filtered seawater served as a control. Symbols represent DMSP concentrations measured in single incubations. DMSP decay rates were calculated from the linear fit of the initial DMSP decline (referred to as 'initial DMSP removal rate' in the text); in (A), light treatments, the pseudo first-order rate constant was determined for calculation of the initial removal rate

removal in the 0.8 µm filtered radiation-exposed treatments consists of photochemical removal (determined in the 0.2 µm filtered radiation-exposed control) and the biological consumption of DMS inhibited by solar radiation. The biotic removal rate due to bacteria was calculated by subtracting the photochemical removal rate from the total removal rate in the corresponding 0.8 µm filtered sample.

The photochemical removal rate was calculated by taking the pseudo first-order rate constant as the slope of the plot of the natural log of the DMS concentration versus time (Kieber et al. 1996, Brugger et al. 1998). By multiplying the rate constant with the initial DMS concentration the photochemical removal rate was obtained. Biological and photochemical removal rates were all corrected for the DMS dynamics in the 0.2 µm filtered dark control.

RESULTS

Reduction of the biological DMSP removal by natural surface solar radiation

In the 0.8 µm filtered seawater incubated in the dark, the *in situ* DMSP concentration decreased due to bacterial removal of DMSP. Initially, the DMSP concentration decreased linearly, in one experiment it leveled off as the DMSP concentrations reached ~3 nM (Fig. 1A). However, another experiment showed a linear decrease throughout the entire incubation period to DMSP concentrations of ~2 nM (Fig. 1B). Exposure to surface solar radiation resulted in a reduction of the initial DMSP removal rate by ~50 to 60% over the 6 to 7 h exposure period as compared to the removal rate in the dark (Fig. 1). In one case (Fig. 1A) DMSP removal rate decreased at a higher DMSP concentration than in the dark treatments.

The potential removal rates measured after DMSP amendments and exposure to natural solar radiation for 7 h are exemplified in Fig. 2. The initial removal rate in the dark of 7.06 nmol l^{-1} h^{-1}, which leveled off at ~15 nM, was reduced by 74% in the radiation-exposed treatments over the first 4 h of incubation. In general, DMSP removal rates varied considerably among different experiments and were not related to initial DMSP concentrations (Table 1). Surface solar radiation levels reduced the initial removal rates measured in the dark in almost all experiments by more than 50%; however, the percentage of reduction varied considerably (Table 1).

In the 0.2 µm filtered natural seawater no significant difference in DMSP concentration between dark and

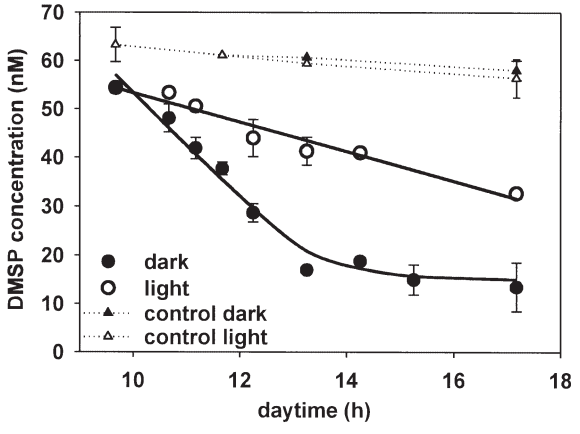

Fig. 2. Example of a time course (obtained 10 July 1997) of the decline in DMSP in 0.8 µm filtered seawater under natural solar radiation and in the dark (circles and solid lines), controls of 0.2 µm filtered seawater are indicated by triangles and dotted lines. DMSP was added to a final concentration of ~55 nM. Symbols are means of duplicate treatments, bars indicate SD

Table 1. Biological DMSP removal rates in 0.8 µm filtered natural seawater exposed to surface solar radiation (BR-rad) compared to biological DMSP removal rates in the dark (BR-dark). Samples in 1996 were taken in the northern Adriatic Sea about 5 km off Ancona, Italy; samples collected in 1997 are from the costal North Sea, Texel, The Netherlands. Asterisks indicate significant difference compared to biological removal rates under dark conditions as determined by Student's *t*-test slope comparison: $^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$

