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A new source of dimethylsulfide (DMS) for the arctic atmosphere: ice diatoms

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Abstract We report the first evidence that pennate diatoms growing within the bottom layer of first-year ice in the Arctic produce significant amounts of particulate dimethylsulfoniopropionate ($DMSP_p$) and dissolved DMSP+DMS. In 1992 in Resolute Passage, a tributary of Barrow Strait, $DMSP_p$ concentrations within the bottom layer of ice reached 1055 mg S m^{-3} at the end of the vernal bloom, a value one order of magnitude higher than the maximum value reported in antarctic ice. Bottom-ice concentrations in $DMSP_p$ and $DMSP_d$+DMS were significantly correlated with the abundance of the dominant pennate diatom *Nitzschia frigida*. Intracellular concentration in DMSP of ice algae was very low (0.001 pg $cell^{-1}$) at the end of April when algae were light-limited and reached 1.17 pg $cell^{-1}$ in mid-May following an increase in light and algal growth. We calculate that the rapid release of the dissolved DMSP+DMS from the ice into surface waters following the ice break-up will generate a sea-to-air DMS flux of 0.7 mg S m^{-2} d^{-1}, a pulse ten times higher than the mean arctic summer flux. We estimate that this 1-d pulse represents up to 5% of the annual DMS emission in the Arctic.

Introduction

Over oceanic basins, dimethylsulfide (DMS) emissions from pelagic microalgae play an important climatic role by providing additional cloud condensation nuclei and increasing the backscattering of solar radiation (Charlson et al. 1987; Ayers and Gras 1991; Falkowski et al. 1992; Malin et al. 1992). In the Arctic, aerosol SO_4^{2-} is 25 to 35% biogenic in summer and less than 14% at other times of the year (Li and Barrie 1993). Arctic concentrations of atmospheric methane-sulfonate (MSA), a photo-oxidation product of DMS in the air, exhibit significant seasonal and long-term variations (Li et al. 1993). Li et al. suggest that the spring peak in MSA is due to marine DMS emissions from the north east Atlantic, while the summer peak is related to more regional Arctic or high-latitude Atlantic and Pacific sources. The analysis of the Vostok ice core in Antarctica has also revealed the existence of important glacial-interglacial variations in atmospheric MSA (Legrand et al. 1991). These variations are attributed to an increased oceanic emissions of DMS during the later stages of glacial periods.

The contribution of local sources of DMS to the atmospheric MSA signal observed in polar regions may have been underestimated. Bates et al. (1987) reported that DMS annual emissions from the Arctic Ocean represented about 1% of the global oceanic flux. This estimate excludes the potential contribution of pelagic blooms of *Phaeocystis pouchetii*, a significant DMS producer (Keller et al. 1989a), recently observed both in the Antarctic (Gibson et al. 1990) and in the Arctic (Smith et al. 1991). Kirst et al. (1991) have shown that ice algae from the Antarctic produce important quantities of particulate dimethylsulfoniopropionate (DMSP) and proposed that they may also release significant amounts of DMS in the atmosphere. Results from Kirst et al. cannot be extrapolated to the Arctic, where dinoflagellates and prymnesiophytes, the taxa apparently responsible for the production of DMSP in the Antarctic, are scarce (Horner 1985).

The goal of the present study was to determine the potential contribution of ice microalgae to the DMS sea-to-air flux in the Arctic. We investigated the vernal accumulation of particulate DMSP and dissolved DMSP+DMS in first year ice during the bloom of ice algae in Resolute Passage, a tributary of Barrow Strait, High Canadian Arctic.

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Possible causes for temporal variations in DMSP quotas in ice algae were also explored.

Materials and methods

We measured the vernal accumulation of chlorophyll *a*, ice algal cells, particulate DMSP ($DMSP_p$) and dissolved DMSP+DMS ($DMSP_d$+DMS) in bottom ice in Resolute Passage (74°41.19N, 95°15.59W; Fig. 1) from 27 April to 21 May 1992. The sampling site was characterized by a water depth of 125 m, an ice thickness of 1.84 to 1.97 m and a snow cover of 5 cm. Measurements were done at least once a week on the lowest 2 cm of ice-cores, taken with a SIPRE ice corer (7.5 cm i.d.). On three occasions, the vertical distribution of algal abundance, chlorophyll *a*, $DMSP_p$ and $DMSP_d$+DMS in the ice was investigated by removing sections of 5 cm thickness at each 25 cm along the ca. 200 cm ice core. To minimize osmotic stress, the ice samples were melted in surface water filtered onto 0.2-µm polycarbonate membranes (Bates and Cota 1986). Salinities and concentrations determined on ice samples were corrected for the dilution effect of the added seawater as described in Cota and Sullivan (1990) and Harrison et al. (1990). Water samples were also collected at seven depths (0, 2.5, 7.5, 30, 60, 90 and 125 m) underneath the ice with 5-litre Niskin bottles.

