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Effects of reduced ultraviolet radiation on aqueous concentrations of dimethylsulfoniopropionate and dimethylsulfide during a microcosm study in the Lower St. Lawrence Estuary

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ABSTRACT: In August 1994, microcosm experiments were conducted with the natural phytoplankton community from the Lower St. Lawrence Estuary, Canada, in order to determine the influence of ultraviolet radiation (UVR) on the production of dimethylsulfoniopropionate (DMSP) and dimethylsulfide (DMS). The planktonic community was exposed for 42 h to 2 different light regimes: natural light conditions and UVR reduced by 95% using UF3 filters. Throughout the experiments, flagellates dominated the algal community. During the first day, the production rate of DMS under reduced UVR was 4 times greater than under natural light conditions, suggesting a decrease in the loss rate of DMS under reduced UVR. There were no significant effects of the light regimes on particulate DMSP ($DMSP_p$), dissolved DMSP ($DMSP_d$), $DMSP_p$/chlorophyll *a* and $DMSP_p$/total algal cell number ratios during the first 24 h. During the second day, $DMSP_p$ concentrations, $DMSP_p$/chlorophyll *a* and $DMSP_p$/total algal cell number ratios increased significantly under reduced UVR whereas these variables decreased in the microcosms exposed to natural light conditions. These results suggest that the reduction of UVR favoured the accumulation of DMSP in algal cells. We conclude that the reduction of UVR affects the DMSP/DMS dynamics in seawater at 2 levels depending on the time frame considered: on a short-term basis (<24 h), it increases the DMS concentration, probably by decreasing its removal; on a long-term basis (>24 h), it increases algal DMSP content, probably by stimulating the synthesis and/or by inhibiting the excretion of DMSP.

KEY WORDS: Dimethylsulfide · Dimethylsulfoniopropionate · Phytoplankton · Ultraviolet radiation · Photooxidation · Bacteria · Microcosms

INTRODUCTION

In the remote atmosphere, marine emissions of dimethylsulfide (DMS) play an important climatic role. They provide the major part of sulfate aerosols and cloud condensation nuclei (CCN) that increase the absorption and scattering of solar radiation (Charlson et al. 1987, Hegg et al. 1991, Lawrence 1993). DMS is produced from dimethylsulfoniopropionate (DMSP), an osmoregulatory molecule present in many microalgae (Challenger & Simpson 1948, Reed 1983, Vairavamurthy et al. 1985, Dickson & Kirst 1986, 1987a, b). DMSP is released in seawater during the senescent phase of blooms via cell autolysis (Nguyen et al. 1988,

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Turner et al. 1988, Matrai & Keller 1993, 1994) and zooplankton grazing (Dacey & Wakeham 1986, Belviso et al. 1990, 1993, Leck et al. 1990, Levasseur et al. 1994b, Cantin et al. 1996). Dissolved DMSP may then be converted into DMS by bacteria (Kiene & Service 1991, Kiene 1992, Wolfe & Kiene 1993, Wolfe et al. 1994). Bacterial degradation, photooxidation and sea-air ventilation represent the 3 major sinks for DMS (Brimblecombe & Shooter 1986, Suylen et al. 1986, Zeyer et al. 1987, Gibson et al. 1990, Kiene & Bates 1990, Malin et al. 1993, Kieber et al. 1996).

Results from recent studies indicate that DMSP synthesis and DMS production may be affected by light intensity. In laboratory studies, Karsten et al. (1990, 1992) demonstrated that DMSP quotas of green macroalgae from polar and temperate regions increase with light intensity. In the north-east tropical Atlantic Ocean, Belviso et al. (1993) found a relationship between light and DMSP accumulation in nanophytoplankton (most likely prymnesiophytes). Levasseur et al. (1994a) also attributed the increase in intracellular DMSP of ice microalgae to an increase in light intensity. In batch cultures, Vetter & Sharp (1993) showed that increase in light intensity stimulates DMS production by the diatom *Skeletonema costatum*.

Changes in light spectral characteristics following the recent increase in ultraviolet radiation (UVR) caused by stratospheric ozone depletion (Watson 1988, Anderson et al. 1991, Smith et al. 1992, Kerr & McElroy 1993) may also affect the dynamics of DMSP/DMS. From water collected on the coast of the North Sea, Brimblecombe & Shooter (1986) demonstrated that an important part of marine DMS can be rapidly photooxidized by natural sunlight. In the Bellingshausen Sea, Antarctica, surface DMS concentrations decreased during peak daylight periods, possibly due to photooxidation (Crocker et al. 1995). Recently, Kieber et al. (1996) showed that, in the oligotrophic equatorial Pacific Ocean, direct photolysis by short wavelengths (<460 nm: blue and UV light) accounts for 7 to 40% of the DMS sink in the surface mixed layer (0 to 60 m). Changes in UVR may also indirectly affect DMS production via their influence on the physiology and ecology of marine organisms, and their production of DMSP. Several works have shown that UVR influences the community composition of phytoplankton (Bidigare 1989, Karentz et al. 1991, Cullen et al. 1992, Bothwell et al. 1994). Since DMSP quotas are highly species-specific (Keller et al. 1989a, b, Keller 1991), these UVR-induced shifts in phytoplankton community may change DMSP production rates. UVR can also affect bacteria (Herndl et al. 1993, Lindell et al. 1995, Müller-Niklas et al. 1995) and zooplankton (Damkaer & Dey 1983, Dey et al. 1988), 2 additional important components of the marine DMS cycle.

The goal of this study was to determine the influence of the natural levels of UVR on DMSP and DMS production by a natural coastal plankton community. To achieve this goal, seawater collected in the Lower St. Lawrence Estuary, Canada, was transported to microcosms and exposed to natural and reduced levels of UV radiation.