Date	Initial DMSP conc. (nM)	BR-dark (nmol l^{-1} h^{-1})	BR-rad in % of BR-dark
17 Aug 1997[a]	6.5	0.73	40**
18 Jun 1997[a]	8.4	1.05	39***
7 Aug 1997	20.7	2.73	19**
15 Sep 1996	28.3	1.40	25***
10 Jun 1997	29.1	2.37	38**
25 Sep 1997	32.0	1.63	34**
6 Sep 1996	32.7	1.40	46**
2 Aug 1997	33.3	2.66	71*
16 Aug 1997	43.0	1.23	31**
11 Sep 1996	46.6	2.11	48*
10 Jul 1997	54.4	7.06	26***
Mean		2.3	37.9
±SD		1.81	14.13

[a]Experiments without amendments of DMSP

radiation-exposed treatments were observed (comparison of slopes with Student's *t*-test ($p > 0.08$; Neter et al. 1996). Free DMSP lyase activity was generally low. Nevertheless, all DMSP removal rates calculated for the 0.8 µm filtered seawater were corrected for the activity of free DMSP lyase.

Effect of different initial DMSP concentrations on the inhibition of DMSP removal by surface solar radiation

In the dark treatments, initial removal rates at various DMSP concentrations usually followed a saturation curve, as shown on one example in Fig. 3A. Under surface solar radiation, the initial removal rates leveled off at significantly lower concentrations than in the dark (Fig. 3A, Wilcoxon, $p < 0.05$, $n = 5$). In Fig. 3B, the initial removal rates at various initial DMSP concentrations are shown, pooled from 3 different experiments. In one experiment, DMSP removal in the dark did not reach saturation at the concentrations applied (~60 nM) and was therefore excluded from the regression analysis. The saturating DMSP concentration of the initial removal rate was significantly lower in radiation-exposed treatments (~30 nM) than in the dark treatments (>80 nM; Fig. 3B, Wilcoxon, $p < 0.001$, $n = 28$). Nevertheless, the initial DMSP removal rates obtained for different initial DMSP concentrations varied considerably between the different dates when experiments were performed. The saturation curve does not follow Michaelis Menten kinetics as checked by linearization using an Eadie Hofstee plot (data not shown).

Reduction of the biological DMSP removal under different radiation regimes

In a set of experiments, the effect of different wavelength ranges of the solar radiation spectrum was tested. Exposure to the full range of surface solar radiation reduced initial removal rates in 0.8 µm filtered natural seawater to 19–71% of the removal under dark conditions, with UV-B radiation contributing, on average, 15.1 ± 11.7% to the total inhibition (Fig. 4). UV-A radiation was responsible, on average,