The melted ice and water column samples were treated as follows: (1) Two subsamples were filtered on Whatman GF/F filters, extracted for 24 h in 90% acetone for fluorometric (Strickland and Parsons 1972) or spectrophotometric chlorophyll *a* determination (Jeffrey and Humphrey 1975); (2) Two subsamples were filtered onto pre-combusted Whatman GF/F filters which were stored frozen in a desiccator for later determination of particulate organic carbon and nitrogen using a Perkin Elmer elemental analyser (Sharp 1974); (3) Four 20-ml vials were filled with either unfiltered or filtered (Whatman GF/F) sample and 1 ml of 5 *M* KOH for the $DMSP_p$ and $DMSP_d$+DMS determinations (Keller et al. 1989b). All vials were immediately sealed with a Silicone-lined serum cap and held in the dark until analyzed. DMSP (as DMS) was measured on a Varian 3400 gas chromatograph equipped with flame photometric detector and a Chromosil 330 Teflon column (Keller et al 1989b). Two 200-ml subsamples were fixed with either hexamine-buffered formaldehyde (4%) or acidic Lugol's fixative for later identification and counting of coccolithophores and diatom/flagellates, respectively, using the Utermöhl technique (Lund et al. 1958). Subsamples of the filtrate from the water column samples were frozen for analysis of nitrate-NO_3, nitrite-NO_2, phosphate-PO_4 and silicate-SiO_4 using a Technicon AutoAnalyser (Strickland and Parsons 1972). Salinity of the melted ice core was determined with a Solomat MPM 2009 conductivity meter.

Results and discussion

Vertical distribution of microalgae and DMSP in the ice and in the water column

As typically observed in first-year ice in spring, detailed analysis of three ice cores has shown that at least 90% of the algal biomass (chlorophyll *a* and $DMSP_p$), $DMSP_d$+DMS and cell number was concentrated in the lowest 5 cm of the cores (Table 1; only data from 21 May are presented). Chlorophyll *a* concentrations, cell number and $DMSP_p$ concentrations were very low in the water column (Table 1) and represented 9, 25 and 10% of the total ice+water integrated concentrations, respectively. The algal assemblage was dominated by pennate diatoms in the ice and by flagellates in the water column.

Vernal variations in ice algal biomass, $DMSP_p$ and $DMSP_d$+DMS

In April–May 1992, chlorophyll *a* concentrations at the bottom of the ice increased from 35 mg m^{-2} to a maximum value of 147 mg m^{-2} (Fig. 2A), a value two times lower