MATERIAL AND METHODS

Sampling and study sites. Microcosm experiments were conducted from 3 to 4 August 1994 at the Pointe-au-Père field station of University of Quebec on the south shore of the Lower St. Lawrence Estuary (LSLE) (Fig. 1). Four plastic enclosures of 1.5 m depth and 200 l volume were filled on 3 August at 01:00 h with LSLE seawater pumped from the pier of the Maurice Lamontagne Institute (68° 20' W; 48° 35' N) (Fig. 1). Before filling the enclosures, the seawater was filtered onto a Nytex filter (202 µm) to remove mesozooplankton. The microcosms were placed in an enclosure cooled with seawater pumped from 10 m depth in front of the shore station in order to simulate *in situ* temperature conditions. Water temperature in the different microcosms was measured every 6 h. Immediately after their filling, 2 microcosms were covered with 4.5 mm thick neutral Plexiglas filters that cut 10% of 3 bandwidths of light, PAR (photosynthetically available radiation, 400 to 700 nm), UV-A (320 to 400 nm) and UV-B (280 to 320 nm), while the 2 others were covered with 4.5 mm thick UF3 filters (Rohm and Haas Company, UK) which cut 10% of incident PAR, 95% of incident UV-A and 98% of in-

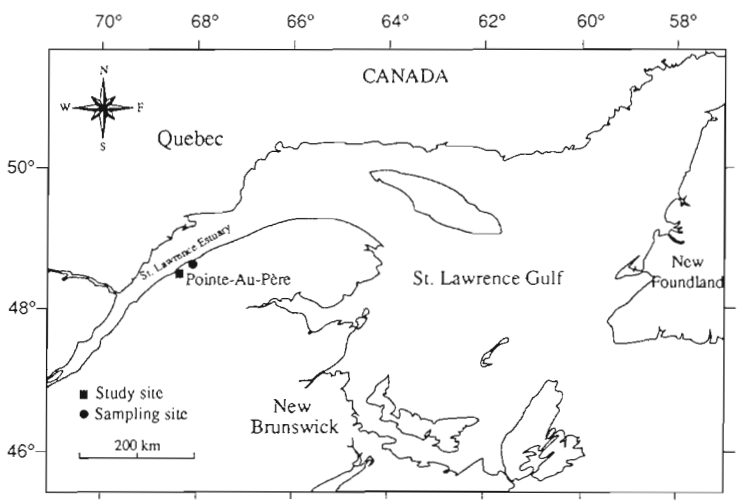

Fig. 1. Location of study and sampling sites

cident UV-B. Incident irradiance (UV and PAR, 280 to 700 nm) was measured with a IL 1700 radiometer (Inter National Light Company) equipped with detectors to measure PAR, UV-A and UV-B. Each light sensor was calibrated at the National Institute of Standards and Technology, Newburyport, MA, USA.

Water samples were collected every 6 h. Before sampling, the microcosms contents were mixed delicately with a paddle, then 10 l of water was collected from each enclosure and temporarily kept in a black bottle. For each sample, we determined in duplicate the concentrations of nutrients (nitrate + nitrite and phosphate), particulate DMSP ($DMSP_p$) and dissolved DMSP ($DMSP_d$), free DMS and chlorophyll *a* (chl *a*) and phytoplankton, microzooplankton and bacterial cell numbers.

Laboratory analyses. For nutrient determination (nitrate + nitrite and phosphate), a 50 ml subsample was filtered through a Whatman GF/F glass-fiber filter and the filtrate was frozen at −20°C for later analysis using a Technicon Auto Analyzer (Strickland & Parsons 1972).

For $DMSP_p$ determination, two 250 ml subsamples were filtered on Whatman GF/F filters (pressure <178 mm Hg). The filters were then placed in serum bottles filled with 18.5 ml of distilled water and 0.8 ml of 5 mol l^{-1} KOH to convert DMSP into DMS (Challenger & Simpson 1948). For $DMSP_d$ + free DMS determination, two 50 ml serum bottles were filled with 46 ml of the filtrate and 2 ml of 5 mol l^{-1} KOH. For free DMS determination, 2 serum bottles were filled with 115 ml of the filtrate and 5 ml of distilled water. All serum bottles were immediately sealed with a Teflon-faced serum cap and kept in the dark at 4°C until analysis. DMS samples were analyzed less than 2 h after the sampling while both DMSP samples were frozen at −20°C and analyzed during the next week. In all cases (free DMS, $DMSP_p$ and $DMSP_d$ + free DMS), DMS was measured on a Varian 3400 gas chromatograph equipped with a flame photometric detector and a Chromosil 330 Teflon column (Supelco) according to a modified method of Leck & Bågander (1988). Samples were sparged with N_2 gas (30 ml min^{-1}) in a heated bubbling chamber (70°C). The extracted gases were then cryotrapped in a Teflon loop submerged in liquid nitrogen. The Teflon loop was subsequently heated (70°C), releasing the extracted gas onto the GC column.

For chlorophyll *a* determination, 1000 ml subsamples were filtered through Whatman GF/F filters, which were subsequently frozen in liquid nitrogen. Each filter was ground in 4 ml of a solution of 98% methanol and 2% ammonium acetate, and the extract centrifuged at 3000 rpm for 5 min. The supernatent was filtered on a Gelman filter (Acrodisc CR PTFE syringe, 0.2 µm) and the filtrate was analyzed using reversed-phase HPLC (High Performance Liquid Chromatography) (Wright et al. 1991).

Subsamples were fixed with the acidic Lugol's solution (Throndsen 1978) for the identification and counting of phytoplankton and microzooplankton with an inverted microscope (Utermöhl 1931). For direct bacterial counts, subsamples (10 ml) were fixed by addition of 1 ml of formaldehyde (final concentration 3.7%) and held at 4°C. The bacterial cells were stained for 1 h at 4°C with DAPI (4',6-diamidino-2-phenylindole) (Sigma) at final concentration of 2.5 µg ml^{-1} (Porter & Feig 1980). Then, they were filtered onto a Nuclepore membrane filter (0.2 µm; 47 mm; black filter) and counted using a Leitz epifluorescence microscope equipped with a 100 W mercury lamp and filters to accommodate excitation and emission wavelengths for DAPI.

Statistical analyses. Before undertaking the different parametric statistical tests, the normality of distribution and the homogeneity of variance were verified with the test of conformity of Kolmogorov-Smirnov (Zar 1984) and the test of Hartley (test of the F_{max}) (Winer 1971), respectively. No transformation was required since the normality and the homoscedacity were respected.

