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NOTE

Dimethylsulfide (DMS) production by size-fractionated particles in the Labrador Sea

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ABSTRACT: We measured the production of dimethylsulfide (DMS) by size-fractionated particles during a cruise in the Labrador Sea in May-June 1997. The experiments were conducted at 2 stations characterised by low levels of nitrate and high levels of phytoplankton biomass and particulate dimethylsulfoniopropionate ($DMSP_p$). Samples were size fractionated to assess the size distribution of $DMSP_p$ and the potential DMS production associated with the different size fractions. The potential for DMS production was estimated by incubating the filters in pre-filtered and boiled seawater amended with 500 nM of dissolved DMSP ($DMSP_d$). At both stations, the highest $DMSP_p$ concentrations were measured in the 2 to 11 and >20 µm size fractions. Elevated potential net DMS production rates were also associated with these 2 size fractions, which were responsible for 40 to 53% and 23 to 31% of the cumulative production, respectively. Only 4% of the potential net DMS production was measured in the 0.7 to 2 µm fraction, which presumably contained many of the free-living bacteria. The potential net DMS production rates of the different size fractions were linearly related (Spearman correlation coefficient = 0.86) to the concentrations of $DMSP_p$ in the fractions. These results suggest that DMSP-cleaving activity was spatially associated with DMSP-producing algae or DMSP-rich detritus (e.g. faecal pellets, marine snow).

KEY WORDS: Dimethylsulfide (DMS) · Dimethylsulfoniopropionate (DMSP) · Bacteria · Phytoplankton · Labrador Sea · Size fraction

Dimethylsulfide (DMS) represents the most important climatically active biogenic gas emitted by the oceans (Lovelock et al. 1972, Andreae 1990, Malin & Kirst 1997). DMS results from the enzymatic cleavage of dimethylsulfoniopropionate (DMSP) (Cantoni & Anderson 1956), a compatible solute found in many phytoplankton species (Keller 1991). The cleavage of DMSP into DMS has been associated mostly with bacteria (Kiene 1990, 1992, Ledyard & Dacey 1994, de Souza & Yoch 1995a, Yoch et al. 1997), but also with a few phytoplankton species (Ishida 1968, Stefels & Dijkhuizen 1996, Wolfe & Steinke 1996). Although dissolved DMSP ($DMSP_d$) concentrations are relatively low in nature (mean of ca 14 nM for the global ocean, Kettle et al. 1999) and very high affinities for DMSP are often measured (Ledyard & Dacey 1996a, Kiene et al. 1998), K_m values for DMSP cleavage in the micromolar range are also commonly reported (Ledyard 1993, Ledyard & Dacey 1996a,b). This suggests that bacteria may frequently encounter $DMSP_d$ concentrations many orders of magnitude higher than concentrations found in the bulk phase of seawater. More generally, multiphasic kinetics for glucose uptake on a very large range of concentrations have also been observed for assemblages of natural bacteria and an isolated oligotrophic marine bacterium (Azam & Hodson 1981, Nissen et al. 1984). This suggests that bacteria may encounter high DOC (dissolved organic carbon) levels which are postulated to be closely associated with phytoplankton cells and with aggregates of marine snow (Mitchell et al. 1985). As suggested by Azam & Ammerman (1984), the existence of very high K_m values is a strong indication that bacteria are acclimated to high substrate concentrations as found immediately surrounding phytoplankton cells or other particulate materials. By extension, high K_m values for DMSP suggest that bacteria involved in DMSP cleavage may be attached to algae (presumably DMSP producers) or imbedded in DMSP-rich detritus (e.g. faecal pellets, marine snow).

During a recent study in the Labrador Sea, we found no saturation of DMSP cleavage for substrate concentrations as high as 5000 nM, with *in situ* $DMSP_d$ levels never exceeding 60 nM in the bulk phase (Schultes et al. unpubl.). Again, these results suggest that DMSP-cleaving organisms were acclimated to high levels of $DMSP_d$. During the same cruise, the size fractionation

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of particulate DMSP ($DMSP_p$) showed that most of the particulate DMSP was found in the 2 to 11 and >20 µm particulate size ranges (Cantin et al. unpubl.). We thus hypothesized that most of the DMSP cleavage was associated with those dominant fractions.

