

## Distribution and metabolism of dimethylsulfoniopropionate (DMSP) and phylogenetic affiliation of DMSP-assimilating bacteria in northern Baffin Bay/Lancaster Sound

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[1] We determined the distribution and bacterial metabolism of dimethylsulfoniopropionate (DMSP) and dimethylsulfide (DMS) in the two dominant surface water masses in northern Baffin Bay/Lancaster Sound during September 2008. Concentrations of particulate DMSP (DMSP<sub>p</sub>; 5–70 nmol L<sup>-1</sup>) and the DMSP<sub>p</sub>:Chl *a* ratios (15–229 nmol μg<sup>-1</sup>) were relatively high, suggesting the presence of DMSP-rich phytoplankton taxa. Photosynthetic picoeukaryotes and total prokaryotes were tenfold and threefold more abundant in Baffin Bay surface water (BBS) than in Arctic surface water (AS), respectively. Heterotrophic bacterial production (0.07–2.5 μC L<sup>-1</sup> d<sup>-1</sup>) and bacterial turnover rate constants for dissolved DMSP (DMSP<sub>d</sub>) were low (0.03–0.11 h<sup>-1</sup>) compared with the values previously reported in warmer and more productive environments. Nonetheless, a relatively large proportion (12%–31%) of the DMSP metabolized by the bacteria was converted into DMS. Additionally, between 40% and 65% of the total bacterial cells incorporated sulfur from DMSP<sub>d</sub>, with *Gammaproteobacteria* and non-*Roseobacter Alphaproteobacteria* (Alf<sub>R-</sub>) contributing proportionally more to total DMSP-incorporating cells. The contribution of Alf<sub>R-</sub> to the total prokaryotic community was 50% higher in BBS than in AS, while the bacterial rate constants for DMSP<sub>d</sub> turnover were 78% higher in BBS than in AS. These results show that the two different Arctic water masses host specific microbial assemblages that result in distinct affinity for DMSP.

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### 1. Introduction

[2] Dimethylsulfide (DMS) is the main vector by which sulfur is transferred from the ocean to the continents via the atmosphere [Lovelock *et al.*, 1972]. Once ventilated to the atmosphere, DMS is oxidized to sulfate aerosols that act as cloud condensation nuclei, which may lessen the radiative flux to the Earth's surface and exert a cooling effect on climate [Charlson *et al.*, 1987]. The impacts of climate

changes on DMS production may be particularly important in the Arctic where the interaction between a larger ice-free surface available for gas exchange and a stimulation of DMS biological production could partly offset the warming caused by the loss of ice albedo [Gabric *et al.*, 2005].

[3] The distribution of DMS is controlled by a suite of abiotic and biotic factors involving all components of the planktonic food web [Simó, 2004]. Both algal and bacterial cells possess enzymes that cleave the algal osmolyte dimethylsulfoniopropionate (DMSP) to DMS [Yoch, 2002; Todd *et al.*, 2007]. Several studies indicate that DMSP uptake and assimilation of sulfur from DMSP (DMSP-sulfur or DMSP-S) are widespread among active marine bacteria, with numbers of DMSP-assimilating cells being comparable to those taking up leucine [Malmstrom *et al.*, 2004; Vila *et al.*, 2004]. The proportion of DMSP taken up by bacteria and converted into DMS (i.e., DMS yield), a key parameter governing DMS production, varies typically between 5 and 30% [Kiene and Service, 1991; Kiene, 1992] depending on bacterial production and availability of DMSP and other labile reduced sulfur sources [Kiene *et al.*, 2000; Pinhassi *et al.*, 2005; Levasseur *et al.*, 2006]. Most studies on bacterial DMSP metabolism have only considered the