The analysis of variance (ANOVA) with repeated measures was used for the comparison of averages (Zar 1984). The null hypothesis (H_0) stipulates that averages of a measured variable are equal between both light regimes. The ANOVA with repeated measures does not test the interaction effects between the sampling time and the UVR treatment (Zar 1984). The ANOVA was completed by *a posteriori* contrast test, the test of Fisher's LSD (Least Significant Difference) (Zar 1984). This test allows the identification of averages that are significantly different between the 2 experimental conditions.

Simple linear regression (Zar 1984) was used to estimate the relationship between biogenic sulfur ($DMSP_p$, $DMSP_d$ and DMS) and sampling time under the natural and reduced light regimes during the first 24 h of the experiment.

Spearman's rank correlations (Zar 1984) were also used to determine the correlation between the biogenic sulfur pools, the different biological variables and the sampling time under both light regimes.

RESULTS

Variations of irradiance, water temperature and nutrients

Temporal variations of light intensities under neutral and UF3 filters are presented in Fig. 2. During the first day, microcosms covered with neutral filters (microcosms

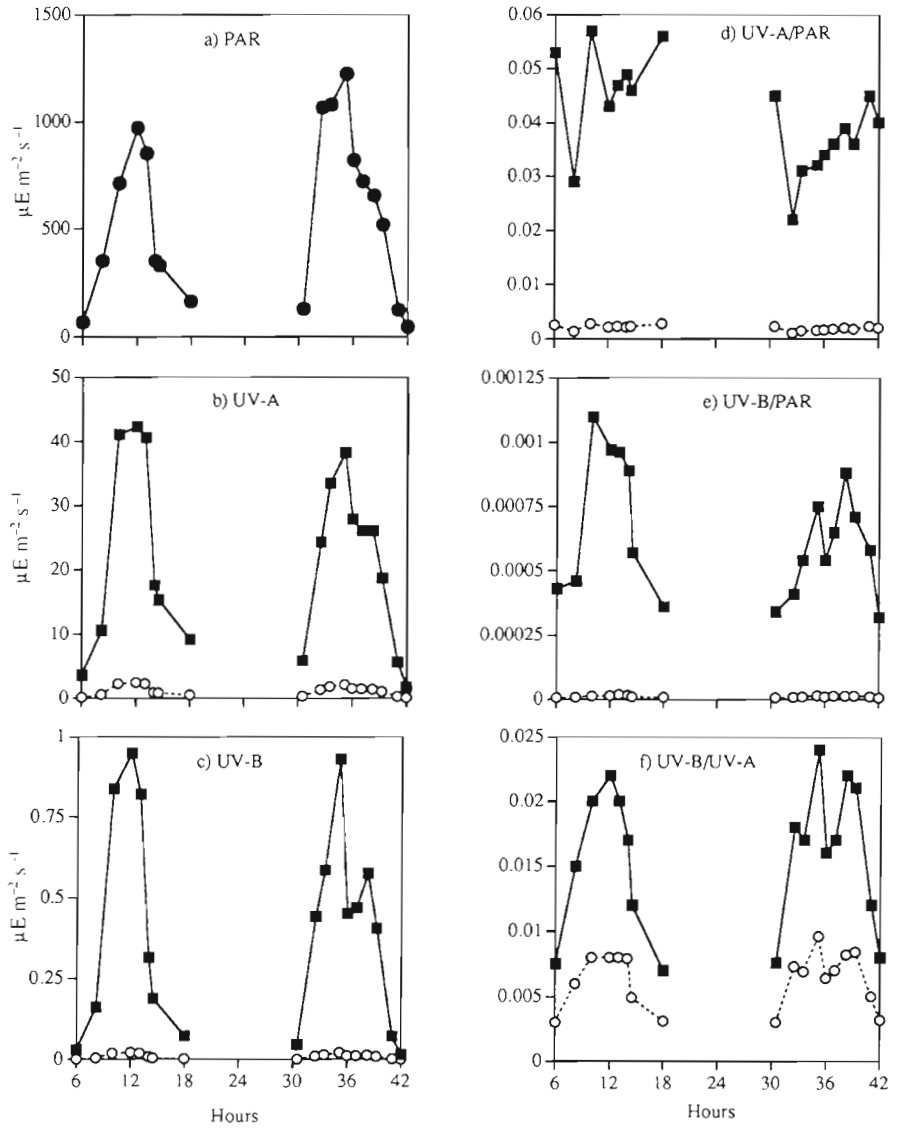

Fig. 2. Temporal variations of (a) PAR (photosynthetically available radiation; 400 to 700 nm), (b) UV-A (320 to 400 nm), (c) UV-B (280 to 320 nm), (d) UV-A/PAR ratio, (e) UV-B/PAR ratio and (f) UV-B/UV-A ratio under neutral density (●, ■) and UF3 (○) filters. In (a), PAR is the same under both light regimes

exposed to natural light conditions) received maximal PAR, UV-A and UV-B intensities of 975, 42.50 and 0.95 µE m^{-2} s^{-1}, respectively (Fig. 2a, b, c). During this day, the maximum value of UV-A/PAR and UV-B/PAR ratios, obtained under natural light conditions, was 0.057 and 0.001, respectively (Fig 2d, e). These maximum values were observed at 10:00 h. On the other hand, the maximum value of UV-B/UV-A ratio (0.022) was obtained at 12:00 h (Fig. 2f). During the second day, maximum intensities of PAR (1224 µE m^{-2} s^{-2}), UV-A (38.50 µE m^{-2} s^{-1}) and UV-B (0.93 µE m^{-2} s^{-1}) under neutral filters were measured at 11:10 h (Fig. 2a, b, c). At this time, the UV-B/UV-A ratio was also maximum (0.024) under the natural light regime (Fig. 2f). Under the same light conditions, the maximum value of the UV-A/PAR (0.045) and UV-B/PAR (0.0009) ratios was reached at 6:30 and at 14:15 h, respectively (Fig. 2d, e).