This working hypothesis was tested on 2 occasions during the same cruise. Surface water samples were collected with Niskin bottles at 2 stations located in the central basin (Fig. 1). Silicone tubing was used to gently transfer water from the Niskin bottles to an acid washed carboy in order to minimise bubbling and avoid rupturing fragile cells. Seawater (350 ml) was then filtered by gravity on a sequential series of four 47 mm filters. The filter series comprised nylon net filters (20 and 11 µm, Millipore), and glass fiber filters (2 µm GMF and 0.7 µm GF/F, Whatman). The filtration protocol was performed in duplicate, the first set of filters being used for the determination of $DMSP_p$, and the second set for the incubation experiments (see below). DMS and DMSP concentrations were measured within 10 min and 3 wk, respectively, with a gas chromatograph equipped with a flame photometric detector following a modified version of the method described by Leck & Bågander (1988) (see Cantin et al. 1996 for details on the techniques).

The high levels of chlorophyll *a* (>6 µg l^{-1}) and low levels of nitrate (<1 µM) measured at both stations (Table 1) indicate that the phytoplankton spring bloom had reached an advanced stage of development at the time of the cruise. The results from the first set of filters showed that $DMSP_p$ concentrations were also high (ca 270 nM) at both stations and were similarly distributed among the different size fractions (Table 2). At these 2 stations, most of the $DMSP_p$ was measured in the 2 to 11 µm and >20 µm fractions, which accounted for 89% of the total $DMSP_p$. On the other hand, the 0.7 to 2 µm and the 11 to 20 µm fractions accounted for a maximum of 6 and 10% of the total $DMSP_p$, respectively.

Table 1. Chemical and biological variables measured at the surface of Stns L4-08 and L6-04. Data from Cantin et al. (unpubl.)

Variable	Unit	L4-08 Concentration	L6-04 Concentration
Temperature	°C	5.0	4.6
Salinity	PSU	34.2	34.5
$DMSP_p$	nM	269.5	267.8
Chl *a*	µg l^{-1}	11.5	6.7
NO_3	µM	0.77	0.16
Phytoplankton	10^6 cells l^{-1}	6.0	4.4
Phaeocystis pouchetii	10^6 cells l^{-1}	0.8	0

The second set of filters was used to test the potential DMS production of the different size fractions. In this case, the filters were placed in a 250 ml dark HDPE bottle and suspended in 250 ml of 0.2 µm filtered seawater that was previously heated in a microwave oven (80 to 90°C for 20 to 40 min) in order to kill the remaining bacteria and deactivate potentially free DMSP-lyase. The bottles had been soaked overnight in 10% HCl, then in nanopure water and finally rinsed with the water used to fill each bottle. The 0.2 µm filtered seawater was also poured into HDPE bottles as a control. All incubation bottles (>20, 11–20, 2–11, and 0.7–2 µm fractions, and <0.7 and <0.2 µm filtered seawater) were amended with $DMSP_d$ (Research Plus Inc.) from a sterile stock solution to obtain a final concentration of 500 nM. Every treatment was duplicated. Bottles were gently inverted to mix the contents and incubated in the dark in a circulating water-bath within 1°C of *in situ* seawater temperature (4 to 6°C). At each timepoint (usually 0 and 3 h, occasionally 0, 2 and 3 h, to check for linearity), 60 ml of water were filtered by low vacuum (never exceeding 5 inches Hg [16.9 kPa]) over a Whatman GF/F glass fiber filter for immediate DMS analysis.