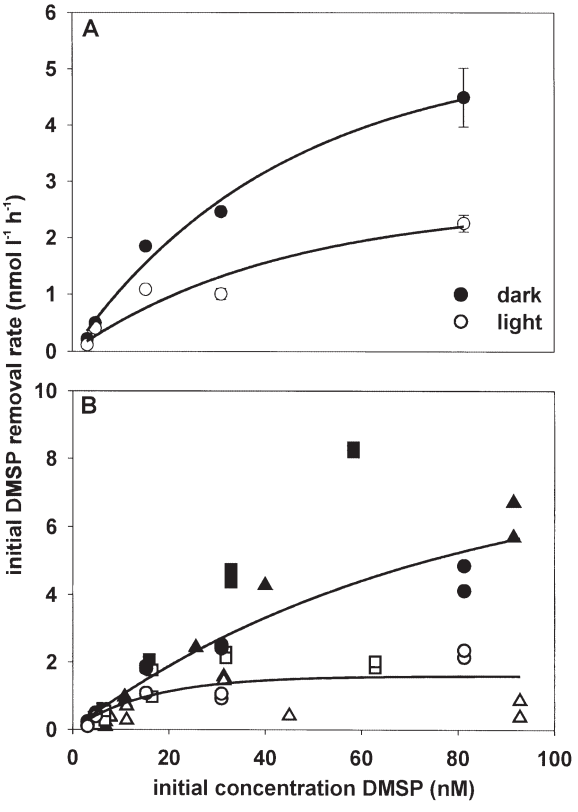

Fig. 3. Dependence of the initial DMSP removal rate on the initial DMSP concentration in 0.8 µm filtered seawater under surface solar radiation and in the dark. The initial DMSP removal rate has been corrected for loss obtained in 0.2 µm filtered controls. (A) Example for one experiment; symbols are mean of duplicate treatments, bars indicate SD. (B) Three experiments pooled, different symbols indicate the different dates of the experiments. Open symbols represent radiation-exposed treatments, solid symbols dark treatments. Solid lines represent exponential fit. Solid squares were excluded from the regression line

for 42.5 ± 29.9%, and PAR for 42.4 ± 32.4% of total inhibition. High standard deviations are due to the fact that in 2 experiments UV-A was the main inhibitory radiation (2 and 16 August), whereas in 2 other experiments the main inhibitory effect was caused by PAR (7 August and 25 September; Fig. 4). In 2 experiments, the contribution of UV-B to the total inhibition effect was rather high (28 and 21% of total inhibition on 16 August and 25 September, respectively) while in the other 2 experiments UV-B contributed only 1 to 10%.

Reduction of microbial DMS removal in comparison to photochemical removal during exposure to surface solar radiation

In 4 experiments, the DMS removal due to both photochemical removal and biological consumption was estimated. In 0.2 µm filtered seawater, DMS concentrations decreased under surface solar radiation, whereas in the treatment incubated in the dark the DMS concentration increased, probably due to DMSP lyase activity, at a rate of 0.46 nmol l^{-1} h^{-1} (Fig. 5). In the 0.8 µm filtered seawater, the DMS concentration in the radiation-exposed treatments decreased at a rate of 0.93 nmol l^{-1} h^{-1}, in the dark treatments at a rate of 0.68 nmol l^{-1} h^{-1} (total removal in light and dark was 1.39 and 1.14 nmol l^{-1} h^{-1}, respectively, corrected for the 0.2 µm filtered dark treatment). By subtracting the photochemical removal rate of 1.02 nmol l^{-1} h^{-1} (derived from the 0.2 µm filtered radiation-exposed treatment, corrected for the dark control) from the removal rate determined in the 0.8 µm filtered radiation-exposed treatment, we calculated a biological removal rate of 0.37 nmol l^{-1} h^{-1} due to bacterial activity. The rather high free DMSP lyase activity might have come from stimulation through the filtration step, as cells of *Phaeocystis* sp. which was still rather abundant in June 1997 in the coastal North Sea (G. Cadee pers. comm.) were disrupted. In Table 2 the DMS removal rates under solar radiation are given in comparison to the biological removal rates in the dark and the photochemical DMS removal rates. Bacterial removal of DMS was reduced in the presence of solar radiation to 25–56% of the biological DMS removal rates under dark conditions. In all experiments, the photochemical removal rate was substantially higher than the bacterial removal under surface solar radiation (Table 2). Only in 1 experiment was DMSP lyase activity high (10 July 1997).

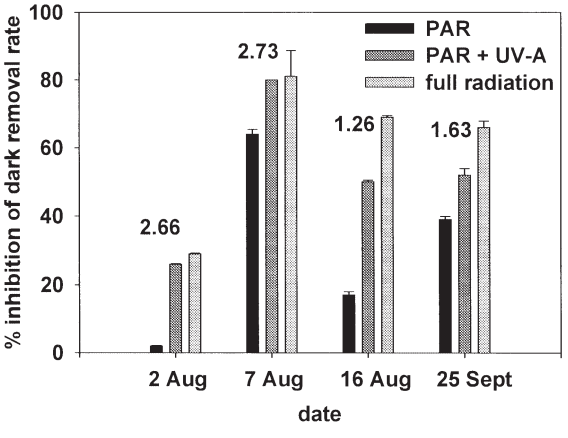

Fig. 4. Contribution of different ranges of natural surface solar radiation to the reduction of biological DMSP removal in 0.8 µm filtered seawater (corrected for DMSP removal in 0.2 µm filtered controls) as compared to the biological DMSP removal rate in the dark. Numbers above the bars indicate the initial removal rates in the dark treatments in nmol DMSP l^{-1} h^{-1}