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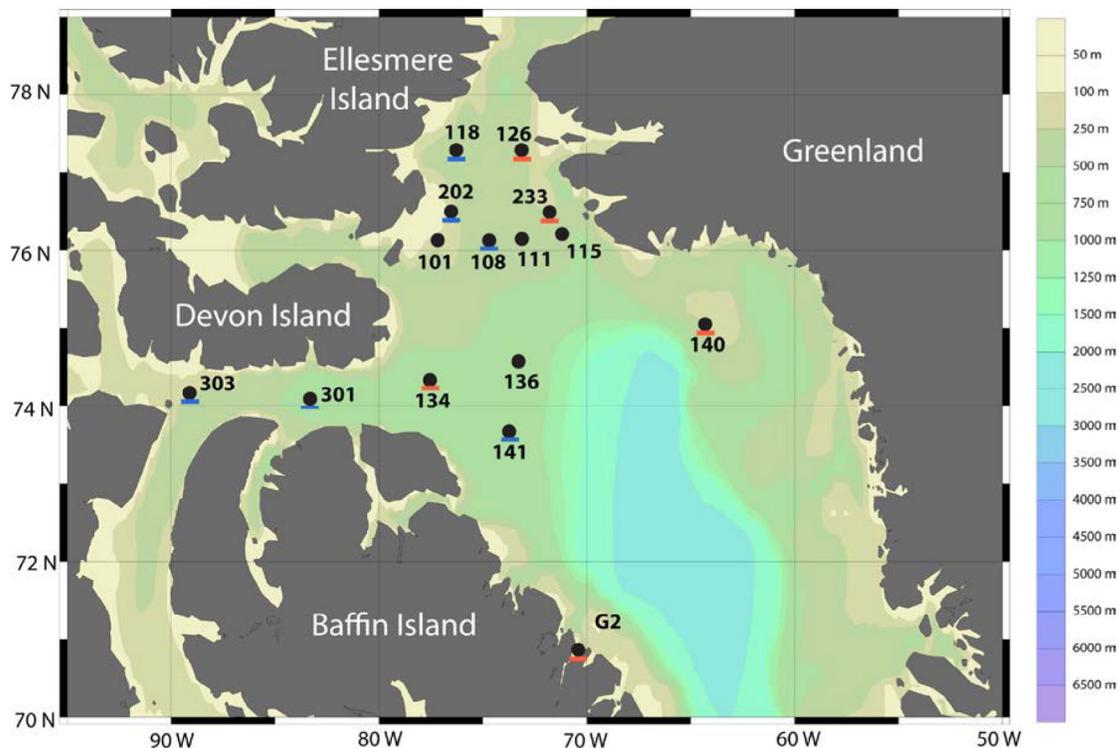
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**Figure 1.** Map of the eastern Canadian Arctic and Baffin Bay showing the locations of the sampling stations. Distribution of the two bacterial clusters determined by the cluster analysis (see Figure 3 and section 3) is also shown: warm Baffin Bay surface water cluster (red dashes), cold Arctic surface water cluster (blue dashes).

response of the whole assemblage, ignoring potential variability among phylogenetic groups. However, there are indications that the affinity for DMSP may vary among major groups of heterotrophic bacteria [Malmstrom *et al.*, 2004; Vila *et al.*, 2004]. Bacteria are also a major sink for DMS in the ocean [Kiene and Bates, 1990]. The coupling between bacterial DMS production and consumption is thus a controlling factor in the DMS distribution in the ocean.

[4] Arctic waters have been sparsely studied and the contribution of bacteria to DMS biological production in these systems is poorly understood. Galí and Simó [2010] reported moderate concentrations of total DMSP (DMSP<sub>T</sub>) and DMS during a *Phaeocystis pouchetii* bloom in the East Greenland Current and West Svalbard Current during the summer retreat of the ice edge, a situation they attributed to a tight coupling of biological DMS production and consumption, and a fast turnover of DMS. Bacterial DMS consumption was the dominant sink of DMS during their study. During a recent study conducted in fall 2007 in the Northwest Passage (Canadian Arctic Archipelago), Luce *et al.* [2011] found that the capacity of the microbial community to take up dissolved DMSP ( $k_{\text{DMSPd}}$ ) and to convert it into DMS increased with increasing phytoplankton biomass, suggesting that DMS production was ultimately limited by organic matter availability. Vila-Costa *et al.* [2008b] used microautoradiography to estimate the proportion of DMSP-degrading bacteria under the ice in the southeast Beaufort Sea during March and May 2004. These authors found a surprisingly low percentage ( $\sim 4\%$ ) of DMSP-assimilating bacteria, compared to values higher than 44% measured at

lower latitudes [Malmstrom *et al.*, 2004]. Whether this low percentage is also representative of other seasons and regions of the Arctic (including ice-free summer conditions) is not known.

[5] The objectives of this study were 1) to quantify the microbial DMSP loss rate constant and DMS yield from DMSP<sub>d</sub> in Lancaster Sound and northern Baffin Bay during late summer, 2) to identify the key bacterial phylogenetic groups present and determine their contribution to the DMSP-incorporating cells, and 3) to compare the different surface water masses in terms of their bacterial assemblages and patterns of DMSP and DMS metabolism.

## 2. Methods

### 2.1. Study Area, Sample Collection and Core Oceanographic Variables

[6] Sampling was conducted from 7 to 27 September 2008 aboard the CCGS *Amundsen* at 15 stations in Lancaster Sound and northern Baffin Bay (Figure 1). Water samples were collected using a rosette equipped with 12 L OceanTest Equipment bottles, an in situ chlorophyll fluorometer (Sea-Point 2465), an irradiance sensor (QCP-2300, Biospherical Instruments) and a Seabird 911*plus* Conductivity Temperature Depth (CTD) probe. Water samples were screened through a 200  $\mu\text{m}$  mesh net to remove large zooplankton grazers.