The level of $DMSP_d$ addition was based on previous experiments conducted dur-

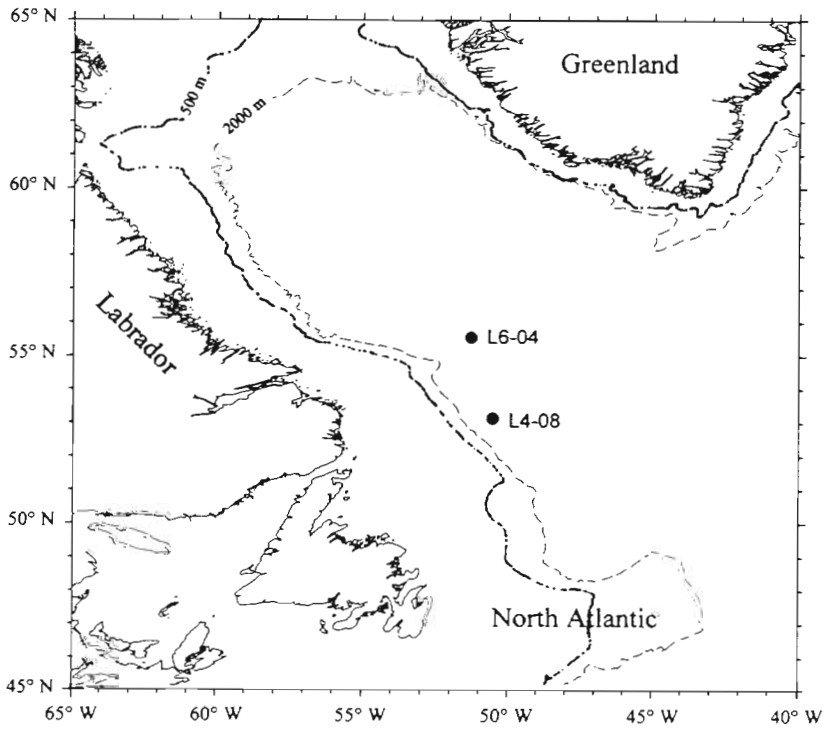

Fig. 1. Locations where experiments were conducted in the Labrador Sea

Table 2. DMSP concentration and potential net DMS production by different size fractions from natural seawater collected at Stns L4-08 and L6-04

Size fraction (µM)	DMSP *in situ* (nM)		(%)		DMS production (nM h^{-1})		(%)	
	L4-08	L6-04	L4-08	L6-04	L4-08	L6-04	L4-08	L6-04
<0.7	2.5[a]	12.0[a]	–	–	14.9	4.0	26	12
0.7–2	3.1	16.9	1	6	2.2	1.0	4	3
2–11	109.5	146.3	41	55	23.0	17.2	40	53
11–20	26.4	13.2	10	5	4.6	0.4	8	1
>20	130.5	91.4	48	34	13.4	10.0	23	31

[a]*In situ* dissolved DMSP concentration

ing the same cruise. Our first choice was to get estimates of *in situ* gross DMS production rates which do not need DMSP addition and require the use of appropriate DMS consumption inhibitors. We tested some inhibitors during the cruise but none gave satisfactory results (data not shown). Thus, the determination of net DMS production became the only choice available. In other experiments conducted during the same cruise, Schultes et al. (unpubl.) and Wolfe et al. (1999) showed that the DMS production and consumption were generally in balance at the stations sampled in the Labrador Sea. Thus, it appeared necessary to add DMSP to shift the equilibrium toward the production in order to get a significant signal.

In general, Schultes et al. (unpubl.), who experimented with different levels of addition from 0 to 5000 nM, began to observe a significant response in terms of production with 500 nM additions during the same cruise. We then decided to use the same level in our experiments. Thus, because there were additions of substrate, the production rates measured during our experiments represent potential production rates. During the same cruise, Schultes et al. (unpubl.) showed linear net DMS production rate in response to DMSP additions up to 5000 nM $DMSP_d$, suggesting that there was no shift in the system properties. Although the ambient concentration of $DMSP_d$ in seawater is typically in the tens of nM, concentrations as high as 200 nM have been observed in open ocean regions (Malin et al. 1993, Palmer Locarnini et al. 1998), corresponding to the dissolved DMSP suddenly released in the water at the end of an algal bloom. There is ample precedent for using elevated substrate levels in the context of kinetics assays. For example, Ledyard & Dacey (1996b) found no sign of saturation for $DMSP_d$ amendments as high as 1 µM in the Sargasso Sea, while the same authors estimated K_m as high as 11.5 µM in the temperate coastal waters in Monterey Bay (Ledyard & Dacey 1996a). Laboratory studies have also shown very high K_m values for bacterial DMSP-lyase ranging from several hundred nM (Ledyard & Dacey 1994) to 2 mM (de Souza & Yoch 1995b). It is thus clear that marine bacteria or phytoplankton have a very large capacity for $DMSP_d$ utilisation, which far exceeds the ambient concentrations of $DMSP_d$ usually found in bulk seawater.