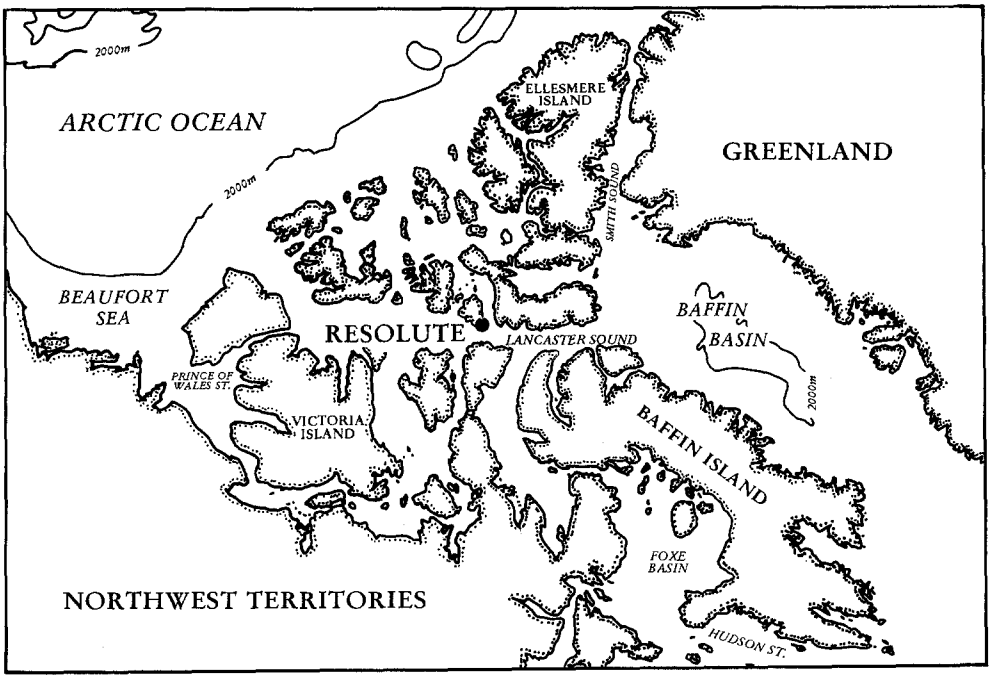

Fig. 1 Location of study site offshore Resolute in Barrow Strait (74°41.19N, 95°15.59W), Northwest Territories, High Canadian Arctic

Table 1 Vertical distribution of chlorophyll *a* concentrations, total cell number, pennate diatoms number, microflagellates number, particulate dimethylsulfoniopropionate ($DMSP_p$) and dissolved dimethylsulfoniopropionate plus free dimethylsulfide ($DMSP_d$+DMS) concentrations in the ice and in the water column on 21 May in Barrow Strait. (*n.d.* not determined)

Depth		Chl *a* (mg m^{-3})	Total cells (10^6 cells m^{-3})	Pennates (10^6 cells m^{-3})	Flagellates (10^6 cells m^{-3})	$DMSP_p$ (mg S m^{-3})	$DMSP_d$+DMS (mg S m^{-3})
Ice depth (cm)							
Top ice	0	1.0	2120	90	0	0.019	0.109
	13	2.0	880	130	50	0.000	0.109
	43	2.1	2950	170	0	0.000	0.089
	73	3.2	n.d.	n.d.	n.d.	0.001	n.d
	103	3.4	4010	190	220	0.000	0.355
	133	11.8	930	370	0	0.000	0.368
	163	16.9	n.d.	n.d.	n.d.	0.000	0.929
Bottom ice	193	2187.2	548083	450700	59600	192.456	481.637
Water depth (m)							
Surface	0	0.20	57.8	6.5	34.2	0.000	0.026
	2.5	0.11	93.2	5.3	62.5	0.000	0.061
	7.5	0.15	141.6	1.8	65.5	0.016	n.d.
	30	0.07	75.5	2.3	35.4	0.029	n.d.
	60	0.07	54.3	4.7	27.7	0.000	n.d.
	90	0.09	53.7	8.8	19.5	0.000	n.d.
	125	0.08	29.5	7.7	11.2	0.000	n.d.

than that measured in previous years at the same location (up to 350 mg m^{-2}, Smith et al. 1990). The growth of ice algae seems to have been light-limited during the whole sampling period, except for a short period of biomass increase (from 6 to 11 May) related to an increase in solar radiation (Gosselin et al. in preparation). During the bloom, particulate DMSP concentrations increased from 0.01 to 34 mg S m^{-2} (Fig. 2C) in the last 2 cm of the core. In this layer, $DMSP_p$ concentration reached 1055 mg S m^{-3}, a value more than two orders of magnitude higher than generally observed in biomass-rich temperate coastal waters (5 mg S m^{-3}, Iverson et al. 1989; 9 mg S m^{-3}, Turner et al. 1988) and one order of magnitude higher than the maximum value reported for the interior ice algal assemblage of the Weddell Sea in the Antarctic (94 mg S m^{-3}, Kirst et al. 1991).