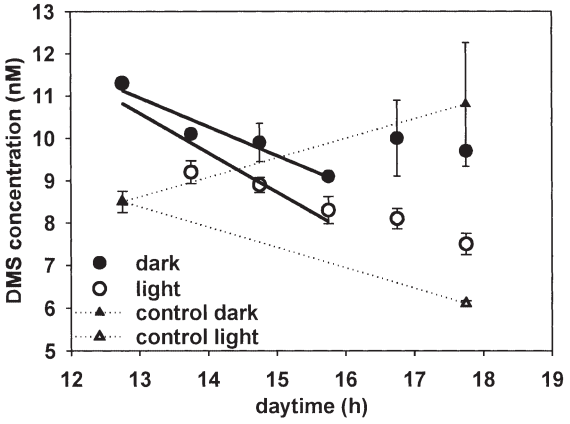

Fig. 5. Time course of the decline of DMS in the dark and under surface solar radiation in 0.8 µm filtered natural seawater, in comparison to the DMS decline in 0.2 µm filtered seawater exposed to solar radiation (control light) indicating photochemical removal. The control dark treatment was 0.2 µm filtered natural seawater kept in the dark by wrapping the flasks in aluminum foil. Symbols are mean of duplicate incubations, bars indicate SD

DISCUSSION

Reduction of the biological DMSP removal by solar surface radiation

In all experiments except one a clear linear decline in DMSP concentration over time was found for the initial phase of incubation in 0.8 µm filtered seawater (Figs 1 & 2). DMSP removal at *in situ* concentrations was significantly reduced in all experiments when exposed to surface solar radiation (Fig. 1). Probably, the enzymes of the bacteria present in the samples

Table 2. Comparison of the biological DMS removal rate in the dark (BR-dark), photochemical DMS removal rates (PR), total DMS removal rates under solar radiation (TR-rad) and biological DMS removal rates under solar radiation (BR-rad). BR and TR were determined in 0.8 µm filtered seawater, PR in 0.2 µm filtered seawater. BR-rad is the difference betweenTR-rad and PR. All rates are given in nmol l^{-1} h^{-1}. For sampling locations see Table 1

Date	Initial DMS conc. (nM)	BR-dark	PR	TR-rad	BR-rad
			(nmol l^{-1} h^{-1})		
10 Jun 1997[a]	8.5	1.10	1.02	1.39	0.37
15 Sep 1996[a]	10.5	0.91	0.64	1.15	0.51
11 Sep 1996[a]	25.0	1.47	1.53	1.90	0.36
5 Aug 1997	34.6	1.16	2.08	2.63	0.55
Mean		1.16	1.32	1.77	0.45
±SD		0.23	0.63	0.65	0.10

[a]Experiments without amendments of DMS

were photochemically degraded by solar radiation (see Müller-Niklas et al. 1995). In some of the DMSP removal experiments, DMSP removal ceased well before the DMSP was completely depleted. This pattern has been observed previously, mostly for unfiltered but also for filtered seawater (Kiene 1996a,b). In our case we used filtered water; therefore algae were excluded. Since no autofluorescent particles were present in our samples, DMSP production by autotrophs can be excluded. Possibly, bacteria containing DMSP and releasing it during the incubation period are responsible for this effect. Exposure to solar radiation might enhance the release, thereby causing the observed decrease in the DMSP removal rate at higher DMSP concentrations in experiment in Fig 1A.

