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NOTE

Particulate dimethyl sulphoxide in seawater: production by microplankton

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ABSTRACT: Dimethyl sulphoxide (DMSO) represents a major pool of dissolved dimethylated sulphur in seawater However, the origin and fate of this compound in the marine environment, and its role in the biogeochemical cycle of dimethyl sulphide (DMS), remain unclear. The only established route for the formation of DMSO in oxygenated seawater is photochemical oxidation of DMS. It is not known whether significant biotic production pathways exist. In a study of methylated sulphur speciation in coastal North Sea waters and cultures of marine unicellular algae, we measured pools of particulate DMSO ($DMSO_p$) at nanomolar and micromolar concentrations, respectively. Analyses of size-fractionated seawater particulates and incubation experiments provided evidence that $DMSO_p$ was associated with microplanktonic organisms. Log-phase cultures of *Amphidinium carterae* and *Emiliania huxleyi* exhibited intracellular dimethylsulphoniopropionate (DMSP) to DMSO molar ratios of 25 and 8, respectively. Our results strongly suggest the existence of biological production and release of DMSO in eukaryotic microplankton.

KEY WORDS: Dimethyl sulphoxide · Phytoplankton · Dimethylsulphoniopropionate · Dimethyl sulphide · *Amphidinium carterae*

Just over a decade ago Charlson et al. (1987) brought attention to the possible role of dimethyl sulphide (DMS) in the global climate. Their hypothesis greatly stimulated research on all aspects of this biogenic trace gas, including the microbial ecology that leads to DMS production and cycling in marine waters and influences its emission to the atmosphere (Saltzman & Cooper 1989, Andreae 1990, Malin et al. 1992). It has generally been assumed that the oxidised form of DMS, dimethyl sulphoxide (DMSO), would also be present in seawater and hence would play a role in the DMS cycle (Wakeham & Dacey 1989). However, this stable and soluble compound has proven difficult to analyse at the nanomolar concentration levels likely in marine aquatic environments. The first data were published by Andreae (1980), and it led him to suggest that phytoplankton were involved in DMSO production and release, but the analytical technique used is now known to be prone to interference from dimethylsulphoniopropionate (DMSP), which is considered the major precursor of DMS. Several methods are now available which overcome this problem (Ridgeway et al. 1992, Hatton et al. 1994, Kiene & Gerard 1994, Lee & de Mora 1996, Simó et al. 1996). These include specific reduction of DMSO with the enzyme DMSO-reductase (Hatton et al. 1994) or sequential hydrolysis of DMSP followed by reduction of DMSO with borohydride (Simó et al. 1996). In both cases the DMS evolved is preconcentrated using a purge-and-cryotrap technique prior to analysis by gas chromatography. As a consequence of the application of all these methods to oceanographic work in the last few years, much more is now known about the distribution of DMSO in marine waters. DMSO concentrations are generally higher than those of DMS in surface and euphotic waters, where they usually range between 2 and 20 nM (Bates et al. 1994, Simó et al. 1995, 1997, Hatton et al. 1996, Lee & de Mora 1996). DMSO is also found in deep marine waters, where DMS and DMSP are below usual detection limits (Hatton et al. 1996). Hence, a considerable pool of DMSO exists in the oceans.

Much less progress has been made regarding the production and turnover pathways of DMSO in the sea. The only routes for the formation of DMSO in oxygenated seawater demonstrated so far are abiotic: the photo-oxidation of aqueous DMS (Brimblecombe &

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Shooter 1986, Kieber et al. 1996) and the deposition of atmospheric DMSO generated by radical oxidation of DMS (e.g. Turnipseed & Ravishankara 1993). Although bacterial DMS-to-DMSO oxidation occurs in microbial cultures and anaerobic environments (Taylor & Kiene 1989, Zhang et al. 1991, Juliette et al. 1993, Taylor 1993), it is not known whether significant biotic production pathways exist in oxic marine waters. In this paper we present data from field and laboratory studies which show, for the first time, the occurrence of a significant pool of particulate DMSO associated with microplankton. Our results suggest that eukaryotic microorganisms, mainly phytoplankton, are involved in DMSO production and release.

Methods. ***Seawater sampling:*** Surface seawater was collected on 3 occasions (samples A, B and C in Table 1) at 07:30 h at an station 5.7 miles (9.2 km) offshore from Great Yarmouth (Norfolk, England). The water column depth was 29 m and seawater temperatures were 14°C (A), 15°C (B) and 18°C (C). 10 l water volumes were taken in glass bottles from just beneath the surface, transported to the laboratory in cool, dark conditions and analysed within 3 h of collection.

