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Influence of phytoplankton taxonomic profile on the distribution of dimethylsulfide and dimethylsulfoniopropionate in the northwest Atlantic

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ABSTRACT: Distributions of dimethylsulfide (DMS) and dimethylsulfoniopropionate (DMSP) were surveyed in surface waters of the NW Atlantic in May 1998, a few weeks after the spring bloom. A triangular transect extending from Nova Scotia to Bermuda and northeast toward Newfoundland encompassed 4 major oceanic biogeochemical provinces: Northwest Atlantic Continental Shelves (NWCS), Gulf Stream (GFST), North Atlantic Subtropical Gyre (NAST) and the North Atlantic Drift (NADR). Surface concentrations of DMS and DMSP were highest in the NADR, with peaks up to 8.9 nM DMS, 44.1 nM dissolved DMSP ($DMSP_d$) and 240 nM particulate DMSP ($DMSP_p$). The phytoplankton assemblage throughout the study area was dominated by dinoflagellates and prymnesiophytes. Statistically significant correlations were observed between the abundance of dinoflagellates and prymnesiophytes and the concentrations of DMS and DMSP along the transect. Size-fractionation of $DMSP_p$ revealed the 2 to 11 µm fraction to be the most important contributor to total DMSP (mean 72%, range 27% to 91% of total). In the region of the highest DMS(P) concentrations, the phytoplankton assemblage was dominated by prymnesiophytes and dinoflagellates, with *Chrysochromulina* spp. and *Gyrodinium flagellare* being the most abundant. The abundance of these taxa showed a marked correlation with total $DMSP_p$ and with the 2 to 11 µm size fraction of DMSP in which these cells are found. This plankton assemblage was observed both early and late in the transect, which may indicate that it is a persistent feature along the northern side of the Gulf Stream at this time of year. Sea-air flux of DMS was calculated based on 2 different models. The results showed peaks in flux corresponding to the peaks in DMS concentration in surface water. Pooling and averaging the values for each biogeochemical province reveals DMS concentrations lower than the average values of an existing global DMS database for the same regions and times.

KEY WORDS: Dimethylsulfide · DMS · Dimethylsulfoniopropionate · DMSP · Prymnesiophyte · Dinoflagellate · *Chrysochromulina* spp. · *Gyrodinium flagellare*

INTRODUCTION

The natural sulfur cycle in the oxic marine environment is dominated by processes involving dimethylsulfide (DMS) and its precursor molecule, dimethylsulfoniopropionate (DMSP). DMSP is produced by phytoplankton, where it may serve as an osmolyte (Vairavamurthy et al. 1985) and cryoprotectant (Kirst et al. 1991). When released into the water column via cell lysis or exudation, it is consumed via 2 principal pathways: the major fraction (>70%) is demethylated by bacteria to 3-methiolpropionate (Kiene & Linn 2000a) while the minor fraction (<30%) is enzymatically

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cleaved to DMS and acrylate, principally by bacteria (Kiene & Service 1991, Ledyard & Dacey 1994, Wolfe 1996) and some species of phytoplankton (Stefels & Dijkhuizen 1996, Steinke et al. 1998). DMS is volatile, and is lost from the surface waters by ventilation to the atmosphere, where it is implicated in a series of physico-chemical reactions that lead to the formation of sulfate aerosols (reviewed by Andreae 1990). Sulfates are amongst the largest natural sources of aerosols, and, over remote marine areas, DMS release from surface waters is the principal source of aerosols in the troposphere (Clarke et al. 1998). Sulfate aerosols play a significant role in the formation of cloud condensation nuclei, the distribution of which controls the formation, persistence and albedo of clouds. A hypothesis has been proposed linking marine phytoplankton populations to long-term climate control via this indirect mechanism (Charlson et al. 1987). However, it is a difficult hypothesis to verify because it encompasses a wide range of temporal and spatial scales and presents considerable difficulty in establishing a link between oceanic and atmospheric measurements. Nevertheless, this so-called 'CLAW' hypothesis (the acronym is derived from initials of the authors) has stimulated much interest in DMS and its distribution in the ocean. A recent compilation of existing DMS data from various sources (Kettle et al. 1999, Kettle & Andreae 2000) paints an approximate global picture of DMS in surface waters, but there are many areas of sparse data coverage, and much remains to be learned about DMS distributions and their controlling mechanisms on both spatial and temporal scales. The present study seeks to fill some of those gaps.

For the purpose of climate modelling, it would be desirable to predict DMS concentrations and fluxes from fundamental oceanographic variables such as temperature, salinity and chlorophyll *a* (chl *a*) concentrations. This goal has proven elusive due to the many processes that influence the production and transformation of DMSP. DMSP production is species-specific, with certain taxonomic groups (principally dinoflagellates and prymnesiophytes) being especially rich in DMSP, while others (including most diatoms) are not (Keller et al. 1989). This, combined with the fact that transformation of DMSP to DMS occurs largely indirectly via bacteria, means that there is no simple relationship between the abundance of phytoplankton and the amount of DMS produced. However, regardless of the many factors which can influence the distribution of DMSP and DMS, it is likely that, in a particular region or ecosystem, a few dominant processes will be the primary determinants of DMS concentration.

This paper uses simultaneous measurements of DMS, DMSP, temperature, chl *a* and phytoplankton abundance, along with other variables, to relate the spatial distributions of organic sulfur to the oceanographic conditions across several biogeographic provinces of the NW Atlantic. Relationships between these variables will be explored, and the significance of 2 phytoplankton taxa (the prymnesiophyte *Chrysochromulina* spp. and the dinoflagellate *Gyrodinium flagellare*) will be highlighted. This approach is based on the rationale of providing broad coverage across ecosystem boundaries to help elucidate the factors that influence DMS distributions. The results of this study suggest that dinoflagellates and prymnesiophytes, including *Chrysochromulina* spp. and *G. flagellare*, may dominate the production and distribution of DMS and DMSP in this region of the NW Atlantic at this time of year. The data presented here comprise part of a larger data set covering several years of observations in this region, including *in situ* and shipboard incubations, which is described in part elsewhere (Scarratt et al. 2000b).

MATERIALS AND METHODS

The May 1998 cruise track extended from Nova Scotia south to Bermuda and northeast to the North Atlantic Drift region (Fig. 1). The cruise track was designed to pass through several of the biogeochemical provinces defined by Longhurst (1998) as follows (abbreviations in parentheses): Gulf Stream (GFST), North Atlantic Subtropical Gyre (NAST), North Atlantic Drift (NADR) and Northwest Atlantic Continental Shelves (NWCS). At 6 h intervals along the transect, profiles were taken for salinity, temperature, and chl *a* fluorescence using a SeaBird 9/11 Plus CTD. A rosette sampler equipped with 10 l Niskin bottles was used to collect water samples. At each station, an initial profile to 200 m identified the depth of the chl *a* fluorescence maximum, and bottles were filled at that depth and just below the surface (ca. 5 m). Related data from concurrent shipboard incubation experiments describing DMS and DMSP production and consumption kinetics at some of these stations are presented by Scarratt et al. (2000b).