UF3 filters cut 10% of the incident PAR but 95 and 98% of incident UV-A and UV-B, respectively (Fig. 2a, b, c). During the 2 days of the experiment, UV-A and UV-B intensities, under UF3 filters, did not exceed 2.35 and 0.02 µE m^{-2} s^{-1}, respectively (Fig. 2b, c).

The total incident irradiance (UV and PAR) received by the microcosms exposed to the natural light regime during the first and the second day was 23.7 E m^{-2} d^{-1} (4.8 MJ m^{-2} d^{-1}) and 34.0 E m^{-2} d^{-1} (6.9 MJ m^{-2} d^{-1}), respectively. Under reduced UVR, the total incident irradiance was 22.8 E m^{-2} d^{-1} (4.5 MJ m^{-2} d^{-1}) and 33.0 E m^{-2} d^{-1} (6.6 MJ m^{-2} d^{-1}) during the first and the second day, respectively.

Temporal variations of the water temperature and nutrients concentrations (nitrate + nitrite and phosphate) are presented in Fig. 3. Water temperature increased from 11.3 to 15.5°C in all microcosms during

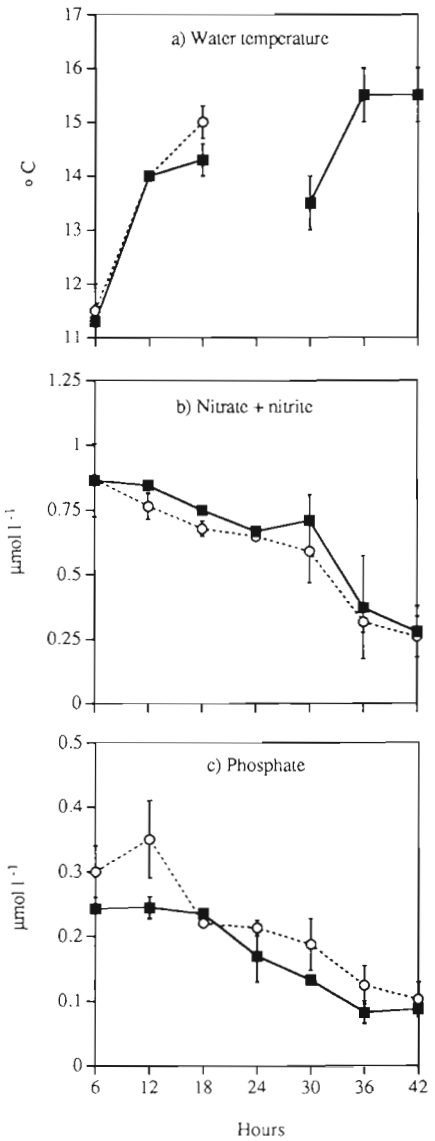

Fig. 3. Temporal variations of (a) water temperature, (b) nitrate + nitrite concentration and (c) phosphate concentration under natural (■) and reduced (○) UVR (average ± standard deviation of duplicates)

the 2 days of the experiment (Fig. 3a). An ANOVA analysis with repeated measures showed, however, no significant difference in mean water temperature between both light regimes (Table 1). Concentrations in nitrate + nitrite and in phosphate were, respectively, 0.86 and 0.27 µmol l^{-1} at the beginning of the sampling period and decreased to values of 0.30 µmol l^{-1} for nitrate + nitrite and 0.10 µmol l^{-1} for phosphate at the end of the experiment (Fig. 3b, c). Concentrations of nitrate + nitrite and of phosphate were similar in microcosms exposed to both light conditions (Table 1). Hence, changes in biological and chemical variables measured between both treatments (see below) cannot be explained from changes in water temperature or in ambient nutrients.

Table 1 Analyses of variance (ANOVA) with repeated measures concerning the effects of sampling time and UVR treatment on water temperature, nutrients (nitrate + nitrite and phosphate), chlorophyll *a*, total phytoplankton, flagellate, dinoflagellate, diatom and *Cryptomonas* spp. abundances, bacterial and ciliate abundances, $DMSP_p$, $DMSP_p$ per chlorophyll *a* and $DMSP_p$ per total algal cell number, $DMSP_d$ and DMS. *Significant at 5%, **significant at 1% and ***significant at 0.1%. ns: non significant

Variables	Sources of variation	
	Sampling time	UVR treatment
Water temperature	***	ns
Nitrate + nitrite	***	ns
Phosphate	**	ns
Chlorophyll *a*	***	ns
Total phytoplankton	***	ns
Flagellates	***	ns
Dinoflagellates	*	ns
Diatoms	*	ns
Cryptomonas spp.	***	ns
Bacteria	*	ns
Ciliates	*	ns
$DMSP_p$	***	**
$DMSP_p$/algal cell	*	*
$DMSP_p$/chlorophyll *a*	*	*
$DMSP_d$	**	**
DMS	***	***

Variations in phytoplankton biomass, abundance and species composition

Temporal variations in chlorophyll *a*, total algal cell number and abundance of the different taxa (flagellates, dinoflagellates and diatoms) are presented in Fig. 4. In the 4 microcosms, chlorophyll *a* concentration and total algal cell number increased during the experiment from 1.35 to 3.75 µg l^{-1} and from 0.60×10^6 to 1.90×10^6 cells l^{-1} (Fig. 4a, b). Flagellate abundance increased from 0.30×10^6 to 1.30×10^6 cells l^{-1} (Fig. 4c). This group was dominated by *Cryptomonas* spp., which increased from 0.13×10^6 to 0.55×10^6 cells l^{-1} at the end of the experiment (Fig. 4d). The abundance of dinoflagellates increased from 0.17×10^6 to 0.50×10^6 cells l^{-1} (Fig. 4e). This group was dominated by *Katodynium* spp. Diatoms, which were dominated by *Thalassiosira* spp., increased from 0.10×10^6 to 0.23×10^6 cells l^{-1} (Fig. 4f). Abundances of the different phytoplankton groups (flagellates, dinoflagellates and diatoms) were not significantly affected by reduced UVR (Table 1). There was no important change in the species composition of the phytoplankton assemblage during the experiment in either treatment. Flagellates