Size fractionation: Size fractionation of a seawater sample was achieved by gravitational filtration through Nytex mesh (200 µm) and Nucleopore 18, 5 and 1 µm filters. 50 ml aliquots of each size fraction were further filtered through GF/F filters, which were then analysed for the particulate species.

Seawater incubation experiment: Unfiltered seawater from sample B was distributed into acid-washed, 1 l glass bottles with Teflon-sided screw caps, and incubated in the dark for 48 h at the *in situ* temperature of 15°C. A microvolume of pure chloroform, used as an 'inhibitor', was added to one of the bottles to a final concentration of 500 µM. The water sample was carefully inverted to mix the contents both following chloroform addition and just before subsampling. Subsamples were withdrawn through Teflon tubing attached to a glass syringe.

Culture experiments: Cultures of *Amphidinium carterae* and *Pleurocrysis carterae* were each grown in F/2-enriched natural seawater medium in a 2 l cylindrical glass culture vessel with a flat base and multi-socket flat-flange lid. The lid ports were sealed with cotton and muslin bungs. The cultures were slowly stirred using a Nalgene floating Teflon stir bar, and incubated at 12°C with a 12 h light/12 h dark cycle. A culture of *Emiliania huxleyi* was grown in a similar medium in a 300 ml glass vessel, and incubated at 18°C with the same light/dark cycle. Cells were counted using a light microscope and a haemocytometer.

Analyses: In freshly collected seawater and incubation experiments, DMS and dissolved DMSP ($DMSP_d$) and DMSO ($DMSO_d$) were determined sequentially using GF/F filtrates, following an adaptation (Simó, Malin & Liss unpubl.) of the borohydride reduction method of Simó et al. (1996). Particulate DMSO ($DMSO_p$) was determined after removal and analysis of DMSP by cold NaOH hydrolysis of the GF/F filters for 24 h. DMSO and $DMSP_p$ were not detected during routine blank analyses of filters. In the *Amphidinium carterae* culture experiment, sulphur species were determined using the methods of Hatton et al. (1994), involving DMSO analysis by enzymatic reduction. Dissolved compounds were measured after filtration through a Millipore AP25 depth filter. $DMSO_p$ was analysed by adding the seawater sample to distilled water, so that cells would burst due to osmotic shock, thus enabling the DMSO reductase enzyme access to cellular DMSO. $DMSO_p$ concentrations were then calculated by subtracting the $DMSO_d$ value. Preliminary measurements in *Pleurocrysis carterae* and *Emiliania huxleyi* cultures were done using this method and the borohydride reduction method, respectively. Phytoplankton speciation and abundance data for North Sea waters were obtained using an inverted microscope, and carbon biomass was estimated by applying appropriate carbon conversion factors.

Results and discussion. Surface seawater was collected at an offshore station in the North Sea on 3 occasions (Table 1). The first visit (A) coincided with a phytoplankton bloom, of which 98% of the biomass was accounted for by *Phaeocystis* sp. A month later (B) the planktonic biomass was substantially lower and dominated by heterotrophic dinoflagellates; and on the third visit (C) the population was dominated by heterotrophic dinoflagellates and diatoms. While carrying

Table 1. Concentrations of particulate and dissolved dimethylated sulphur species (nM, all values are means of duplicate measurements), chlorophyll *a* (mg m^{-3}), total biomass and dominant eukaryotic microplankton species and group biomasses (mg C m^{-3}) in North Sea waters

	A June 19, 1996	B July 18, 1996	C August 2, 1996
$DMSO_p$	16	3.9	2.7
$DMSO_d$	25	4.9	2.3
$DMSP_p$	340	5.2	7.1
$DMSP_d$	150	4.3	4.0
DMS_d	65	1.6	0.8
Chl *a*	13.26	1.33	2.74
Phaeocystis sp.	268	–	–
Diatoms	1.20	2.51	13.4
Flagellates	4.62	2.96	4.79
Ciliates	7.42	1.88	1.63
Heterotr. dinoflagellates	23.7	27.0	26.6
Other	0.04	0.10	0.33
Total biomass	305	34.5	46.8