[7] Temperature, salinity and chlorophyll fluorescence profiles were recorded at all stations. In situ fluorescence data were calibrated against measurements of extracted

chlorophyll *a* (Chl *a*) from water samples collected at 5 discrete depths between 5 and 100 m following the acidification method of *Parsons et al.* [1984]. Chl *a* concentrations were determined with a Turner Designs Model 10-AU fluorometer.

[8] Duplicate surface water samples (5 mL) for the determination of picophytoplankton (0.2 to 2  $\mu\text{m}$ ) and nanophytoplankton (2 to 20  $\mu\text{m}$ ) abundances were fixed with glutaraldehyde (0.1% final concentration [*Marie et al.*, 2005]), stored in liquid nitrogen and kept frozen at  $-80^{\circ}\text{C}$  until analysis. Samples were analyzed using an EPICS ALTRA flow cytometer (Beckman Coulter) equipped with a 488 nm laser. Pico- and nanophytoplankton were distinguished based on forward scatter calibration with polystyrene microspheres of known size (1  $\mu\text{m}$ , Fluoresbrite plain YG, Polysciences). The flow cytometer configuration used in the present study allowed the discrimination of phycoerythrin-containing cyanobacteria, whereas phycocyanin-containing cyanobacteria, if present, were counted with the eukaryotic phytoplankton.

## 2.2. Bacterial Diversity, Abundance and Production

[9] Identification of selected clades of bacteria was made by Catalyzed Reporter Deposition–Fluorescence In Situ Hybridization (CARD-FISH) following the protocol described by *Pernthaler et al.* [2002]. Surface water samples were fixed with paraformaldehyde (2% final concentration) for 24 h at  $4^{\circ}\text{C}$ , and then filtered onto polycarbonate membranes 0.2  $\mu\text{m}$  GTTP (Millipore). Cellulose nitrate filters 0.45  $\mu\text{m}$  (Whatman 25 mm) were used underneath the polycarbonate membrane filters to smooth the filtration surface and improve the uniformity of the cell distribution. The polycarbonate membrane filters were stored at  $-20^{\circ}\text{C}$  until subsequent analysis. Sections were cut from each filter and hybridized with different HRP-probes (Biomers.net) specific to *Alphaproteobacteria* Alf968 [*Neef*, 1997], *Betaproteobacteria* Bet42a [*Manz et al.*, 1992], *Gamma-proteobacteria* Gam42a [*Manz et al.*, 1992], a putative *Roseobacter* Ros537 [*Eilers et al.*, 2001] and a general *Eubacteria* probe Eub338 [*Amann et al.*, 1990]. A negative control was conducted with the probe Non338 [*Wallner et al.*, 1993] to check for potential non-specific hybridization. The detailed CARD-FISH protocol steps are described by *Garneau et al.* [2006].

[10] Enumeration of total prokaryotic and CARD-FISH cells was performed by epifluorescence microscopy (Olympus BX51 inverted microscope) using UV light for 4',6-diamidino-2-phenylindole (DAPI) stained cell fluorescence [*Porter and Feig*, 1980] and blue light for carboxy-fluorescein (CARD-FISH). A minimum of 15 fields, 500 DAPI-stained cells and 100 FISH-positive cells were counted per sample [*Pernthaler et al.*, 2001]. Negative controls with probe Non338-HRP yielded no fluorescently labeled cells. For each probe, the results are expressed as the proportion of hybridized cells (FISH positive (+) cells) in comparison with total prokaryotic cells (DAPI+ cells) on each filter expressed as %. Multiplication of total prokaryote abundance (DAPI+) by the percentage of hybridized cells gives the cell abundance for each group. It should be noted that DAPI+ and CARD-FISH cells were enumerated on separate sections of the same because the CARD-FISH protocol can cause some cells to detach from the filter and be

lost. As done in previous studies, we assumed that there was no bias in phylogenetic affiliation to any cells lost during the CARD-FISH protocol. The cells that hybridized with a probe, for example the Eub probe (later referred to as Eub FISH<sup>+</sup> cells), represent the Bacteria. The DAPI-stained cells that did not hybridize with the Eub probe are hereafter referred to as unidentified prokaryotes. The non-*Roseobacter Alphaproteobacteria* (Alf<sub>R</sub>) term represents the fraction of Alf FISH<sup>+</sup> cells that were not positive for our putative *Roseobacter* (Ros) probe. The Alf<sub>R</sub> abundance was calculated as the difference between Alf FISH<sup>+</sup> cells and Ros FISH<sup>+</sup> cells.