Seawater samples for DMS and DMSP analyses were collected from the Niskin bottles immediately after the rosette was lifted aboard. Water was transferred from the Niskins into 500 ml HDPE bottles using a short length of silicone tubing. The tip of the tubing extended to the bottom of the bottle to minimize the formation of bubbles. The bottles were filled to the top, leaving minimal headspace, and water was allowed to overflow before sealing. Processing the samples for DMS and DMSP analyses (see below) was begun immediately after collection. Samples for other analyses

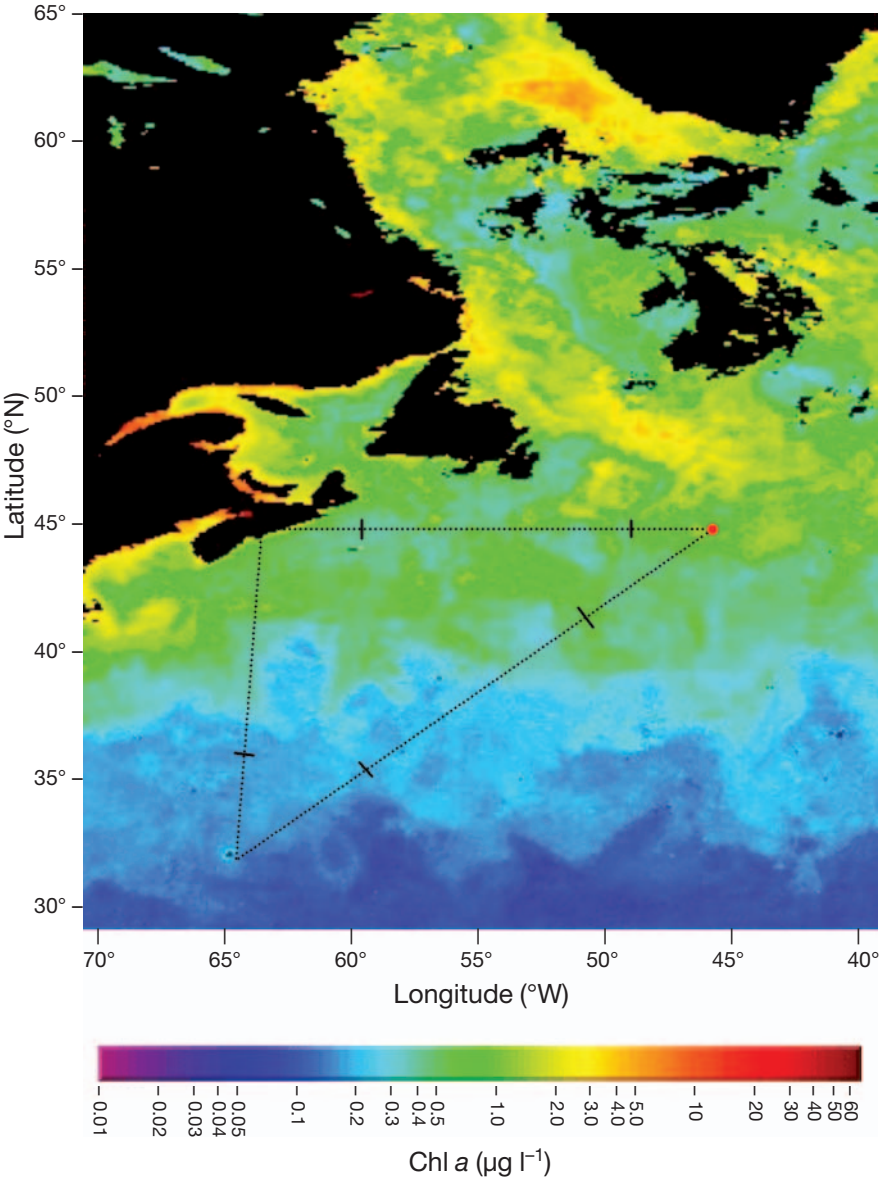

Fig. 1. Map of study region showing the cruise track (dashed line). Tick marks along transect denote 500 nautical mile intervals. The red dot indicates the approximate location of maximum dimethylsulfide (DMS) and dimethylsulfoniopropionate (DMSP) concentrations as well as the profile shown in Fig. 5. The color background is a SeaWiFS composite image of chlorophyll *a* for May 1998

were collected from the Niskin bottles into 7 l, foam-insulated carboys (Thermos) from which sub-samples were taken. Nitrate samples were stored frozen and analyzed after the cruise using a Technicon Auto-Analyser (Strickland & Parsons 1972). Salinity samples were processed aboard ship using a Guildline Autosal 8400B salinometer. Chl *a* samples were filtered on 25 mm GF/F filters, extracted in 90% acetone, and analyzed aboard using the fluorometric procedure of Parsons et al. (1984). Samples were also fixed in acidic Lugol's solution for later identification, enumeration and size determination of phytoplankton and microzooplankton (Lund et al. 1958). Picoplankton were not enumerated.

Size-fractionation of particulate DMSP ($DMSP_p$) was performed by gravity filtration of 100 to 250 ml of seawater on a sequential series of four 47 mm filters. The filter series comprised 20 and 11 µm nylon net filters (Millipore), plus 2 and 0.7 µm glass-fiber filters (GMF and GF/F Whatman, respectively). Filtration of 100 ml of seawater lasted <1 min for the 20, 11 and 2 µm filters and <10 min for the 0.7 µm filter. Each filter was placed in a 25 ml serum bottle filled with 23 ml of nanopure water and 1 ml of 10 N KOH crimp-sealed with a gray butyl septum and aluminum seal. For dissolved DMSP ($DMSP_d$) determination, 23 ml of the final filtrate (<0.7 µm) was added to 1 ml of 10 N KOH and immediately sealed. DMSP was allowed to react for a minimum of 24 h in the dark at 4°C. The strong alkali treatment decomposes DMSP quantitatively and stoichiometrically to DMS and acrylate (Dacey & Blough 1987). The measured quantity of DMS in filtered samples following KOH addition thereby represented the total amount of $DMSP_d$ plus DMS. $DMSP_d$ was computed as the difference between $DMSP_d$ + DMS and DMS. All DMSP samples were analyzed within 4 wk. Experiments conducted in our laboratory have shown that DMSP samples may be stored for this period of time without significant deterioration. For DMS determination, filtrate from the final stage was decanted carefully into a serum vial and immediately sealed. To save time, DMS samples were collected before the entire 250 ml of filtrate had passed through the apparatus, and thus were typically analyzed within 15 min of being taken from the Niskin bottles. Organic sulfur analyses were performed by gas chromatography using the methods described by Scarratt et al. (2000a,b). Most of the DMSP samples were measured on a Varian 3400 gas chromatograph (GC) equipped with a flame photometric detector (FPD) and a Chromosil 330 Teflon column (2.4 m, 1/8 inch o.d., Supelco). All the DMS samples and the more dilute DMSP samples were measured on a Varian STAR 3400 CX GC equipped with

a pulsed flame photometric detector (PFPD) and a SPB-1 Sulfur capillary column (30 m, 4.0 µm thickness, 0.32 mm i.d., Supelco). DMSP standards were prepared from a volumetric solution of DMSP-hydrochloride (Research Plus) and dispensed into KOH-containing serum vials as for the samples above. DMSP standards were prepared at intervals during the cruise so that the stored DMSP samples could be calibrated against standards of the same age. DMS standard gas (DMS in He) was prepared using a permeation tube apparatus (Kin-Tek) connected directly to the purge-and-trap system. The analytical method has a precision of ca. 10% and a minimum quantification limit for both DMS and $DMSP_d$ of ca. 0.08 nM.