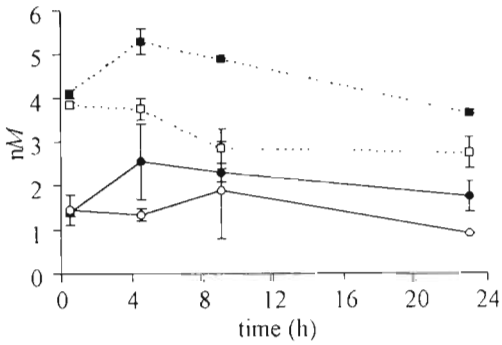

Fig. 1 Time course of the concentrations of particulate DMSP (squares) and DMSO (circles) during incubation of water sample B (see Table 1), with (open symbols) and without (solid symbols) addition of chloroform. Samples were incubated in the dark at the *in situ* temperature of 15°C. Error bars indicate the scatter of duplicate analyses

out DMS, $DMSP_d$ and $DMSP_p$, and $DMSO_d$ analyses, we found that DMSO could be detected on the GF/F filters which had been used to filter the seawater. Using the same criteria as those for DMSP analysis, it seemed likely that this non-filterable DMSO could be particulate in origin.

Supporting evidence for a pool of particulate DMSO was obtained during an incubation experiment, in which chloroform was used as an inhibitor of bacterial DMS metabolism. Chloroform is used to measure DMS consumption rates (Kiene & Bates 1990) with the assumptions that it has no effect on the production of DMS or the partitioning of the total DMSP pool. However, in some cases chloroform seems to cause $DMSP_p$-to-$DMSP_d$ release from microbial cells, which may be due to induced cell mortality or effects on cell membrane properties (Wolfe & Kiene 1993). During the first 24 h of dark incubation of water sample B (Table 1), chloroform addition caused a 25 to 50% decrease of the $DMSP_p$ and $DMSO_p$ relative to the control series (Fig 1), with a concomitant increase in the dissolved pools. It is well established that $DMSP_p$ is mostly contained in the cells of certain types of marine phytoplankton (Keller et al. 1989). Thus, the observed parallel effects of chloroform on DMSO and DMSP partitioning between the particulate and dissolved phases suggests that a pool of DMSO exists in planktonic cells.

From Table 1 it can be seen that for all 3 seawater samples, concentrations of $DMSO_p$ were of the same order as those of $DMSO_d$. This indicates that its concentration within cells (a minor portion of the total seawater volume) was orders of magnitude higher than its concentration in the dissolved pool. Hence, $DMSO_p$ was unlikely to have derived from uptake of DMSO from seawater by diffusion. Although in-cell production seems more likely, to date there has been no definitive evidence for the biosynthesis and occurrence of DMSO in any marine microorganism. In the present study $DMSO_p$ and $DMSP_p$ occurred at similar moderate concentrations in samples B and C (Table 1), and at much higher levels during the bloom of *Phaeocystis* sp. (sample A), an organism that is known to contain high levels of DMSP (Liss et al. 1994).

In addition to phytoplankton, microzooplankton grazers and bacteria might also have contributed to the $DMSO_p$ observed in the seawater samples. Herbivorous ciliates and heterotrophic dinoflagellates play a significant role in the seawater DMS cycle via processing of $DMSP_p$ during grazing and digestion of phytoplankton cells (Belviso et al. 1990, Christaki et al. 1996, Wolfe et al. 1997). Bacteria could also accumulate DMSO either as a substrate for growth or as a product of DMS or DMSP metabolism (Taylor 1993). However, size fractionation of sample C showed that $DMSO_p$ was mostly detectable in particles >5 µm (Fig. 2). This distribution indicates that $DMSO_p$ was not largely confined to the free bacterial fraction but to eukaryotic organisms, though we cannot preclude that some of the $DMSO_p$ could be associated with detritus and faecal pellets.

To test whether DMSP-containing phytoplankton can be a direct source for DMSO, we monitored $DMSO_p$, $DMSO_d$, DMS, $DMSP_p$, $DMSP_d$ and cell numbers in a batch culture of the dinoflagellate *Amphidinium carterae* (Fig. 3). $DMSO_p$ occurred at significant concentrations during the whole experiment, and increased exponentially with cell number and $DMSP_p$.