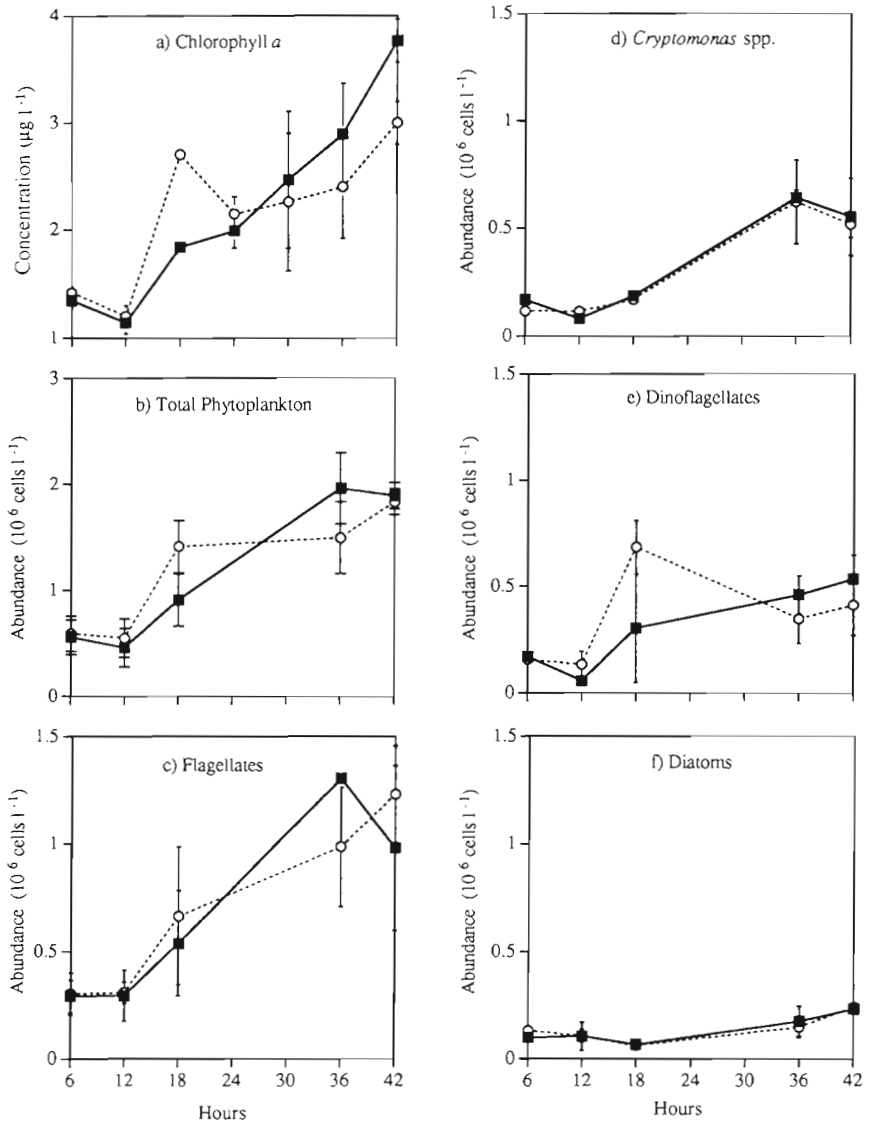

Fig. 4. Temporal variations of (a) chlorophyll *a* concentration, (b) total phytoplankton abundance, (c) flagellate abundance, (d) *Cryptomonas* spp. abundance, (e) dinoflagellate abundance and (f) diatom abundance under natural (■) and reduced (○) UVR (average ± standard deviation of duplicates)

dominated the phytoplankton community, representing approximately 60% of the total algal cell number. Dinoflagellates and diatoms represented 20 to 34% and 6 to 20% of the total algal abundance, respectively.

Variations in $DMSP_p$, $DMSP_d$ and DMS

Temporal variations in $DMSP_p$, $DMSP_d$ and free DMS are presented in Fig. 5. At the beginning of the sampling period, $DMSP_p$ concentrations were approximately 109 nmol l^{-1} in the 4 microcosms (Fig. 5a). During the first day, $DMSP_p$ concentrations increased similarly under the natural and reduced light regimes at rates of 9.30 and 9.90 nmol l^{-1} h^{-1}, respectively (Fig. 5a, Table 2). After 24 h, $DMSP_p$ concentrations measured under reduced UVR began to increase as compared to those measured under the natural light regime (Fig. 5a). Under natural light conditions, $DMSP_p$ concentrations remained relatively stable around 285 nmol l^{-1} between 24 and 36 h and then decreased to 220 nmol l^{-1} at the end of the experiment (Fig. 5a). On the other hand, $DMSP_p$ levels measured under reduced UVR continued to increase during the second day (Fig. 5a). At 42 h, $DMSP_p$ concentrations measured under reduced UVR reached a value 2.5 times greater than under the natural light regime (Fig. 5a). Under both light conditions, $DMSP_p$ concentration was correlated with chlorophyll *a* concentration and flagellate abundance (Tables 3 & 4). Under the reduced UVR regime, $DMSP_p$ concentration was also correlated with the abundance of the flagellate *Cryptomonas* spp. (Table 4).

Table 2. Least squares linear regression statistics between biogenic sulfur ($DMSP_p$, $DMSP_d$ and DMS) and sampling time under the natural and reduced light regimes during the first 24 h of the experiment. For the regressions, only the 4 first points of Fig. 5a, b, c are used. $^{\bullet}0.01 < p \leq 0.05$, $^{\bullet\bullet}0.001 < p \leq 0.01$, $^{\bullet\bullet\bullet}p \leq 0.001$

	Slope (nmol l^{-1} h^{-1})		Intercept (nmol l^{-1})		Correlation coefficient	
	Natural UVR	Reduced UVR	Natural UVR	Reduced UVR	Natural UVR	Reduced UVR
$DMSP_p$ and sampling time	9.30	9.90	60	71	$0.94^{\bullet\bullet}$	$0.96^{\bullet\bullet\bullet}$
$DMSP_d$ and sampling time	1.30	1.25	46	40	$0.78^{\bullet}$	$0.72^{\bullet}$
DMS and sampling time	0.15	0.58	13	11	$0.95^{\bullet\bullet\bullet}$	$0.99^{\bullet\bullet\bullet}$