Generally, we calculated the removal rates according to Ledyard & Dacey (1996a) because the linear decline indicates that there are no interfering feedback mechanisms. Data points were used for calculation as long as they showed a linear relationship; however, at least the first 4 to 5 sampling points were used. For the data shown in Fig. 1A, the decline in DMSP was not linear. We therefore calculated the rates for the radiation-exposed incubations according to Kiene (1996b) by determining the first-order rate constant and multiplying it with the initial DMSP concentration. For the dark incubations both ways of calculation resulted in essentially the same rate (0.72 and 0.73 nmol l^{-1} h^{-1}, for first and zero orders, respectively). In general, calculating the DMSP removal rates by applying first-order rate constants resulted in slightly higher initial removal rates (<15%); however, in 2 cases the differences were >60%. The percent inhibition remained rather constant except for the latter 2 cases.

In order to determine the potential DMSP removal rate, we performed experiments with additions of DMSP and followed the decline in DMSP concentrations under surface solar radiation and in the dark. From this kind of experiment the turnover rate can be calculated by multiplying the removal rate with the *in situ* concentration according to Kiene (1996b). Exposure to natural surface solar radiation resulted in significantly reduced DMSP removal rates ranging between 29 and 81% of the DMSP removal in the dark (mean 62.1 ± 14.1%, Table 1); hence the turnover will be affected to the same extent. Absolute turnover rates could not be calculated, as the *in situ* concentrations were not always determined. In the 0.2 µm filtered controls no difference in the decline of DMSP was observed between the radiation-exposed and dark treatments, implying that free DMSP lyase was not affected. However, free DMSP lyase activity in our experiments was generally rather low; therefore a significant difference between light and dark treatments could remain obscure. Scarratt et al. (1999) also found that free DMSP lyase activity accounted for only 2% of total DMSP cleavage. In the only case with higher DMSP lyase activity (10 June 1997, Fig. 5) no difference was detected between solar radiation and dark treatments; however these are too few data to exclude any effect of solar radiation on free DMSP lyase activity. Dissolved DMSP added to autoclaved, natural seawater remained stable under exposure to solar radiation (data not shown). Therefore, photochemical DMSP cleavage did not occur as was previously suggested by Hefu & Kirst (1997).

In the experiments to determine the dependence of the biologically mediated DMSP removal rates on the initial DMSP concentration, the saturating DMSP concentration was significantly lower in the radiation-exposed treatments than in the dark (Fig. 3A). These findings indicate that even if DMSP removal is stimulated by, for example, a sudden release of DMSP by phytoplankton exposed to UV radiation the inhibition will increase with increasing DMSP concentration. There was a remarkable consistency within the treatments collected at a single date, but considerable variability between different sampling dates was observed; one case even showed no saturation at all (Fig. 3B). Despite the high variability among sampling dates the general trend of a significantly lower saturation concentration in radiation-exposed treatments was always observable.

A high spatial and temporal variability of the DMSP removal was also shown by Kiene (1996b), Ledyard & Dacey (1996a,b), Simó & Pedrós-Alió (1999), Scarratt et al. (2000), and Schultes et al. (2000). Kiene (1996b) determined the turnover of DMSP in estuarine and shelf waters and found highly variable turnover rates with no

discernable distinct seasonal pattern. Ledyard & Dacey (1996b) examined turnover, uptake and lyase kinetics of DMSP in coastal waters and also found high spatial and temporal variability, as observed in this study. Scarratt et al. (2000) investigated the kinetics of the potential DMS production from DMSP cleavage in North Atlantic waters and found an inverse exponential relation to chl *a* concentrations. Besides the high short-term variability of rates, Simó & Pedrós-Alió (1999) further found that coupling and decoupling of DMSP consumption, DMS production and DMS consumption occurred on very short time scales within the water body of an eddy. Within a few days, DMS production accounted for 100% to only 6% of the DMSP consumed.