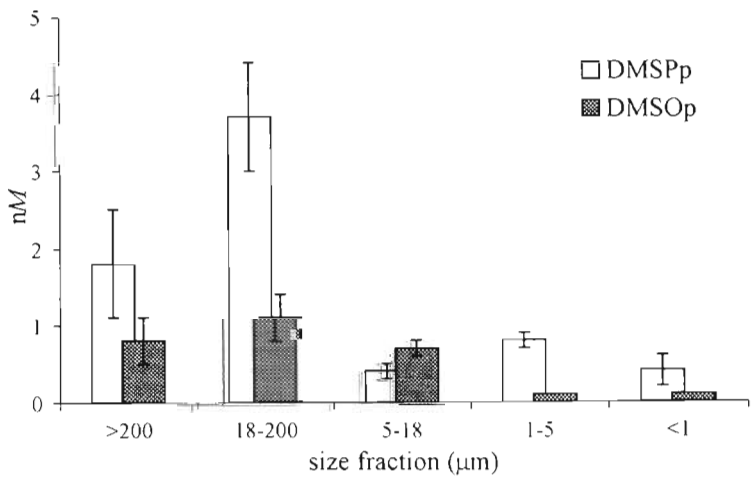

Fig. 2. Concentrations of $DMSO_p$ and $DMSP_p$ in size fractions of sample C. Error bars indicate the scatter of duplicate analyses. See Table 1 for the DMSO and DMSP concentrations and the microplankton composition of the whole water sample

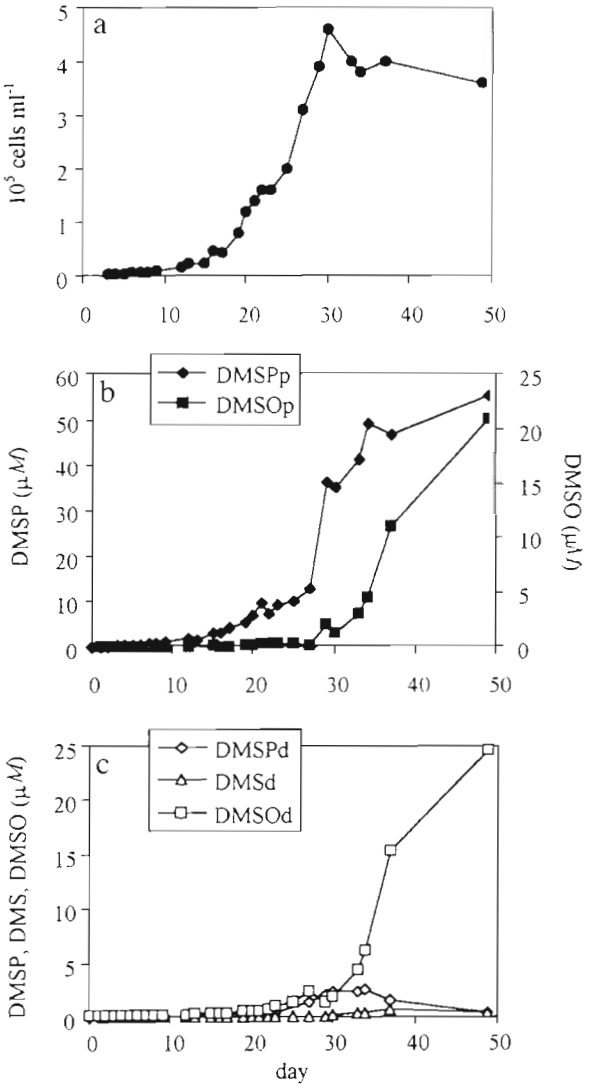

Fig. 3. *Amphidinium carterae*. Time course of the concentrations of (a) cells, (b) particulate DMSP and DMSO, and (c) dissolved DMSP, DMSO and DMS in a batch culture of the dinoflagellate