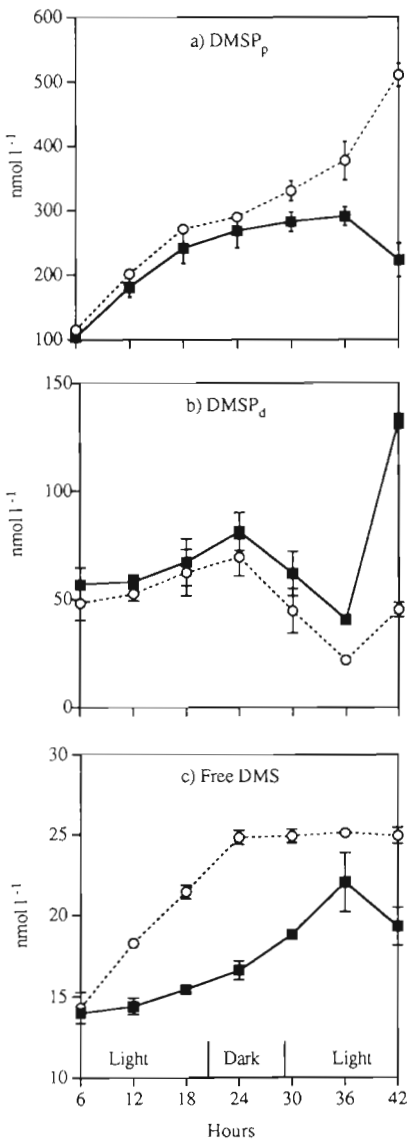

Fig. 5. Temporal variations of (a) particulate DMSP ($DMSP_p$), (b) dissolved DMSP ($DMSP_d$) and (c) free DMS under natural (■) and reduced (o) UVR (average ± standard deviation of duplicates)

Table 3. Spearman's rank coefficients of correlation between biogenic sulfur, different biological variables and sampling time under the natural light regime for the whole duration of the experiment ($DMSP_p$, $DMSP_d$, DMS, chl *a* and bacterial abundance, n = 14; for the other variables, n = 10). $^{\bullet}0.01 < p \leq 0.05$, $^{\bullet\bullet}0.001 < p \leq 0.01$, $^{\bullet\bullet\bullet}p \leq 0.001$

Natural UVR	$DMSP_p$	$DMSP_d$	DMS
$DMSP_d$	−0.068		
DMS	**0.758**$^{\bullet\bullet}$	−0.024	
Chl *a*	**0.547**$^{\bullet}$	0.236	**0.842**$^{\bullet\bullet\bullet}$
Total phytoplankton	**0.709**$^{\bullet}$	−0.097	**0.709**$^{\bullet}$
Flagellates	**0.806**$^{\bullet\bullet}$	−0.353	**0.806**$^{\bullet\bullet}$
Dinoflagellates	0.467	0.347	0.636
Diatoms	0.030	0.347	0.030
Cryptomonas spp.	0.632	0.073	**0.806**$^{\bullet\bullet}$
Katodynium spp.	0.600	0.226	0.644
Thalassiosira spp.	0.273	0.122	0.624
Bacteria	−0.246	0.582	−0.246
Ciliates	−0.116	0.086	0.226
Sampling time	**0.585**$^{\bullet}$	0.195	**0.930**$^{\bullet\bullet\bullet}$

Table 4. Spearman's rank coefficients of correlation between biogenic sulfur, different biological variables and sampling time under the reduced UVR regime for the whole duration of the experiment ($DMSP_p$, $DMSP_d$, DMS, chl *a* and bacterial abundance, n = 14; for the other variables, n = 10). $^{\bullet}0.01 < p \leq 0.05$, $^{\bullet\bullet}0.001 < p \leq 0.01$, $^{\bullet\bullet\bullet}p \leq 0.001$

Reduced UVR	$DMSP_p$	$DMSP_d$	DMS
$DMSP_d$	−0.464		
DMS	**0.869**$^{\bullet\bullet\bullet}$	−0.337	
Chl *a*	**0.757**$^{\bullet\bullet}$	−0.101	**0.693**$^{\bullet\bullet}$
Total phytoplankton	**0.806**$^{\bullet\bullet}$	−0.370	**0.796**$^{\bullet\bullet}$
Flagellates	**0.879**$^{\bullet\bullet}$	−0.382	**0.790**$^{\bullet}$
Dinoflagellates	0.644	−0.055	0.644
Diatoms	0.430	−0.491	0.395
Cryptomonas spp.	**0.794**$^{\bullet\bullet}$	−0.382	**0.833**$^{\bullet\bullet}$
Katodynium spp.	0.588	−0.055	0.644
Thalassiosira spp.	0.576	−0.685$^{\bullet}$	0.657$^{\bullet}$
Bacteria	0.206	0.287	0.114
Ciliates	0.345	−0.370	0.438
Sampling time	**0.983**$^{\bullet\bullet\bullet}$	0.416	**0.847**$^{\bullet\bullet}$

$DMSP_d$ concentrations measured under natural and reduced light regimes increased during the first day at similar rates of 1.30 and 1.25 nmol l^{-1} h^{-1}, respectively (Fig 5b, Table 2). During the second day, $DMSP_d$ varied similarly under both light regimes up to the last 6 h of experiment (Fig. 5b). At the end of the experiment, $DMSP_d$ concentrations in the microcosms exposed to the natural light increased by almost a factor of 3, reaching a value of 130 nmol l^{-1} (Fig. 5b). During the same period, $DMSP_d$ only reached 40 nmol l^{-1} under reduced UVR (Fig. 5b).

In contrast to $DMSP_p$ and $DMSP_d$, DMS concentrations measured under reduced UVR increased 4 times more rapidly (0.58 nmol l^{-1} h^{-1}) over the first 24 h than those measured under the natural light regime (0.15 nmol l^{-1} h^{-1}) (Fig. 5c, Table 2). During the second day, DMS levels in the microcosms exposed to the natural light continued to increase until 36 h, then decreased during the last 6 h of the experiment (Fig 5c). Under reduced UVR, DMS concentrations stabilized around 25 nmol l^{-1}, but always remained higher than those measured under the natural light regime (Fig. 5c). In all microcosms, the concentration of DMS was strongly correlated with the chlorophyll *a* concentration and the abundances of flagellates and *Cryptomonas* spp. (Tables 3 & 4).