In addition to the Niskin bottle samples described above, samples were also collected from the ship's continuous seawater pump while the vessel was underway (intake depth 3 m). Samples were taken every 2 h between the profile stations for the same variables as in the Niskin-derived samples, beginning after the ship passed Bermuda (ca. Mile 700) and continuing until the end of the transect. Temperature was measured with a thermistor probe in the pump outlet, while all other measurements were performed as described above for the Niskin-derived samples. Wind speed was recorded every 30 min on the ship's bridge, and these data (along with surface water temperature and DMS concentration) were used to calculate the Schmidt number, piston velocity and sea-air flux of DMS for all surface DMS measurements (both Niskin bottles and pump). The parameterizations of Saltzman et al. (1993) were used for the Schmidt number, and those of Liss & Merlivat (1986) and Wanninkhof (1992) for piston velocity and DMS flux.

On 11 May 1998, the ship passed through a region of elevated DMS concentrations near 44° 1′ N, 45° 52′ W (Mile 1825 of the transect), where the profile in Fig. 5 was obtained. After proceeding further northeast to undertake other experiments, the ship returned to the high-DMS region, where several profiles and pump samples were taken to determine the vertical distribution of the DMS patch and its horizontal extent (approximately 20 n miles in diameter). The interval between the first and second visits to the high-DMS region was approximately 36 h. The positions occupied were not exactly the same, but the CTD profiles indicate that they were representative of the same water mass and that their DMS concentrations were similar.

RESULTS

General conditions

The background of Fig. 1 is a SeaWiFS chl *a* false-color composite image of the NW Atlantic for the month of May 1998, which clearly shows the difference between the oligotrophic waters of the Sargasso Sea and the nutrient-rich waters to the north. Several Gulf Stream meanders are clearly visible. This image also shows that there were no regions of high chl *a* near the cruise track, with maximum detected concentrations <2 µg l^{-1}. Images of the same region during the month prior to the cruise (April 1998) show chl *a* concentrations as high as 5 µg l^{-1}, indicating that an intense spring bloom had occurred prior to the cruise period. Fig. 2 shows the prevailing conditions of sea-surface temperature (SST), salinity, chl *a* and nitrate concentration as determined from surface rosette (≤5 m) and pump samples along the transect. The graph is divided into vertical sections corresponding with the approximate boundaries of the biogeochemical provinces of Longhurst (1998) (NWCS, GFST, NAST, NADR). The positions of the boundaries between provinces were determined based on disconti-

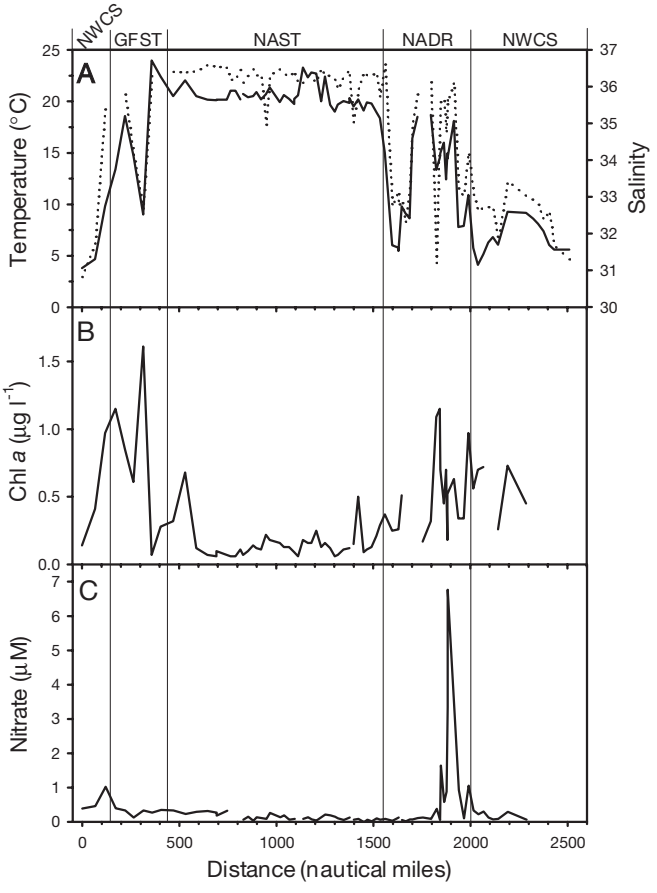

Fig. 2. Surface values (Niskin and pump samples) for entire transect of (A) sea surface temperature (solid line) and salinity (dotted line), (B) chlorophyll *a*, and (C) NO_3^- concentration. Breaks in the lines indicate missing data. Vertical lines show approximate divisions of biogeochemical provinces (Longhurst 1998), see 'Materials and methods' for unabbreviated designations

nuities in the surface temperature and salinity data (Fig. 2A) and by visual inspection of SeaWiFS and AVHRR (SST) satellite images (not shown). This cruise took place after decline of the spring bloom, so the water column was generally stratified with low nitrate and chlorophyll concentrations at the surface. Sea-surface temperatures (Fig. 2A) varied from a minimum of 3.8°C on the continental shelf (NWCS) to 24°C in the GFST, with a large region (NAST) near 20°C. The temperature data clearly show the prominent feature of a Gulf Stream meander or ring early in the transect as well as the cold southern extension of the Labrador Current in the NADR region. These features are also clearly visible in the salinity data (Fig. 2A), which showed a very similar pattern. Chl *a* concentrations near the surface (Fig. 2B) were generally low along most of the transect, varying between 0.06 and 1.6 µg l^{-1} (mean = 0.35 µg l^{-1}). Maximum concentrations were measured in the GFST and NADR regions, while very low levels were observed in the NAST. Nitrate concentrations in the surface water (Fig. 2C) were low throughout the study area (mean = 0.43 nM). The exception was the NADR region, where a shallow nitricline and surface nitrate concentrations up to 6.7 nM were observed, coinciding with slightly higher chl *a* levels than in the surrounding waters.

DMS and DMSP distributions

Fig. 3 shows DMS, $DMSP_d$ and $DMSP_p$ concentrations in surface samples (<5 m depth). DMS concentrations remained relatively low (mean = 1.9 nM) across much of the study area, although there was considerable variation, with some stations in the Gulf Stream and near Bermuda having undetectable levels of DMS (Fig. 3A). As the transect continued northeastward, the DMS concentrations generally increased. Peaks of DMS up to 8.9 nM occurred in the NADR region with a further isolated peak on the continental shelf near the end of the transect. As will be shown below, these peaks were associated with elevated abundances of dinoflagellates and prymnesiophytes. $DMSP_d$ concentrations followed a similar trend (mean = 11.3 nM), with low levels being observed in the southern part of the study area and increasing concentrations to the northeast (Fig. 3B). Peaks in $DMSP_d$ up to 44 nM were present in the NADR region, close to but not necessarily coincident with those of DMS. Similarly, $DMSP_p$ concentrations remained below 50 nM (mean = 44.1 nM) for much of the transect, but increased markedly to a maximum of 240 nM in the NADR before declining again on the continental shelf (Fig. 3C). The peaks of $DMSP_p$ were coincident with those of $DMSP_d$ but not necessarily DMS.