Results from these incubation experiments obtained at Stn L4-08 are presented in Fig. 2. The largest DMS accumulation was measured in the 2 to 11 µm size fraction (up to 85 nM), followed by the >20 and <0.7 µm size fractions. Very little DMS accumulation was observed in the 0.7 to 2.0 µm and in the 11 to 20 µm size fractions. As expected, no production occurred in the control (heated 0.2 µm filtered seawater). Data from Stn L6-04 which give similar results are presented in Table 2 only. Tests conducted during these experiments showed clear linear responses in DMS accumulation during the 3 h incubations (see Fig. 2 for an example). Moreover, during the same cruise, Schultes et al. (unpubl.) always observed a linear response during incubations conducted at 9 different stations in the Labrador Sea. We thus assume that DMS generally accumulated at a linear rate during our experiments. Based on this assumption, we calculated the potential net DMS production rates for the 2 stations (Table 2).

The pattern of DMS production among the 5 fractions was similar at both stations, with higher production rates measured in the 2 to 11 µm size fraction

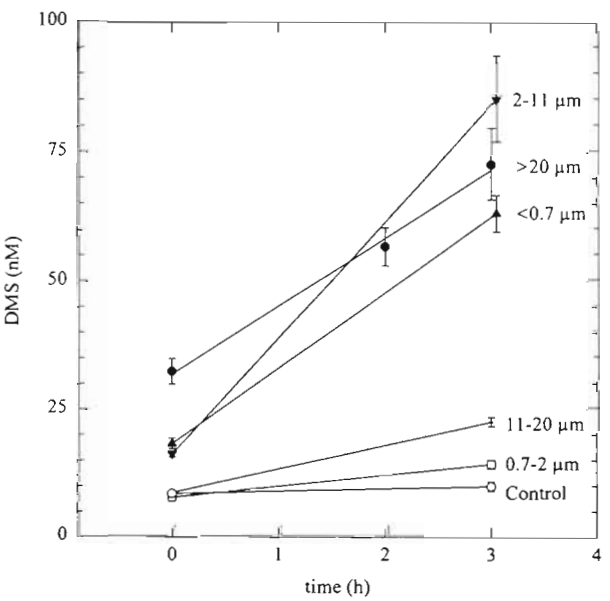

Fig. 2. An example of dimethylsulfide (DMS) net production by different size fractions following an addition of 500 nM of dissolved dimethylsulfoniopropionate ($DMSP_d$) (Stn L4-08). Mean values ± SD on 2 replicates

(17 to 23 nM h^{-1}) and the >20 µm size fraction (10 to 13 nM h^{-1}). The 11 to 20 µm size fraction showed low DMS net production (0.4 to 4.6 nM h^{-1}) at both stations. The 0.7 to 2 µm fraction, which presumably contained the largest portion of the free-living bacteria present in our samples, also showed a very low DMS production rate (1 to 2 nM h^{-1}) at both stations. This suggests that the largest free-living bacteria made a relatively small contribution to DMS production in comparison with attached bacteria or phytoplankton during our experiments. A fairly high concentration of free-living bacteria may also be found in the <0.7 µm size fraction. Lee et al. (1995) estimated that as much as 40% of the free-living bacteria may pass through GF/F filters. If this is the case, our results suggest that the small bacteria are more active in terms of DMS production than the ones retained by the 0.7 µm filter (Table 2). However, as discussed below, free DMSP-lyase seems to have been responsible for most of the DMS production in the <0.7 µm size fraction.