In addition to particulate DMSP, dissolved DMSP+DMS were also found in extremely high concentrations in the bottom layer of the ice, reaching 4.3 mg S m^{-2} (Fig. 2D). Dissolved DMSP+DMS represented ca. 82% of the total DMSP+DMS pool during the initial low biomass period (27 April to 7 May) and ca. 15% during the subsequent period of higher biomass. Similar percentages have been observed in pelagic coastal environments (Turner et al. 1988; Iverson et al. 1989; Matrai and Keller 1993; Levasseur et al. 1994). Dissolved DMSP and DMS are thought to be produced by the lysis of senescent cells (Turner et al. 1988; Matrai and Keller 1993), zooplankton grazing (Dacey and Wakeham 1986; Leck et al. 1990; Levasseur et al. 1994) and bacterial degradation (Kiene 1992). The relative importance of these biological processes to the dynamics of DMS production at the bottom of the ice is still to be determined. It is possible that the low light conditions which prevailed in late April and early May were responsible for the very high fraction of the DMSP pool found in the dissolved phase. As discussed later, the cellular DMSP content of the algae was very low during this period (Fig. 2E), suggesting that DMSP exhudation was important.

Although our sampling protocol and analytical technique do not discriminate between dissolved DMSP and free DMS, freshly collected samples of ice algae had a strong smell of sulfur, indicating that free DMS was present in the ice. Accumulation of DMS at the bottom of the ice may result from the slow rate of gas diffusion through the ice cover (Fanning and Torres 1991; Staubes and Georgii 1993). The low irradiance level at the bottom of the ice (ca. 8 µmol photons m^{-2} s^{-1}; Gosselin et al. in preparation) may also contribute to the accumulation of DMS in bottom ice by preventing the photo-oxidation of DMS to dimethylsulfoxide (DMSO), a DMS loss term reported to be as important as sea-to-air diffusion in the ocean (Brimblecombe and Shooter 1986).

The high $DMSP_p$ and $DMSP_d$+DMS concentrations measured in bottom ice were unexpected since pennate diatoms which were thought to produce very little DMSP (Keller et al. 1989a) represented 91% of the total algal assemblage (Fig. 2B). The pennate diatom assemblage was dominated by *Nitzschia frigida*, *Pseudogomphonema septentrionale*, *Navicula* sp. 6 and two unidentified *Nitzschia* species. Dinoflagellates and prymnesiophytes, the major DMSP producers in the open ocean (Keller et al. 1989a; Gibson et al. 1990) and the presumed producers in antarctic ice (Kirst et al. 1991), represented less than 0.05% of the assemblage. We further investigated the relationship between the variations in DMSP concentrations and the abundance of the major taxa by submitting the data to a Pearson's correlation analysis (Table 2). The concentra-