In addition to the high variability in DMSP dynamics reported previously, the present study clearly shows that the reduction in DMSP removal rate upon exposure to surface solar radiation also varies considerably. Variations in the intensity and in the ratios of different wavelength regimes of solar radiation might be a possible explanation for the observed variability, although all our experiments were performed under a cloudless sky. Unfortunately irradiation measurements are not available for all the experiments that were conducted, but the ratios between UV-B, UV-A and PAR from 6 to 8 August 1997 only varied by <5% and the daily integrated radiation over this period also varied by <5% (J. H. Vosjan pers. comm.). On 7 August, the biological removal of DMSP (20.7 nM initial concentration) in radiation-exposed treatments was inhibited by 81% as compared to the removal rate in the dark (Table 1). From the saturation experiment on the 6 and 8 August (triangles and squares, respectively; Fig. 3B), we calculated the removal rates for radiation-exposed and dark treatments for the same concentration by applying an exponential or linear fit to the data obtained for each day (as in the example in Fig. 3A). Inhibition of the removal rates in radiation-exposed treatments accounted for 62 and 51% of the removal in the dark for 6 and 8 August, respectively. Obviously total radiation and the ratios of UV-B to PAR or UV-A were not responsible for the differences observed in the inhibition of the bacteria involved in DMSP removal.

The composition of the bacterial community might be of major importance in determining the variability of DMSP removal. Arrieta et al. (2000) demonstrated that bacterial strains are highly variable in their sensitivity to UV radiation and in their ability to recover from previous UV stress. Additionally, differences in DMSP lyase expression among different members of the bacterial community might enhance the observed variations in biological DMSP removal rates and their reduction due to exposure to solar radiation. On 3 occasions bacterial production as a general activity parameter was determined by the incorporation of [^{3}H] leucine (according to Kirchman et al. 1985) for the experiments performed in the Mediterranean Sea. In Table 3 the bacterial production and DMSP removal in the dark are listed; in addition, the percent inhibition after exposure to surface solar radiation is given. From our few experiments we conclude that absolute DMSP removal was not coupled to the amount of bacterial production, which is in contrast to findings of Kiene & Linn (2000), who report a close relation between DMSP turnover and bacterial production in oceanic and shelf regions of the Gulf of Mexico. Furthermore, the degree of inhibition differed between bacterial production and DMSP removal (Table 3), indicating that these 2 metabolic processes were affected differently by solar radiation in the Mediterranean Sea.

Table 3. Bacterial production (BSP) and DMSP removal by bacteria (BR) in dark and radiation-exposed treatments determined in 0.8 µm filtered natural seawater. BSP was measured by the incorporation of tritiated leucine ([^{3}H] leucine) for 30 min immediately after exposure to solar radiation. Samples were taken from the northern Adriatic Sea about 5 km off Ancona, Italy

Date	BSP-dark (µg C l^{-1} d^{-1})	BSP-rad in % of BSP-dark	BR-dark (nmol l^{-1} h^{-1})	BR-rad in % of BR-dark
6 Sep 1996	0.51	41	1.4	46
11 Sep 1996	0.47	13	2.11	48
15 Sep 1996	0.73	19	1.40	25

Influence of different radiation ranges on biological DMSP removal rates

Radiation-induced inhibition in the metabolic activity and damage of organisms in aquatic systems was previously thought to be largely mediated by UV-B radiation. There is evidence accumulating now, however, that UV-A contributes the same or even a larger extent to the inhibition of activity (Bailey et al. 1983, Sieracki & Sieburth 1986, Herndl et al. 1997, Sommaruga et al. 1997, Visser et al. 1999). Our experiments reveal that UV-B radiation contributes, on average, ~15% to the observed total reduction of DMSP removal rate, whereas UV-A and PAR each contribute ~42% to the total inhibition (Fig. 4). In 2 experiments, PAR radiation caused the main inhibitory effect; in 2 other experiments UV-A was responsible for most of the inhibition (Fig. 4). Sieracki & Sieburth (1986) showed that UV-A radiation was mainly responsible for the observed growth delay of marine bacteria, whereas PAR did not cause any inhibition. Other authors could also attribute a small inhibitory effect on bac-

terial activity to PAR radiation (Bailey et al. 1983, Sommaruga et al. 1997, Visser et al. 1999). In a study performed in the Gulf of Mexico, Aas et al. (1996) showed that there was no consistent response pattern in bacterial activity to different wavelength ranges, consistent with our results on DMSP removal.