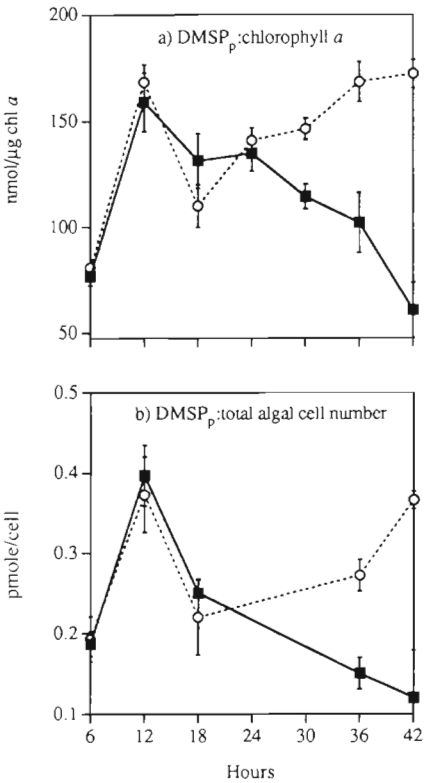

Fig. 6. Temporal variations of (a) $DMSP_p$ per chlorophyll *a* and (b) $DMSP_p$ per total algal cell number under natural (■) and reduced (○) UVR (average ± standard deviation of duplicates)

Variations in $DMSP_p$/chlorophyll *a* and $DMSP_p$/total algal cell number ratios

Fig. 6 presents the temporal variations of $DMSP_p$/chl *a* and $DMSP_p$/total algal cell number ratios. Under natural light regime, these 2 ratios increased during the first 6 h, then decreased gradually from 160 to 60 nmol per µg chl *a* and from 0.40 to 0.11 pmol per algal cell number, respectively (Fig. 6a, b). $DMSP_p$/chl *a* and $DMSP_p$/total algal cell number ratios were significantly influenced by reduced UVR (Table 1). The 2 ratios evolved similarly under both light conditions during the first day (Fig. 6a, b). After 24 h, $DMSP_p$/chl *a* and $DMSP_p$/total algal cell number ratios increased from 135 to 172 nmol per µg chl *a* and 0.21 to 0.38 pmol per algal cell, respectively, under reduced UVR (Fig. 6a, b).

Variations in bacterial and ciliate abundances

Fig. 7 presents the temporal changes in bacterial and ciliated protozoan (the dominant group of zooplankton) abundances. Bacterial number under both treatments varied between 1.25×10^9 and 2.40×10^9 cells l^{-1} (Fig. 7a). The bacterial abundance was maximum for each day at 18:00 h (18 and 42 h) (Fig. 7a). The reduced UVR had no significant effect on the bacterial abundance (Table 1). During the experiment, ciliates numbers under natural light and reduced UVR regimes varied between 3×10^3 and 9×10^3 cells l^{-1} (Fig. 7b). The ciliate abundance was not influenced by reduced UVR (Table 1).

DISCUSSION

Our experiments were conducted under typical summer light conditions with a clear sky in the study area. Incident UV-B varied between 0.02 and 0.95 µE m^{-2} s^{-1} and the UV-B/PAR ratio varied from 0.0003 to 0.00115. These values are similar to that of 0.2 to 1 µE m^{-2} s^{-1} and 0.0005 to 0.0008 obtained by Ferreyra (1995) on the south shore of the Lower St. Lawrence Estuary in August 1993. However, the incident UV-B and UV-B/PAR ratio at our sampling site were much smaller than values of 0.01 to 10 µE m^{-2} s^{-1} and 0.002 to 0.008 observed by Bothwell et al. (1993) at South Thompson River in British Colombia at a similar latitude (50° 49' N). Despite the lower UVR prevailing during our experiment, direct effects of UVR diminution were observed on the net production of DMS and on the DMSP cellular contents of phytoplankton.

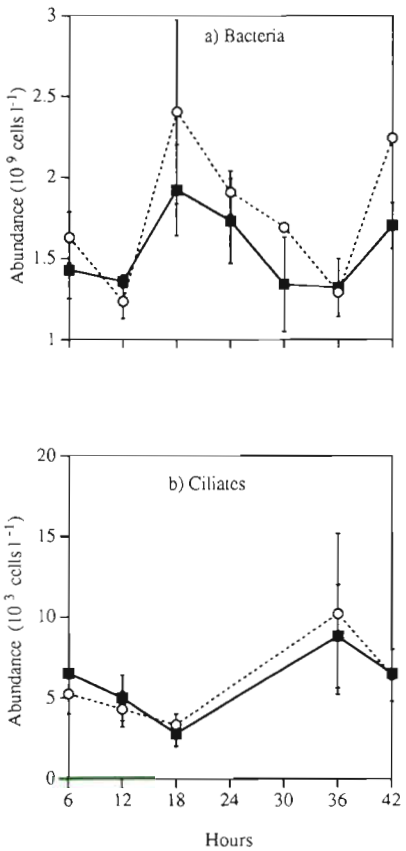

Fig. 7 Temporal variations of (a) bacterial abundance and (b) ciliate abundance under natural (■) and reduced (○) UVR (average ± standard deviation of duplicates)

During our study, the microalgal community was dominated by small flagellates and dinoflagellates which represented, on average, 60 and 30% of total algal cell number, respectively. Diatoms represented only 6 to 20% of the total phytoplankton abundance. The specific composition of phytoplankton was typical of that generally observed in the Lower St. Lawrence Estuary in midsummer (Levasseur et al. 1984). Under natural and reduced UVR, the phytoplankton dynamics were characterized by a gradual increase in algal biomass and total cell abundance (Fig. 4a, b) accompanied by a decrease in nutrient concentrations (nitrate + nitrite and phosphate) (Fig. 3b, c). The abundance of the different phytoplankton taxa (flagellates, dinoflagellates and diatoms) evolved in a similar manner under both light regimes during the whole experiment (Fig. 4c, e, f). After 2 d, there was no important change in taxonomic composition of phytoplankton under reduced UVR. This is not surprising since a change in phytoplankton composition (i.e. algal succession) in response to a modification of the physico-chemical environment generally occurs after a week or more (Harris 1980), a period longer than the duration of our experiment.