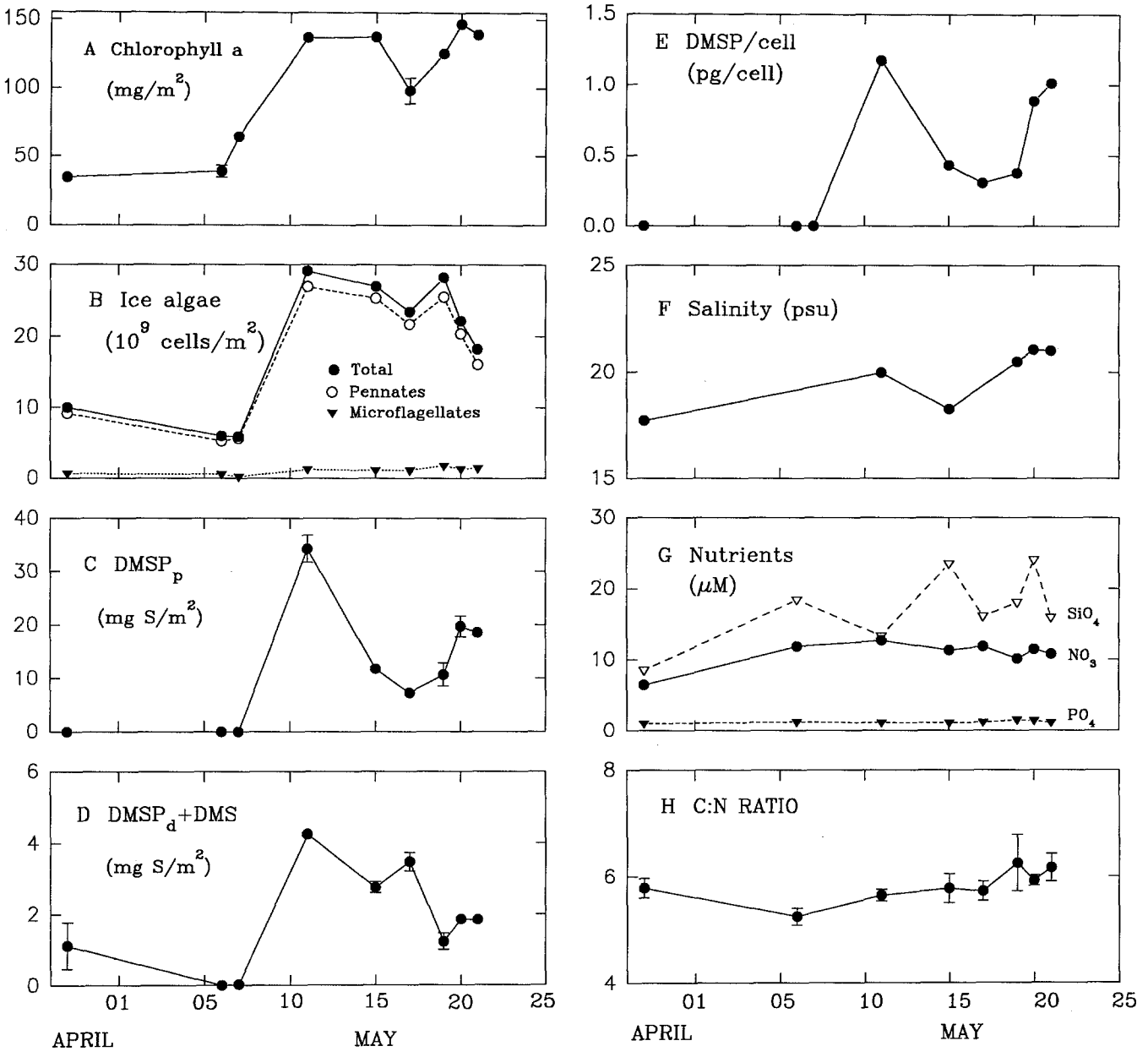

Fig. 2 Vernal variations in: **A** bottom ice chlorophyll *a* concentration; **B** ice algal cell number; **C** bottom ice particulate dimethylsulfoniopropionate ($DMSP_p$) concentration; **D** bottom ice dissolved DMSP+dimethylsulfide ($DMSP_d$+DMS) concentration; **E** DMSP quota of ice algae; **F** salinity of bottom melted ice; **G** nutrient (nitrate-NO_3^-, silicate-SiO_4 and phophate-PO_4) concentrations in surface water underneath the ice; and **H** ratio of particulate organic carbon to particulate organic nitrogen (C:N by weight) of ice algae in Resolute Passage, a tributary of Barrow Strait, High Canadian Arctic. In **A**, **C**, **D** and **H**, all data points represent mean of duplicate samples; error bars represent ±1 SD

tions of $DMSP_p$ and $DMSP_d$+DMS were significantly correlated with the abundance of pennate diatoms and *N. frigida* ($P \leq 0.01$, $N=9$). The correlations between the numbers of microflagellates, dinoflagellates and prymnesiophytes and the concentrations of both $DMSP_p$ and $DMSP_d$+DMS were not significant ($P \geq 0.05$).

Vernal variations in DMSP quotas

DMSP is thought to play an osmoregulatory and cryoprotectant role and it has been hypothesized that ice algae have high intracellular DMSP content as an acclimation to their high salinity and low temperature environment (Kirst et al. 1991). To explore this hypothesis, we estimated the intracellular DMSP content of the arctic ice algal assemblage by dividing the $DMSP_p$ concentrations with the corresponding total algal concentration. The DMSP quotas of the cells exhibited considerable variability, ranging from less than 0.001 to 1.17 pg cell^{-1} (Fig. 2E). The highest value of 1.17 pg cell^{-1} was lower than the maximum value of 1.45 pg DMSP cell^{-1} previously reported for pennate diatoms in culture (Keller et al. 1989a). The elevated DMSP concentrations found in the arctic ice seem to reflect the high ice algal biomass rather than abnormally high DMSP cellular content.