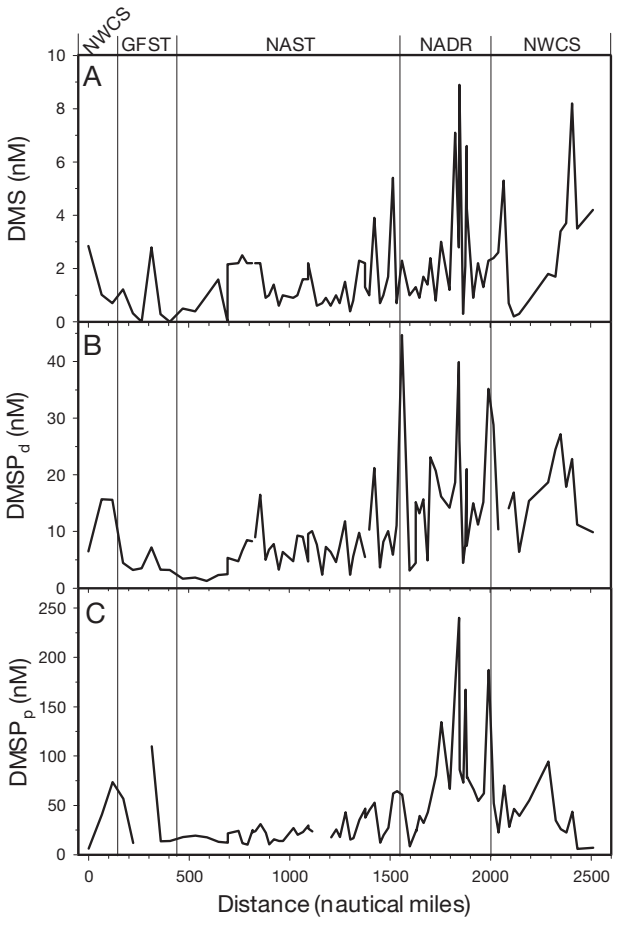

Fig. 3. Surface values (Niskin and pump samples) for entire transect of (A) DMS, (B) $DMSP_d$ (dissolved) and (C) $DMSP_p$ (particulate) concentrations. Breaks in the lines indicate missing data. Vertical lines show approximate divisions of biogeochemical provinces (Longhurst 1998)

Plankton species assemblage

Enumeration and identification of phytoplankton and microzooplankton were performed at selected stations in each biogeochemical province (19 stations in total). Picophytoplankton (<2 µm diameter) were not enumerated, so their contribution to the overall population (and chl *a*) cannot be estimated, though they probably represent a large fraction, especially in oligotrophic waters (Agawin et al. 2000). At several places along the transect (especially in the NADR region), large populations of prymnesiophytes were detected, mainly *Chrysochromulina* spp. (up to 1.4×10^6 cells l^{-1}) as well as the dinoflagellate *Gyrodinium flagellare* (up to 4.8×10^5 cells l^{-1}). Fig. 4A shows the abundances of 4 major taxonomic divisions (diatoms, dinoflagellates, prymnesiophytes and other species), in addition to the abundances of *G. flagellare* and *Chrysochromulina* spp. for 19 stations along the transect. At several

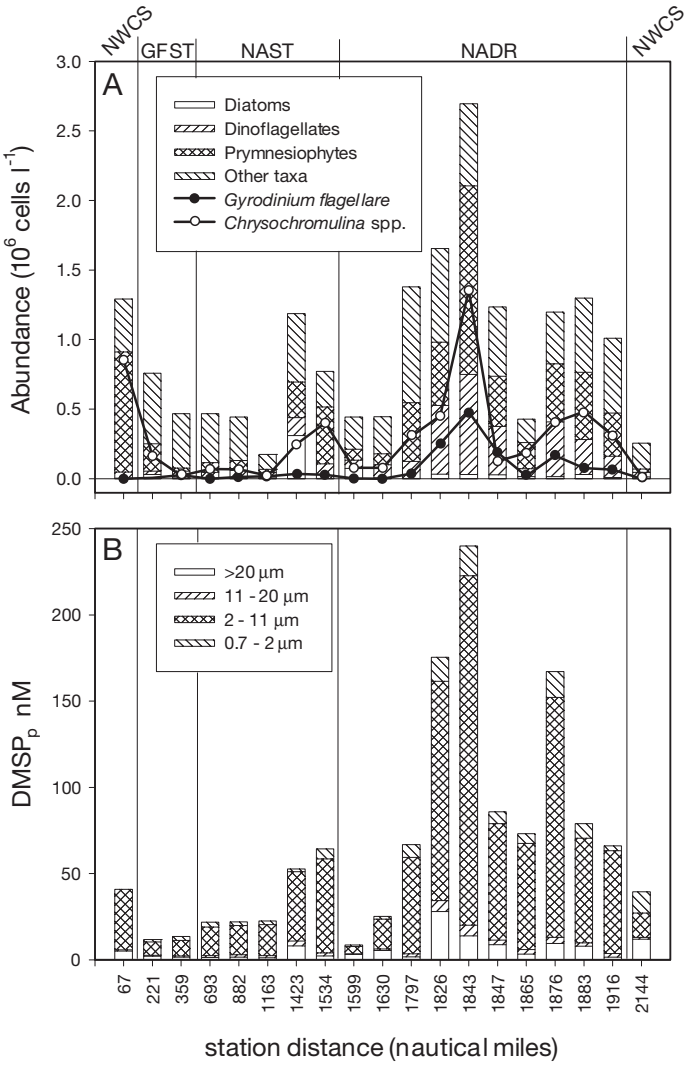

Fig. 4. (A) Bars: Abundance of major phytoplankton groups in surface samples at 19 stations. Lines: Abundance of the dinoflagellate *Gyrodinium flagellare* and the prymnesiophyte *Chrysochromulina* spp. (B) Size-fractionation of $DMSP_p$ in surface samples at the same 19 stations. Vertical lines show approximate divisions of biogeochemical provinces (Longhurst 1998). Note that to improve the clarity of the plot, the *x*-axis scale is nonlinear, and the stations are not in reality equidistant

stations, *G. flagellare* and *Chrysochromulina* spp. together comprised >50% of the total phytoplankton population (Fig. 4A). At 1 station, *Chrysochromulina* spp. alone accounted for 66% of the population. The maximum abundance of dinoflagellates and prymnesiophytes occurred at 1 station in the NADR region, which was also the location of the maximum $DMSP_p$ and $DMSP_d$ concentrations. Two adjacent stations (also rich in the same taxa) had the maximum concentrations of DMS and high concentrations of $DMSP_d$ and $DMSP_p$.