The only difference we noted between the 2 stations was associated with the dissolved fraction (<0.7 µm). Stn L6-04 showed a relatively low production rate (4 nM h^{-1}) for this fraction while Stn L4-08 had a production rate (15 nM h^{-1}) as high as the >20 µm fraction (13 nM h^{-1}). *Phaeocystis pouchetii* was present at this station (Table 1). The high production observed in the dissolved fraction may thus result from the existence of free DMSP-lyase already present in the water or released by *P. pouchetii* during the filtration procedure or from small (<0.7 µm) DMS-producing bacteria.

Our results support the current belief that significant concentrations of active free DMSP-lyase may exist in marine waters. DMS production has been observed in 0.2 µm filtered seawater from a coastal pond on the east coast of the United States (Wakeham et al. 1987), in the English Channel (Turner et al. 1988), and in coastal seawater near the mouth of the Duplin River in the United States (Kiene 1990), leaving open the possibility that soluble DMSP-lyase enzymes are present in seawater. Similarly, we found a significant production of DMS in the <0.7 µm size fraction at both stations which we attribute to small bacteria or free enzymes (Table 2). Interestingly, the DMS production rate for the dissolved size fraction (<0.7 µm) was almost 4 times higher at Stn L4-08, where a significant concentration of *Phaeocystis pouchetii* was found, compared to Stn L6-04 (Table 2). This higher DMS production rate might have been associated with exudation or leakage of DMSP-lyases by the *P. pouchetii* cells which are known to produce an extracellular DMSP-lyase (Stefels & Dijkhuizen 1996, Stefels & van Boekel 1993). Furthermore, the 0.2 µm filtered seawater used at Stn L6-04 showed a significant production (4.1 nM h^{-1}, see Table 2 for comparison) of DMS before heating and no significant production after the heating treatment, suggesting the presence of active dissolved enzymes.

The examination of the data presented in Table 2 suggests the existence of a relationship between the distribution of $DMSP_p$ within the different size fractions and the potential DMS production exhibited by each fraction. The 2 to 11 and >20 µm size fractions showing the highest potential DMS production (40 to 53 and 23 to 31% of the cumulated production, respectively) were also those containing most of the $DMSP_p$ (34 to 55%). After pooling the results of the 2 experiments, we found a significant relationship (Spearman correlation coefficient = 0.86, p = 0.007) between the concentrations of $DMSP_p$ in the different size fractions and the potential net DMS production rates (Fig. 3). Therefore, our results show that most of the DMSP-lyase activity was found where most of the $DMSP_p$ was present. These results lead to 2 possible interpretations. First, if the potential net DMS production was mainly controlled by the abundance of bacteria attached to the particles, the strong DMSP producers or high DMSP-containing particles could have thus attracted more DMSP-cleaving bacteria. One study has already demonstrated a bacterial chemotaxis to DMSP in experiments with a marine bacterium (Zimmer-Faust et al. 1996). Second, if microalgal cells were the main organisms involved in DMSP cleavage, our results suggest that the DMSP-lyase synthesised by the phytoplankton was mainly produced by algae present in the size fraction where most of the DMSP was found. Within a single species, variation in DMSP-lyase activity does not necessarily happen to correlate with intracellular DMSP. Indeed Steinke et al. (1998) observed that the DMSP-lyase activity did not correlate with the intracellular DMSP concentrations during

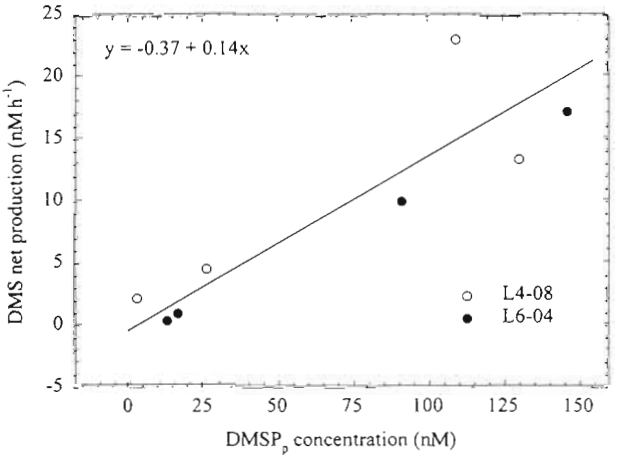

Fig. 3. Linear regression Model II (Sokal & Rohlf 1969) between concentration of DMSP in each fraction and potential DMS net production

experiments with axenic cultures using 6 strains of *Emiliania huxleyi*. But the question of whether different algal species having higher levels of intracellular DMSP generally show higher DMSP-lyase activity remains to be answered.