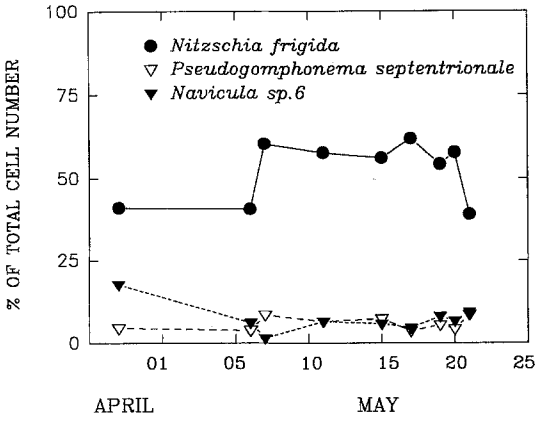

Fig. 3 *Nitzschia frigida, Pseudogomphonema septentrionale* and *Navicula* sp. 6. Temporal variations of the relative contribution (in percentage) of the three dominant pennate diatom species to total cell number

Table 2 Pearson's coefficient of linear correlation between concentrations of particulate dimethylsulfoniopropionate ($DMSP_p$) and dissolved dimethylsulfoniopropionate plus dimethylsulfide ($DMSP_d$+*DMS*) and abundance of the major taxa (*=$P \leq 0.01$)

	$DMSP_p$	$DMSP_d$+DMS
Pennate diatoms	0.73*	0.81*
Nitzschia frigida	0.72*	0.84*
Microflagellates	0.64	0.52
Dinoflagellates	0.28	0.38
Prymnesiophytes	0.05	0.47

The drastic increase in DMSP quotas observed in early May may result either from a change in species composition or in the physiological status of the ice algae. DMSP quotas are highly species-specific in microalgae (Keller et al. 1989a). As shown in Fig. 3, the relative abundance of the dominant pennate diatoms remained relatively constant during the sampling period. Thus, a shift in species cannot explain the increase in DMSP quota observed in May. DMSP quotas of algae are sensitive to changes in salinity and temperature (Vairavamurthy et al. 1985; Karsten et al. 1992). The salinity of the melted bottom ice was also relatively constant (Fig. 2F) and we found no significant relationship between the variations in salinity and DMSP quotas. Although the actual salinity of the bottom-ice brine channels may be as high as 60 psu in first-year ice (Wakatsuchi and Ono 1983), our salinity index suggests that no important variations in salinity have occurred during the sampling period. Algae may respond to small changes in salinity by altering their cellular ion content. Hence, the absence of correlation between the DMSP quota of ice algae and the small variations in salinity observed during our study should not be taken as proof against the role of DMSP as an osmolyte compound. Temperature at the sea-ice interface was also very stable during the sampling period, varying between −1.72 and −1.78°C (R. Ingram, personal communication).

Nitrogen supply may also influence DMSP quotas in macro- and micro-algae (Vairavamurthy et al. 1985; Turner et al. 1988; Gröne and Kirst 1992). DMSP, glycine betaine and proline are compatible solutes and it has been suggested that microalgae would preferentially synthesize the N-free solute DMSP under nitrogen-stress conditions (Vairavamurthy et al. 1985; Turner et al. 1988). Again, we must reject this explanation since our data indicate that the ice algae were never nitrogen deficient during the sampling period. This is supported by the fact that nitrate concentrations in surface water were always higher than 5 μM (Fig. 2G) and that C:N ratios of the particulate matter in bottom-ice remained close to the critical value of 5.7 observed in nutrient sufficient microalgae (Fig. 2H; Redfield et al. 1963).

In conclusion, neither shifts in species composition, salinity, temperature or nitrogen supply can explain the drastic change in DMSP quotas. The correspondence between the increase in DMSP quotas and algal biomass argues for a light control of DMSP biosynthesis, as evidenced for macro-algae by Karsten et al. (1992). Further work is needed to test this hypothesis.

Contribution of ice algae to the arctic sea-to-air DMS flux

DMS produced in bottom ice will probably vent to the atmosphere by three major mechanisms acting on different spatio-temporal scales: (1) through openings in the ice during the entire season, as was recently shown for bromoform gases produced by ice algae (Sturges et al. 1992); (2) at the ice margin during the ice melt when under-ice water carrying sedimented ice algae is advected to open water; (3) during ice break-up over a wider area.