Intracellular contents of DMSO and DMSP during the log-phase averaged 0.3 ± 0.2 and 11 ± 4 pg cell^{-1}, respectively (n = 15), with a mean value of ca 25 for the $DMSP_p/DMSO_p$ molar ratio, which had a minimum value of approximately 3 during the stationary phase. $DMSO_d$ was the major dissolved species, and its concentration paralleled that of $DMSO_p$ throughout the experiment. This indicates that the major source for the dissolved DMSO was partitioning from the intracellular pool rather than transformation of dissolved DMS. We believe that these data provide strong evidence for the production and release of DMSO by dinoflagellate cells. We have also found submicromolar levels of $DMSO_p$ in 2 preliminary experiments on cultures of the DMSP-producing prymnesiophytes *Emiliania huxleyi* and *Pleurochrysis carterae* (data not shown). Log-phase *E. huxleyi* cells contained 0.1 pg DMSO cell^{-1} and 1.4 pg DMSP cell^{-1}, and had a mean $DMSP_p/DMSO_p$ molar ratio of 8 (n = 4). Hence, $DMSO_p$ production does not appear to be restricted to dinoflagellates. It is worth stressing that 2 independent analytical methods were used for DMSO determination in coastal seawaters (Simó et al. 1996, Simó, Malin & Liss unpubl.) and algal cultures (Hatton et al. 1994, Simó, Malin & Liss unpubl.), and both revealed the existence of a particulate DMSO pool.

Our discovery of significant amounts of $DMSO_p$ has implications for the complexity of the biogeochemical cycle of DMS in the marine environment (Malin et al. 1994). The results suggest that DMSO is not only produced via photo-oxidation of dissolved DMS (Kieber et al. 1996), but may also be a significant metabolite of biological methylated sulphur transformations within marine pelagic food webs. Ongoing investigation in our groups aims to ascertain the origin and pathways of $DMSO_p$ production. All aerobic organisms have developed mechanisms to deal with reactive oxygen species, such as hydrogen peroxide and singlet oxygen, which are produced as by-products of photosynthesis, photo-oxidative stress and respiration. If the final steps of DMSP biosynthesis in unicellular algae occur in the chloroplast, as is the case in higher plants (Trossat et al. 1996), then it seems likely that $DMSO_p$ could be generated via reaction of DMS with strong oxidants of this type. In the natural environment, another potential source for $DMSO_p$ might be enzymatic reactions in the guts, feeding vacuoles or faecal pellets of grazers, where local anaerobic conditions appropriate for bacterial or enzymatic DMS oxidation (Taylor 1993) could occur. Grazing experiments with protists feeding on DMSP-containing prymnesiophytes and bacteria reveal an imbalance between $DMSP_p$ ingested and $DMSP_p$ processed through $DMSP_d$ and DMS_d, thus indicating that a significant part of the algal/bacterial DMSP is metabolised by the grazer (Wolfe et al. 1994, Christaki et al. 1996, Wolfe 1996). Whether some of the metabolised DMSP is converted to DMSO is not yet known.

Once released by plankton in pelagic waters, DMSO may undergo loss processes such as transport to deeper waters (Hatton et al. 1996) and consumption by bacterioplankton capable of utilising it aerobically as carbon and energy source or anaerobically as an electron acceptor (Taylor 1993). If microbial reduction of aqueous DMSO is shown to occur in seawater, as observed in cultured bacteria (Taylor & Kiene 1989, Zhang et al. 1991, Taylor 1993), $DMSO_p$ would represent a new planktonic DMS precursor.

Especially intriguing is the role of DMSO in phytoplankton, whether it is a by-product of sulphur metab-

olism or has any additional function. DMSP is known to act as a compatible solute, osmolyte and cryoprotectant, and is suggested to function as a methyl donor and act as a transient pool for excess of intracellular sulphur (Kiene et al. 1996). As a zwitterion, it can only be released from cells whose membranes are damaged, or by active transport. In contrast, DMSO is a dipolar aprotic hydroscopic substance which easily diffuses across intact membranes. This would explain why it appears to leak out of healthy dinoflagellate cells and increase in the dissolved phase faster than DMSP (Fig. 3). Because it is also nontoxic and does not cause irreversible damage to membranes, DMSO has been used extensively to protect algal, bacterial and protozoan cells against the adverse effects of freezing-thawing in cryogenic preservation methods (Kirsop & Doyle 1991). Hence, in view of its properties, we can speculate that DMSO might play diverse physiological roles in microplankton, such as protect cells against photo-generated oxidants and cryogenic damage, or serve as a sulphur and carbon transporter through membranes. Whether DMSO formation is involved in the control of DMSP and DMS production by plankton is something that should be investigated in future research. In the meantime, our findings suggest that it would be worthwhile to incorporate $DMSO_p$ analyses alongside determinations of DMS_d, $DMSP_d$, $DMSP_p$, $DMSO_d$, methanethiol$_d$ and methiolpropionate$_d$, in order to get a more complete picture of the cycling of methylated sulphur compounds in seawater.

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