$DMSP_p$ size fractionation

Fig. 4B shows the concentrations of particulate DMSP in 4 size fractions at the same stations as the phytoplankton abundance data in Fig. 4A. The dominant size fraction at most stations was 2 to 11 µm (mean 72%, range 27 to 91% of total $DMSP_p$). The >20 µm fraction ranked second at several stations, especially in the NADR region. The 0.7 to 2 µm and 11 to 20 µm fractions were minor contributors, although at the DMSP-rich stations of the NADR the 0.7 to 2 µm fraction was consistently present at concentrations >2 nM. The similarity of the overall pattern in Fig. 4A,B illustrates graphically the correspondence between $DMSP_p$ and phytoplankton abundance. It should also be noted that the major size fraction (2 to 11 µm) should encompass the majority of cells of both *Chrysochromulina* spp. and *Gyrodinium flagellare*, whose mean diameters were both measured at approximately 8 µm. This is reflected in the Spearman correlations described below.

Spearman rank correlations

Table 1 shows the results of 2-tailed Spearman nonparametric rank correlations of DMS, $DMSP_d$ and size-fractionated $DMSP_p$ (total plus 4 size classes) with the abundance of the 4 major taxonomic divisions, plus *Chrysochromulina* spp., *Gyrodinium flagellare* and the total chl *a* biomass for the same 19 stations. These correlations include data from surface samples only and do not take into account concentrations at depth. A very significant relationship ($r_s = 0.83$) was observed between total $DMSP_p$ concentration and the abundance of dinoflagellates. Significant correlations ($0.72 \leq r_s \leq 0.75$) were also present between total $DMSP_p$ and prymnesiophytes and between $DMSP_d$ and both dinoflagellates and prymnesiophytes. DMS concentration was very significantly correlated with dinoflagellate abundance but more weakly correlated with prymnesiophytes. Similarly, significant correlations were obtained between total $DMSP_p$ and abundances of *Chrysochromulina* spp. and *G. flagellare*, respectively, the most abundant prymnesiophyte and dinoflagellate. However, the relationships between these 2 genera and $DMSP_d$ and DMS were weaker. No significant correlation was observed between any of the 3 major sulfur pools and diatom abundance, and only weak relationships were present with other taxa. When size-fractionated $DMSP_p$ was used, the strongest relationships were between algal abundance (dinoflagellates and prymnesiophytes, including *G. flagellare* and *Chrysochromulina* spp.) and the 2 to 11 µm size fraction. This is the size fraction in which these taxa were found, based on microscopic examination of the samples. Sig-

Table 1. Spearman's rank correlation coefficient (r_s) between DMS, $DMSP_d$, size-fractionated $DMSP_p$, chlorophyll *a* and the abundance of major taxonomic groups of phytoplankton in surface samples at 19 stations along the transect (2-tailed tests: $^{*}0.01 < p \leq 0.05$, $^{**}0.001 < p \leq 0.01$, $^{***}p \leq 0.001$)

Phytoplankton taxon	DMS	$DMSP_d$	$DMSP_p$				
			Total	0.7–2 µm	2–11 µm	11–20 µm	>20 µm
Diatoms	0.14	0.18	0.19	0.09	0.15	0.34	0.61**
Dinoflagellates	0.72***	0.72***	0.83***	0.58*	0.83***	0.78***	0.53*
Prymnesiophytes	0.63**	0.74***	0.75***	0.39	0.72***	0.45	0.48*
Chrysochromulina spp. only	0.56*	0.68**	0.72***	0.36	0.70**	0.42	0.44
Gyrodinium flagellare only	0.56*	0.63**	0.82***	0.68**	0.84***	0.81***	0.41
All other taxa	0.42	0.64**	0.47*	0.32	0.44	0.42	0.32
Chlorophyll *a*	0.40	0.63**	0.70**	0.43	0.67**	0.63**	0.72***

nificant correlations were also present between the various DMSP pools (except the 0.7 to 2 µm size fraction) and chl *a*, as might be expected in an environment where the phytoplankton biota is dominated by DMSP-producers. There were no significant correlations with either temperature or nitrate concentrations (results not shown).

Profiles in the *Chrysochromulina* spp./*Gyrodinium flagellare* bloom region

Several profiles were taken while the ship crossed and re-crossed this area of elevated DMS concentrations. Fig. 5A shows profiles of water temperature, salinity and density (σ_t) from a representative station in this region (44° 1′ N, 45° 52′ W). Fig. 5B shows chl *a* (by *in situ* fluorometer), DMS, $DMSP_p$ and NO_3^- from the same station. High abundances of *Chrysochromulina* spp. (4.5×10^5 cells l^{-1}) and *Gyrodinium flagellare* (2.5×10^5 cells l^{-1}) were found in the surface waters at this location, representing 27 and 10%, respectively, of the total phytoplankton population. The temperature structure of the water column was complex, with interleaving layers of warmer and cooler water in the upper 100 m, although similar variations in salinity result in a fairly smooth density structure. The profiles of DMS(P) show that the surface concentrations of DMS and

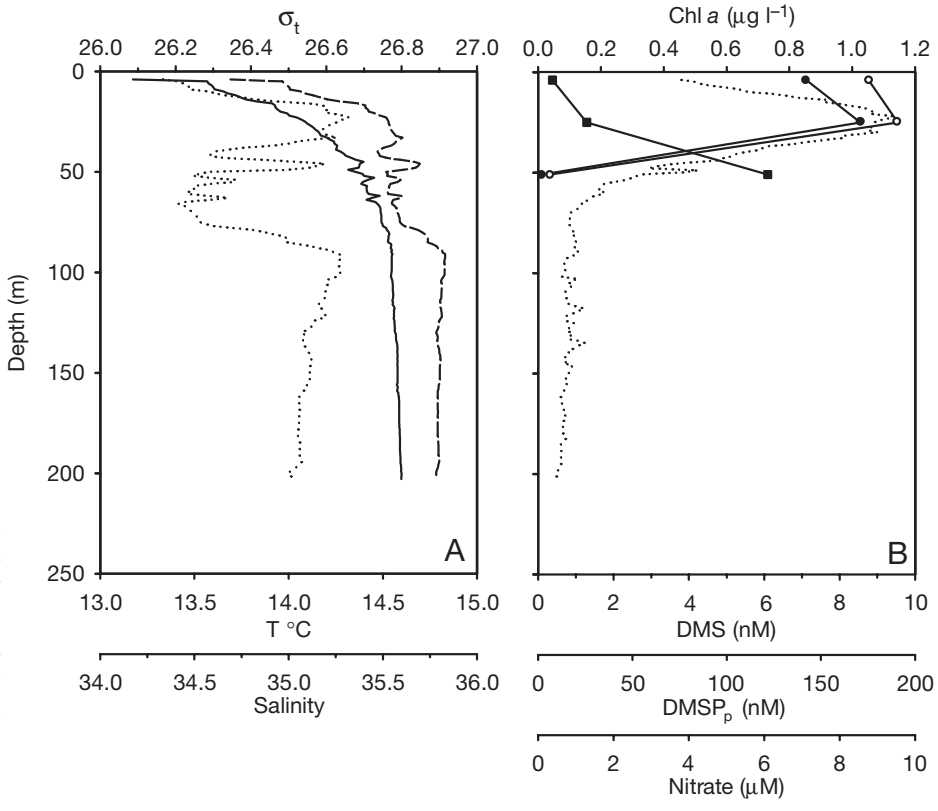

Fig. 5. Profiles at a single station (44° 1′ N, 45° 52′ W), where abundant *Chrysochromulina* spp. and *Gyrodinium flagellare* populations were found, along with high concentrations of DMS and DMSP: (A) water temperature (dotted line), salinity (dashed line) and density (σ_t, solid line). (B) Chlorophyll *a* fluorescence (dotted line), DMS (●), $DMSP_p$ (○), and NO_3^- (■)