The fact that longer wavelengths (UV-A and PAR) are mainly responsible for the inhibition of biological processes implies that removal rates of DMSP can be affected to considerable depths in the oceanic water column. Obernosterer et al. (2001) found that biologically and photochemically effective UV radiation penetrates to depths of ~60 m in the open subtropical Atlantic, which comprises about half of the euphotic layer (Obernosterer et al. 2001). As turnover and removal rates of DMSP have always been determined in samples incubated in the dark (Kiene 1996b, Ledyard & Dacey 1996a,b), the removal rates of DMSP reported in previous studies have to be considered as maximum estimates. The actual biological DMSP removal rates in the upper layers of the ocean are probably lower due to partial inhibition of DMSP removal by solar radiation.

Biological versus photochemical DMS removal

The experiments conducted to compare biological with photochemical DMS removal clearly show that biological removal of DMS is inhibited, on average, by 59.6 ± 14.0% (Table 2). Photochemical removal rates were determined by assuming pseudo first-order kinetics (Kieber et al. 1996, Brugger et al. 1998). Bacterial DMS removal under solar radiation is substantially lower than photochemical DMS removal when exposed to surface radiation levels (Table 2). Kieber et al. (1996) investigated the relation between photochemical and biological DMS removal and atmospheric ventilation but incubated the treatments to estimate the biological DMS removal in the dark. The authors compared the biological DMS removal to photochemical removal and loss via atmospheric ventilation in different layers of the euphotic zone. In 5 out of 8 experiments, biological removal exceeded the photochemical removal in the 0 to 1 and 0 to 20 m surface layers (Kieber et al. 1996). The present study suggests, however, that inhibition of the removal of DMS by bacteria and the photochemical removal might be high in the first few meters during daytime. Furthermore, the total DMS removal rate under surface solar radiation (biological and photochemical) measured in different environments always exceeded the biological removal rate in the dark, indicating that in the first few meters DMS concentrations decline at a higher rate during the day than in the night. In deeper layers, where solar radiation is increasingly attenuated, the photochemical effect will decline exponentially (Kieber et al. 1996) and the biological removal will approach rates obtained in dark incubation. Simó & Pedrós-Alió (1999) estimated the photochemical DMS removal by subtracting the calculated DMS concentration (from the DMSP and DMS consumption and the DMS production rates) from the measured *in situ* DMS concentration. Again these rates were determined in dark incubations; therefore the photochemical DMS removal might be underestimated for the near-surface layers.

We did not distinguish between DMSP cleavage and demethylation. If we assume, in a rough estimate, that bacterial cleavage and demethylation processes are affected by solar radiation at approximately the same rate, on average, about 60% less DMS would evolve from DMSP cleavage in our radiation-exposed treatments (Table 1). The lower amount of DMS ready for consumption in radiation exposed bottles increases the differences from the dark treatments; therefore, the reduction of the biological DMS removal would be underestimated by a factor of approximately 1.6 (derived from the calculation of 100/60).

The impact of solar radiation on the bacterial removal of DMSP and DMS has received surprisingly little attention despite intense research on the effect of UV radiation on organisms. In our study, surface radiation intensities were chosen, which implies that our results represent the upper limit of what can be expected in nature.

CONCLUSIONS

In our study we demonstrated that the biological removal of both DMS and DMSP is reduced by ~60% of the dark removal rates due to natural surface solar radiation. High spatial and temporal variability of the removal rates in the dark, but also their sensitivity to solar radiation, was observed. The responsible wavelength ranges for inhibiting DMS and DMSP removal are mainly UV-A and PAR, while UV-B contributes only ~15% to the total radiation-mediated inhibition. Consequently, DMS and DMSP turnover is considerably reduced by solar radiation in the upper mixed layer of the oceanic water column, possibly down to a depth of ~60 m. Photochemical DMS removal is higher than the biological DMS removal under solar radiation in the near-surface water layers.

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