The protocol used during this study does not allow us to specify the origin (algal versus bacterial) of the DMSP-lyase activity measured in the different particulate size fractions. At Stn L4-08, DMSP-lyase produced by *Phaeocystis pouchetii* was most probably responsible for a significant portion of the DMS production measured in the size fraction (>20 µm) which corresponds with the size of the colonies. On the other hand, the absence of known phytoplanktonic DMSP-lyase producers (data not shown) in the other particulate size fractions at this station, and in all size fractions at Stn L6-04, suggests that attached bacteria were responsible for most of the DMS production. Bacteria are commonly found attached to the surface of phytoplankton cells, particularly during the senescent phase of a bloom (Kogure et al. 1982, Fukami et al. 1983, Smith et al. 1995). The advanced stage of the phytoplankton bloom at our 2 experimental stations may have favoured the growth of attached bacteria as compared to free-living bacteria. The protocol used during this study does not allow us to estimate the relative importance of phytoplankton and attached bacteria in the production of DMS by the particulate material at both stations.

The observation that an important part of the DMS production was controlled by attached bacteria or phytoplankton during our study may provide an explanation for the very high apparent K_m of DMSP-lyase sometimes measured in seawater. When phytoplankton cells exude DOC, e.g. $DMSP_d$, the microenvironment surrounding the cells may contain very high concentrations of $DMSP_d$, orders of magnitude higher than the nanomolar concentrations found in the bulk-phase of seawater. Thus, in contrast with the DMSP-lyases associated with free-living bacteria, the DMSP-lyase systems associated with phytoplankton cells and their microenvironment should be acclimated to very high $DMSP_d$ concentrations and exhibit high K_m values. The experimental results of de Souza & Yoch (1995a) provide support for this hypothesis. They found that a free-living marine bacterium (*Pseudomonas doudoroffii*), presumably exposed to relatively low levels of $DMSP_d$, had an apparent K_m for DMSP at least 100 times lower than that of a bacterium found in a different environment potentially rich in DMSP (*Alcaligenes* sp. strain M3A which was isolated from the surface of salt marsh sediment). Stefels & Dijkhuizen (1996) and Ishida (1968) also found K_m values of 2.25 and 1.5 mM DMSP for crude extracts of axenic *Phaeocystis pouchetii* and *Gyrodinium cohnii* cells, respectively. These observations suggest that an experimental approach which would allow a discrimination between free-living bacteria, attached bacteria, and phytoplankton contained in the same water sample should result in widely different K_m values depending on the type of organisms considered. In support of this hypothesis, Azam & Hodson (1981) have observed multiphasic kinetics for glucose utilisation by a marine microbial assemblage with a broad range of K_m values reflecting the complexity of the microbial environment where substrates are heterogeneously distributed. Thus, K_m estimated from the bulk-phase of seawater may reflect the combined characteristics of free-living bacteria, attached bacteria, and phytoplankton. The variation in the relative importance of free-living bacteria, attached bacteria, and DMSP-lyase containing phytoplankton could play a key role in DMS dynamics, which could explain the strong spatio-temporal variability in K_m values for DMS production observed by Ledyard (1993). Future studies should discriminate between the role of attached bacteria and phytoplankton cells in the production of DMS by particulate material. In addition, studies should look at the variation of the relative role of free and attached bacteria or phytoplankton themselves on DMS production during the different phases of phytoplankton blooms. This information may considerably increase our capacity to predict (model) *in situ* DMS concentration in seawater, and hence its flux to the atmosphere.

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