$DMSP_p$ were high (7.1 and 175.5 nM respectively), with a slight subsurface maximum, declining rapidly to near-0 concentrations at 50 m. Chl *a* peaked at ca. 1.1 µg l^{-1} at a depth of 25 m, declining to low levels below 50 m. Nitrate was low at the surface, increasing rapidly below the chlorophyll maximum.

DMS:chl *a* and $DMSP_p$:chl *a* ratios

The ratios of DMS:chl *a* and $DMSP_p$:chl *a* are indices of the relative concentrations of sulfur compounds in terms of phytoplankton biomass (Fig. 6). Values of DMS:chl *a* were generally higher in the NAST than in more northerly regions, with a minimum value near 0 in the GFST and a maximum near 40 nmol μg^{-1} in the NAST northeast of Bermuda. As the transect progressed northeastwards, the ratio diminished to approximately 10 nmol μg^{-1}, with transient spikes in the range of 20 to 30 nmol μg^{-1}. $DMSP_p$:chl *a* showed a similar pattern overall, but with values more than an order of magnitude higher. An isolated large spike occurred in the NADR (790 nmol μg^{-1}), though in general the values here were less than in the NAST, where they ranged from 100 to 300 nmol μg^{-1}, with occasional values near 400 nmol μg^{-1}.

Sea-air DMS flux and comparisons to modelled distributions

The sea-air flux of DMS is of prime interest in terms of climate. Fig. 7 shows the calculated sea-air flux of DMS based on the models of Liss & Merlivat (1986) and Wanninkhof (1992) along the whole transect. The Wanninkhof model yields DMS fluxes ca. 2-fold higher than that of Liss & Merlivat. The latter is based on artificial tracer studies in a small lake and as such may not perform well in open-ocean systems where fetch is unlimited (Wanninkhof 1992). The Wanninkhof model probably overestimates fluxes at high wind speeds, but wind speeds in this study were generally moderate, so this effect should be limited.

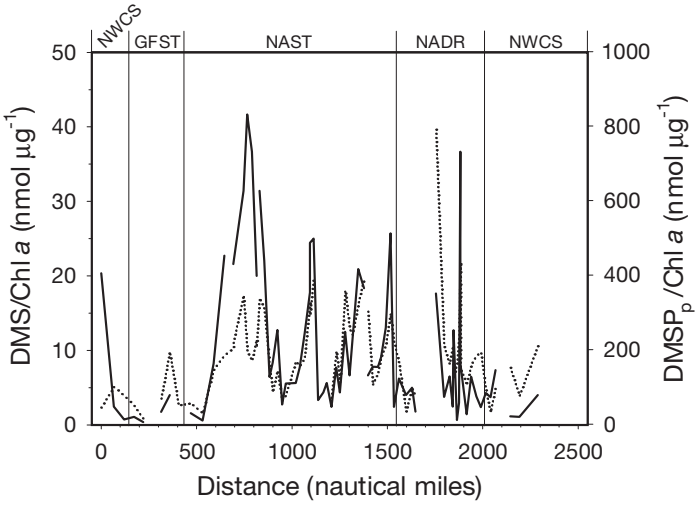

Fig. 6. Ratios of DMS:chlorophyll *a* (solid line) and $DMSP_p$: chlorophyll *a* (dotted line) in surface Niskin bottle and pump samples for the entire transect. Breaks in the lines indicate missing data. Vertical lines show approximate divisions of biogeochemical provinces (Longhurst 1998)

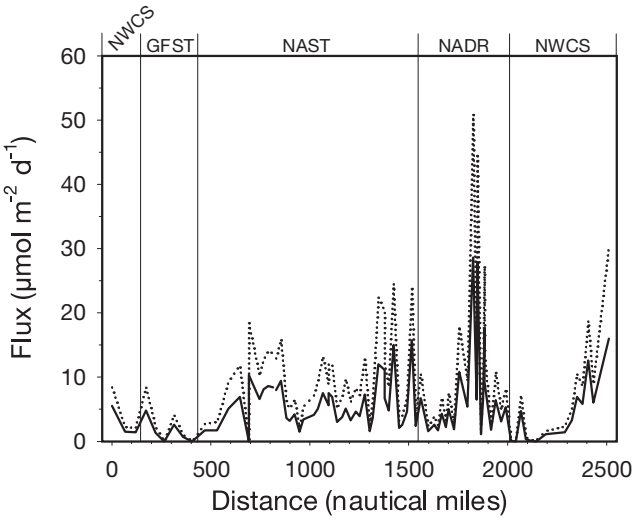

Fig. 7. Calculated DMS fluxes based on surface concentrations (Niskin and pump samples) and smoothed wind speeds (2 h sliding average) for entire transect based on 2 different flux models: Liss & Merlivat (1986, solid line) and Wanninkhof (1992, dotted line). Breaks in the lines indicate missing data. Vertical lines show approximate divisions of biogeochemical provinces (Longhurst 1998)

To facilitate comparison of these data with an existing global database of DMS measurements (Kettle et al. 1999, Kettle & Andreae 2000), the transect was divided into four biogeochemical provinces (Longhurst 1998) as explained above, and the surface DMS(P) concentrations in each province were grouped together and averaged. Table 2 summarizes the means of all DMS(P) observations in each province and also shows the mean sea-air DMS flux for each province calculated using the 2 flux models described above. Table 2 also presents the global database means for each province in the month of May (Kettle et al. 1999, Kettle & Andreae 2000).