In spite of the uncertainty associated with the relative importance of the mechanisms involved in the release of DMS to the atmosphere, we estimated the maximum contribution of ice algae to the DMS ocean-atmosphere flux in the Arctic. To keep our estimate conservative, we first assumed that none of the particulate DMSP will make its way to the atmosphere due to the rapid sinking of the particles following the ice break-up. We then assumed that DMS represented 20% of the $DMSP_d$+DMS pool (Turner et al. 1988) and that the minimum and maximum amounts of DMS found in bottom ice in May are abruptly released and mixed into the upper mixed layer of 2 m which normally forms during the ice break-up (Lepage and Ingram 1991; Fortier et al. in press). The resulting DMS concentrations would be 0.12 and 0.43 mg S m^{-3}, respectively, values one order of magnitude higher than the mean summer DMS concentrations (Bates et al. 1987). It is important to note that a deepening of the mixed layer will proportionally reduce the DMS concentration in the water and sea-to-air flux. Bates et al. (1987) estimated a summer sea-to-air flux of DMS in the Arctic of 0.067 mg S m^{-2} d^{-1}. Using the same exchange coefficient (Vp=1.53 m d^{-1}) and our estimated minimum and maximum near-surface DMS concentrations after break-up, we obtain DMS sea-to-air

fluxes varying between 0.18 and 0.66 mg S m^{-2} d^{-1}, values ten times higher that the mean summer flux. Since the system is not in steady-state, the fluxes will last 1 to 2 d and their intensity will decrease with the decline of the surface DMS concentration. Although not considered in our calculations, the ice $DMSP_p$ pool may also contribute to the magnitude and duration of the DMS flux following the ice break-up. The flushing of the ice algae into a low salinity environment after break-up may lead to a rapid exudation of osmoprotecting molecules such as DMSP, providing an additional source of DMS via the degradation of dissolved DMSP.

The vernal pulse of DMS may contribute significantly to the summer increase of atmospheric MSA in the Arctic (Li and Barrie 1993; Li et al. 1993). Interannual variations in nutrient supply and extent of first-year sea ice affect significantly the magnitude of ice algal blooms (Cota et al. 1991) and presumably also the DMS production. Ice diatoms may thus be also responsible for the changes in atmospheric MSA concentrations observed in polar regions from year to year (Li and Barrie 1993; Li et al. 1993) and between glacial and inter-glacial periods (Legrand et al. 1991).

We estimated the total emission of DMS by ice algae in the Canadian Archipelago and the entire Arctic by multiplying the extent of the annual ice area by the estimated DMS fluxes of 0.18 and 0.66 mg S m^{-2} d^{-1} previously calculated. This assumed that most of the DMS produced by ice algae will make its way into the atmosphere in a 1-d pulse as discussed above. It also assumed that vernal accumulation of DMSP observed in the Barrow Strait is representative of the whole Arctic area, which is probably not the case. The ice algal biomass found at the end of the vernal bloom in the Barrow Strait is generally higher than found in other parts of the Arctic (Cota et al. 1991; Legendre et al. 1992). Thus, our estimated DMS flux should probably be viewed as a potential maximum. Ice algae will then produce between 0.07 and 0.26×10^6 kg S yr^{-1} in the Canadian Archipelago and between 1.3 and 4.6×10^6 kg S yr^{-1} in the entire Arctic (Table 3). These calculations suggest that the spring ice algal bloom could be responsible for at most 5% of the annual ocean flux of DMS in the arctic atmosphere. The contribution of ice algae to the arctic DMS flux seems to be slightly less that their contribution to the total annual primary production in the Arctic Ocean (north of the 65° latitude), which is currently estimated at 4 to 26% (Legendre et al. 1992).

Table 3 Estimated global emissions of dimethylsulfide (*DMS*). Estimate for entire Arctic comes from Table 6 in Bates et al. (1987), but excludes area covered with multi-year ice (ca. 8×10^{12} m^2)

Source	Area (10^{12} m^2)	Emission (10^6 kg S yr^{-1})
Canadian Archipelago annual ice algae (present study)	0.4	0.07–0.26[a]
Arctic annual ice algae (present study)	7.0	1.3–4.6[a]
Arctic open water (from Bates et al. 1987)	11	89

[a] Emission rates based on minimum and maximum bottom ice $DMSP_d$+DMS concentrations measured in May

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