During our experiment, $DMSP_p$ concentrations were strongly correlated with flagellate abundance, more particularly with *Cryptomonas* spp. (Tables 3 & 4). These results agree with those of Gibson et al. (1996), who found a strong correlation between the cellular contents of $DMSP_p$ and *Cryptomonas criophyllum* abundance in antarctic waters. Despite the fact that species composition of phytoplankton remained relatively stable during the experiment, $DMSP_p$ concentrations under reduced UVR increased after 24 h as compared to those measured under natural light conditions (Fig. 5a). Since we observed no significant effect of the light regime on phytoplankton cell abundance, the increase in $DMSP_p$ under reduced UVR most probably results from a change in DMSP cellular content. These results suggest that a reduction of UVR may enhance the accumulation of DMSP in microalgal cells. This accumulation can result from an increase in the cellular synthesis rate of DMSP. DMSP synthesis depends partly on the availability of its precursor, methionine (Andreae 1986). The metabolism of this amino acid involves ATP, membrane bounded proteins and enzymes (Andreae 1990). It has been shown that the synthesis of these compounds is negatively impacted by UVR (Döhler 1985, Vosjan et al. 1990). In the north Pacific Ocean, Goes et al. (1995) showed that exposure of natural phytoplankton populations to UVR led to a marked decline in the overall rate of carbon incorporated into amino acids and a reduction in the pool size of total cellular amino acids. At stations where flagellates were abundant, they also noted a marked decrease in the synthesis of methionine in the presence of UVR. These results suggest that a reduction in UVR can favour methionine synthesis and, therefore, DMSP synthesis in microalgae. The DMSP accumulation observed in phytoplankton under reduced UVR could also result from a decrease in DMSP excretion rate.

During the last 6 h of the experiment, $DMSP_d$ concentrations under reduced UVR became significantly lower compared to those measured under natural light (Fig. 5b). $DMSP_d$ production is governed by its release rate in the seawater (by algal senescence, zooplankton grazing, and excretion) and its bacterial degradation rate (Dacey & Wakeham 1986, Nguyen et al. 1988, Kiene & Service 1991, Matrai & Keller 1994). A UV-induced change in these rates may have been responsible for the accumulation of $DMSP_d$ at the end of the experiment in the natural light microcosms. However, we detected no effect of reduced UVR on total bacterial number or on ciliated protozoan abundance, the main potential grazers in the microcosms.

The reduction of UVR had a strong and rapid impact on DMS. Indeed, reduced UVR caused an increase in DMS concentrations in microcosms during the first day

(Fig 5c). During this day, the accumulation rate of DMS under reduced UVR was 4 times greater than under natural light conditions (Table 2). During the second day, DMS levels in microcosms exposed to reduced UVR stabilized around 25 nmol l^{-1} (Fig. 5c). This suggests that a new balance between production and sink processes of DMS was established after 24 h. However, concentrations of DMS stayed higher under reduced UVR than under the natural light regime.

During the first 24 h, the increase in the DMS accumulation rate under reduced UVR may have resulted from an increase in the DMS production rate or a decrease in the DMS loss rate. Our results demonstrated that reduced UVR had no effect on $DMSP_p$ and $DMSP_d$, the precursors of DMS, during the first day. Consequently, the rapid accumulation of DMS in microcosms exposed to reduced UVR probably results from a decrease in DMS loss rate. Ventilation, bacterial degradation and photooxidation are the principal sinks for DMS (Brimblecombe & Shooter 1986, Zeyer et al. 1987, Gibson et al. 1990, Kiene & Bates 1990, Malin et al. 1993, Kieber et al. 1996). During our experiment, microcosms were covered with filters and submitted to the same mixing conditions before sampling. Consequently, it can be assumed that ventilation made a similar contribution to the DMS sink under both light regimes. Bacterial degradation plays an important role in the marine DMS cycle (Kanagawa & Kelly 1986, Suylen et al. 1986, Zeyer et al. 1987, Kwint & Kramer 1995). During this study, reduced UVR had no effect on the bacterial dynamics (Fig. 7a, Table 1). Since the activity of the bacteria which specifically degrade DMS was not measured, the possibility that reduced UVR can cause an inhibition of DMS-consuming bacterial activity cannot be completely eliminated. Light can also oxidize DMS into dimethylsulfoxide or other products (Brimblecombe & Shooter 1986, Kieber et al. 1996). Hence, the increase in DMS accumulation rate under reduced UVR can result from a decrease in DMS photooxidation rate. This is consistent with laboratory experiments conducted on surface seawater samples collected in the equatorial Pacific Ocean which show that maximal rates of DMS photolysis occur in the UV-B range and for wavelengths between 380 and 460 nm (Kieber et al. 1996). When these rates are normalized to average springtime solar irradiance incident at the sea surface at the sampling site, Kieber et al. (1996) concluded that photolysis of DMS in seawater occurs predominantly between 380 and 460 nm. In the present study, the UF3 filters cut out wavelengths of 400 nm and below, so that DMS photolysis may have been reduced. In coastal waters, the photolysis of DMS by UVR will probably be limited to the upper few meters of the euphotic layer since UVR is rapidly absorbed by water molecules (Müller-Niklas et al. 1995).

In summary, the results of this study show that natural UVR, even at low levels, can affect the DMSP/DMS dynamics in seawater. Reduced UVR effects were observed at 2 temporal scales. At short time scales (<24 h), reduced UVR favors DMS accumulation, probably by decreasing its removal (photolysis and/or biological consumption). At long time scales (>24 h), it increases algal DMSP content, probably by enhancing the synthesis and/or by decreasing the metabolic excretion of DMSP.

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