DISCUSSION

In May 1998, the distribution of biogenic sulfur along the transect generally increased from south to north, and corresponded roughly with the standing stock of

Table 2. Mean DMS(P) concentrations (at surface) and fluxes in each biogeographic province in May 1998. All observations were assigned to 1 of 4 biogeographic provinces (after Longhurst 1998), and means and standard deviations (SD) were calculated for each province. Fluxes were calculated from the DMS concentrations and 2 h averages of wind speed using the air-sea exchange models of Liss & Merlivat (1986) and Wanninkhof (1992). Database values (italics) for DMS concentration (month of May) and flux (month of July) in each province are from Kettle et al. (1999) and Kettle & Andreae (2000), respectively

Province	n	DMS (nM)			$DMSP_d$ (nM)		$DMSP_p$ (nM)		Calculated DMS flux (μmol m^{-2} d^{-1})		Database DMS flux (July) (μmol m^{-2} d^{-1})	
		Mean	SD	*Database*	Mean	SD	Mean	SD	L & M	Wanninkhof	L & M	Wanninkhof
GFST	6	0.8	1.1	*7.0*	4.2	1.6	41.2	42.8	1.6	2.6	*9*	*16*
NAST	44	1.5	1.0	*2.3*	7.9	7.0	26.1	14.3	5.7	9.7	*5*	*10*
NADR	17	2.6	2.3	*4.7*	16.5	9.5	84.6	61.2	6.8	11.0	*7*	*12*
NWCS	21	2.5	2.1	*4.0*	16.4	6.8	39.3	24.8	3.9	6.3	*5*	*9*

phytoplankton. The NADR and NWCS regions were generally richer in biogenic sulfur than the oligotrophic waters of the NAST. Non-parametric regression of $DMSP_p$ against chl *a* for the entire transect (all stations, not just those used in Table 1) yields a weakly significant Spearman rank correlation ($r_s = 0.63$, $\alpha < 0.05$). This is expected since biogenic sulfur ultimately derives from phytoplankton. However, the DMSP cell quota of phytoplankton is highly species-dependent, and the final concentrations of DMSP and DMS in the water column are influenced by other processes such as biological consumption rates and (in the case of DMS) wind-driven ventilation to the atmosphere. Nevertheless, these data support the general concept that more productive environments produce more DMSP and hence more DMS, a fact which has been noted by other authors (Uher et al. 2000 and references therein). The region of elevated DMS concentrations in the NADR coincided with elevated concentrations of nitrate in the surface water relative to the surrounding stations (Figs. 2C & 3A). NO_3^- concentrations were generally low along the rest of the transect. The localized NO_3^- peak in the NADR coincided with the maximum phytoplankton abundance and elevated chl *a* concentrations (Figs. 2B,C & 4A). Although in terms of chl *a* biomass the phytoplankton standing stock in the NADR was not particularly high (0.7 μg l^{-1}), the abundances of dinoflagellates and prymnesiophytes (including *Gyrodinium flagellare* and *Chrysochromulina* spp.) were very high compared to adjacent stations (Figs. 2B & 4A). It therefore seems likely that this assemblage was sustained by the high availability of NO_3^-. This region is hydrographically complex, being a frontal region where the Labrador Current and the Gulf Stream converge (Clarke et al. 1980). This could stimulate localized mixing and vertical nutrient flux. If this is true, it means that DMS production in this region is associated with elevated nutrient conditions, leading to increased phytoplankton productivity. This appears to contradict the concept that DMSP production is characteristic of nitrogen-depleted conditions (Simó 2001 and references therein). However, in this case, the potential stimulation of the growth of DMSP-producing phytoplankton in otherwise low-biomass (and hence DMSP-poor) waters by enhanced nutrient supply is an important factor. By implication, this region of high DMSP production may be a semi-permanent feature of the NW Atlantic at this time of year.

In interpreting the taxonomic data, it is recognized that the method of preservation of the phytoplankton samples (acidic Lugol solution) makes it impossible to rule out the presence of coccolithophorids. The North Atlantic supports large populations of the coccolithophorid *Emiliania huxleyii* in the late spring and summer months. This species has received much attention as a major producer of DMSP and DMS (e.g. Steinke et al. 1998, Simó et al. 2002). It is possible that its presence in these samples may have gone unnoticed, since acidic Lugol solution would destroy the coccoliths and the cells might thus have been misclassified. However, examination of SeaWiFS images for the study region and period in question shows a very low radiance signal in the 555 nm band (the characteristic waveband for coccolith reflectance). It thus seems unlikely that there were significant populations of *E. huxleyi* in these samples.

The DMS:chl *a* ratio has been used by other authors as a measure of the concentration of DMS relative to total phytoplankton biomass. Uher et al. (2000) found high DMS:chl *a* ratios in the oligotrophic waters of the NE Atlantic, and also noted a seasonal variation with higher ratios in summer compared to winter. In the present study, DMS:chl *a* was higher in the low-biomass, oligotrophic waters of the Sargasso Sea than in the more productive waters of the North Atlantic Drift. In the latter region, the ratio reached the levels seen in oligotrophic waters only in isolated locations, in particular, at stations where *Chrysochromulina* spp. and *Gyrodinium flagellare* were abundant. This is at least partially related to the abundance of DMSP,

which is a function of the abundance and DMSP cell quota of the phytoplankton (discussed below). However, bacterial activity is thought to be of primary importance in determining DMS production (Kiene & Service 1991, Ledyard & Dacey 1994, Wolfe 1996, Kiene & Linn 2000b). It is known, for example, that bacterial activity per unit chl *a* is relatively higher in oligotrophic waters than in eutrophic waters (Biddanda et al. 2001 and references therein). In the present study, high bacteria:chl *a* ratios were observed in the Sargasso Sea (Scarratt et al. 2000b), which could help explain the high DMS:chl *a* ratio measured there. Similarly, in the NADR, the highest bacteria:chl *a* value was associated with elevated prymnesiophyte (*Chrysochromulina* spp.) populations, coincident with the highest DMS concentrations. However, there is probably no simple relationship between bacterial abundance and DMS, since the latter is also subject to biological consumption, which is mediated largely by bacteria. Scarratt et al. (2000b) reported for the same cruise that the DMS consumption rate was low in the Sargasso Sea but high at the *Chrysochromulina* spp. stations. In addition, since the DMS concentration is affected by the physical process of ventilation, the DMS:chl *a* will be influenced by physical processes as well.

The $DMSP_p$:chl *a* ratios in this study were generally high across the NAST region and lower elsewhere, with the exception of a large spike in the NADR. In general, DMSP production and the $DMSP_p$:chl *a* ratio are heavily influenced by the phytoplankton species assemblage and its trophic status. Keller et al. (1989) showed that the DMSP quota of phytoplankton is highly variable, depending on the species, with *Chrysochromulina* spp. being one genus identified as an important DMSP producer. In general, dinoflagellates and prymnesiophytes have higher cell quotas of DMSP, while diatoms and other taxa have low quotas. Most of the stations in the present study showed a predominance of prymnesiophytes and dinoflagellates, which may explain why the distributions of chl *a* and $DMSP_p$ were generally similar. It must be acknowledged that picophytoplankton were not enumerated in this study, and thus their potential influence on organic sulfur distributions cannot be directly evaluated here. However, the relatively low DMSP concentrations in the 0.7 to 2 µm fraction (Fig. 4) and the absence of any correlation between this size fraction and either chl *a* or the abundance of 'other species' (Table 1) would suggest that the influence of picoplankton on DMSP production in this study is negligible. The correlations in Table 1 reveal strong relationships between DMSP concentrations (both particulate and dissolved) and the abundance of prymnesiophytes and dinoflagellates. Similar results, including significant relationships with *Chrysochromulina* spp. and *Gyrodinium* sp. as well as other taxa, have been reported for the Gulf of St. Lawrence (Levasseur et al. 1994, Cantin et al. 1996). DMS also shows significant relationships with dinoflagellate and prymnesiophyte abundance, including weak correlations with *Chrysochromulina* spp. and *G. flagellare*. The presence or absence of DMSP-lyase in these taxa is presently unknown. The list of eukaryotic species positively identified as possessing DMSP-lyase is still quite limited (Stefels & Dijkhuizen 1996, Steinke et al. 1998, Wolfe 2000, Niki et al. 2000), but it includes the dinoflagellate *Cryptothecodinium* (=*Gyrodinium*) *cohnii* (Ishida 1968). It is therefore possible that the activity of dinoflagellate DMSP-lyase may have been a significant factor in determining the DMS distributions. It is also possible that these results demonstrate the effect of grazing on DMS production. Grazing by microzooplankton on DMSP-producing species is known to enhance DMS production rates (Wolfe & Steinke 1996, Wolfe et al. 2000). Although the *G. flagellare* observed here appeared to contain chloroplasts, the genus is known to have heterotrophic or mixotrophic members (L. Bérard-Therriault pers. comm.). It is possible, therefore, that *G. flagellare* or other species might be feeding on *Chrysochromulina* spp. or other DMSP producers, and this could result in enhanced release and cleavage of $DMSP_d$ to DMS.

The results here contrast with those of Belviso et al. (2001), who used chemotaxonomic pigment analysis to correlate DMSP abundance with phytoplankton taxa in a large dataset across several ocean basins. They found good correlations between DMSP abundance and the presence of prymnesiophytes and chrysophytes, but not with dinoflagellates. However, the authors also point out that differences in the pigment profile of some dinoflagellates could have affected the results. In a related study (Belviso et al. 2000a), they obtained better correlations using dinoflagellate abundance than through chemotaxonomic analysis. The strong relationship between DMSP and phytoplankton abundance found in the present study and the correspondence between phytoplankton cell sizes and the DMSP size fractionation underscore the influence of phytoplankton taxonomy and size distribution on the concentration of $DMSP_p$. The most abundant $DMSP_p$ fraction (2 to 11 µm) is also the one which contains both *Chrysochromulina* spp. and *Gyrodinium flagellare*, whose cell sizes measured in these samples fall generally in this range. The variation in the concentration of DMSP in this fraction was almost exactly coincident with the changes in abundance of the 2 major species (Fig. 4), and there was a significant Spearman correlation between the 2 to 11 µm size fraction of $DMSP_p$ and the abundances of *Chrysochromulina* spp. and *G. flagellare*.

The regions where the phytoplankton community was heavily dominated by DMSP-producing taxa and where DMSP and DMS concentrations were high were precisely those areas where warm oligotrophic waters mix with colder, more nutrient-rich waters. Frontal regions often produce local phytoplankton blooms and have also been associated with elevated concentrations of DMS, presumably a result of increased biological activity, higher grazing rates and faster turnover of phytoplankton material (Belviso et al. 2000b). The juxtaposition of different water masses may also contribute to the uncoupling of these various processes from each other, leading to an imbalance of one process over another. In the present case, this may help to explain the accumulation of DMS. On a larger scale, Belviso et al. (2000b) found elevated DMS concentrations in association with areas of surface divergence and upwelling in the Atlantic. Their analysis relied on sealevel anomalies derived from satellite altimeter data and as such was not able to resolve small-scale features (<250 km); nevertheless, the implication is that regions of higher nutrient supply and biological turnover are richer in DMS. Although in our study the elevated concentrations of nitrate do not coincide exactly with either the peaks in phytoplankton abundance or those of DMS(P), one possible interpretation is that the enhanced nitrate supply in this frontal region is responsible for supporting the prymnesiophyte/dinoflagellate assemblage.

The spatial correlation of DMS(P) with prymnesiophytes and dinoflagellates, including *Chrysochromulina* spp. and *Gyrodinium flagellare*, along the transect underscores the importance of these taxa to the DMS(P) distribution in the NADR region. Since relatively high DMS and DMSP concentrations and abundant *Chrysochromulina* spp. were found both early in the transect (around Mile 0 to 200) and later in the NADR region, this type of plankton assemblage may be a general feature along the northern side of the Gulf Stream at this time of year. With results from just 1 yr, inter-annual variation is impossible to estimate, but if this is the case, this region may be of significant importance to the regional and global DMS flux. It is possible that similar mechanisms may underlie the more widespread relationships observed by Belviso et al. (2000b) between sea-level anomaly and DMS.

The calculated sea-air DMS flux along the transect shows that, although the flux is a function of both DMS concentration and wind speed, the highly variable DMS concentration in this dataset dominates the resulting fluxes. For both models, the regions of elevated flux all coincide with areas of high DMS concentrations. These are the areas in which prymnesiophytes and dinoflagellates were most abundant. The calculated fluxes also compare well with the database values. Although the database of Kettle & Andreae (2000) provides no DMS flux estimates for the month of May, the fluxes calculated in this study fall very close to the July values from the global database for the NAST and NADR regions. This is in spite of the consistently lower DMS concentrations, and presumably reflects the effects of wind.

It is clear that the DMS concentrations observed here are consistently lower than the database means. This illustrates the potential importance of spatial and temporal (especially inter-annual) variability in DMS distributions. Alternatively, differences in sampling protocol may lead to a bias between different studies. In the present case, sampling DMS from the final filtrate stage could result in consistently lower values. Another factor is the possible tendency for measurements to be biased towards regions of particular interest (i.e. areas with high DMS concentrations), which may explain the higher database values. However, in that sense, this study may be similarly biased, since a large part of the sampling effort was concentrated in the region where high DMS(P) concentrations were found. This emphasizes both the strengths and weaknesses of sampling *in situ* DMS distributions. While there is a need for *in situ* data such as these to provide better coverage of global DMS and DMSP distributions, the variability in those distributions can only be understood by investigating the underlying food web processes.

CONCLUSIONS

In conclusion, this study demonstrates the influence of phytoplankton taxonomy on the distribution and concentration of DMS(P) in ocean waters, as evidenced by the significant correlations between the abundance of certain taxa (prymnesiophytes and dinoflagellates) and the concentrations of organic sulfur pools. Elevated DMSP concentrations were observed in an abundant assemblage dominated by the prymnesiophyte *Chrysochromulina* spp. and the dinoflagellate *Gyrodinium flagellare* in the NADR. Since these 2 species belong to algal groups known to possess DMSP-lyase, the potential importance of phytoplankton DMSP-lyase on DMS distributions in this region must also be recognized. Size fractionation of particulate DMSP reinforces the conclusion that organic sulfur distributions in this region and season are associated with these taxa. The *Chrysochromulina* spp./*G. flagellare* assemblage was found within an oceanographically complex area on the northern side of the Gulf Stream, and could be a regular phenomenon in this region of the ocean in the late spring/early summer. Comparison of the concentrations of DMS observed in this study with an existing global database shows that these mea-

surements are consistently lower than the database values. This suggests that global averages of DMS concentration may have been hitherto overestimated, at least in the NW Atlantic at this time of year. However, in the NAST and NADR regions, the calculated DMS fluxes are similar to the database values.

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