[11] Bacterial production was estimated from  $^{14}\text{C}$ -leucine incorporation rates measured according to *Simon and Azam* [1989]. Triplicate surface water samples were amended with  $^{14}\text{C}$ -leucine and incubated at in situ water temperatures in the dark for 4 to 6 h in sterile polycarbonate bottles. Samples were filtered onto 0.2  $\mu\text{m}$  Nuclepore membrane filters and rinsed with 0.2  $\mu\text{m}$  filtered seawater and ice-cold 5% TCA. Filters were placed in glass vials and frozen at  $20^{\circ}\text{C}$  with 2 mL 5% TCA, until extraction in 5 mL of hot ( $95^{\circ}\text{C}$ ) TCA for 1 h. The insoluble residue was collected onto a 0.2  $\mu\text{m}$  membrane filter [*Kirchman and Ducklow*, 1993; *Rivkin and Anderson*, 1997], and radioactivity was counted. Bacterial production was calculated assuming the standard conversion factor (CF) of 3.1 kg C mol<sup>-1</sup>  $^{14}\text{C}$ -leucine incorporated [*Simon and Azam*, 1989]. Different CFs have been used in the Arctic, ranging from 1.5 to 3.1 kg C mol<sup>-1</sup> [*Garneau et al.*, 2008]. We chose to use the maximum value of 3.1 kg C mol<sup>-1</sup> because it is a commonly used CF value allowing for a direct comparison to other measurements of bacterial production.

## 2.3. Determination of Dimethylated Sulfur Compounds

[12] Triplicate surface water samples were collected for determination of dimethylated sulfur compounds. For total DMSP (DMSPt), 3.5 mL were collected directly from the Niskin bottle into a sterile 15 mL polypropylene screw-cap tube (Falcon). Dissolved DMSP (DMSPd) was sampled using the small-volume gravity drip filtration (SVDF) procedure [*Kiene and Slezak*, 2006]. Following this technique, 50 mL of seawater was filtered through a polysulfone magnetic filter funnel (Whatman 47 mm GF/F filter) and only the first 3.5 mL of filtrate was collected for DMSPd measurement. Samples of DMSPt and DMSPd were preserved with 50  $\mu\text{L}$  of 50%  $\text{H}_2\text{SO}_4$  and stored in the dark at  $4^{\circ}\text{C}$  for 24 and 48 h. Particulate DMSP (DMSPp) concentrations were obtained by subtracting DMSPd from DMSPt concentrations. For DMS sampling, 25 mL of seawater was gently collected from the Niskin bottle into a serum vial, avoiding bubbling and the presence of headspace. The sealed vials were then kept on ice in the dark and processed within one hour of collection.

[13] For DMS determination, the seawater samples were purged and the extracted gas was cryo-trapped in liquid nitrogen. Details of the purge and trap technique are described by *Levasseur et al.* [2006]. Analysis was performed on a gas chromatograph (GC, Varian CP-3800) equipped with a Pulsed Flame Photometric Detector (PFPD). DMSPt and DMSPd samples were hydrolyzed into DMS by injecting 1 mL of 5 mol L<sup>-1</sup> NaOH followed by the 3.5 mL DMSP sample directly into the purge vessel. The DMS thus

produced was analyzed as described above. Previous tests with DMSP standards showed a complete conversion of DMSP into DMS after 4 min of sparging at 70°C.

## 2.4. <sup>35</sup>S-DMSP Incubation Experiments

[14] Microbial DMSP uptake and metabolism were investigated at 10 stations using duplicate surface water samples incubated with the radiolabeled tracer <sup>35</sup>S-DMSP, following the protocol of *Kiene and Linn* [2000] and methods described by *Merzouk et al.* [2008]. In brief, <sup>35</sup>S-DMSP was added in trace amounts (0.0011 nmol L<sup>-1</sup> final concentration) to seawater samples, an addition that generally represented less than 1% of the in situ DMSPd concentrations. It should be noted that in situ DMSPd concentrations were below the quantification limit (0.3 nmol L<sup>-1</sup>) at Stations 202, 115, 111, 126 and 233. The total initial radioactivity in each water sample was determined by first gently mixing the sample and then removing a subsample of the water and counting the <sup>35</sup>S activity by liquid scintillation methods. The <sup>35</sup>S-DMSP-spiked water samples were incubated for 3 h in the dark at the in situ temperature (-1.3 to 3.8°C depending on the station). After 0, 60, 120 and 180 min, subsamples were taken to measure amounts of <sup>35</sup>S in the following fractions: particulates, trichloroacetic acid (TCA)-insoluble macromolecules, dissolved non-volatiles and volatiles according to a slightly modified version of the methods described by *Merzouk et al.* [2008]. In this study, Ellman's reagent was used to bind methanethiol (MeSH), another volatile product of DMSP degradation, in order to obtain solely <sup>35</sup>S-DMS in the volatile fraction.

[15] Radioactivity in all subsamples was measured onboard the ship using a Tri-Carb 2900 TR scintillation counter. In this study, a fraction of the <sup>35</sup>S-DMSP taken up into bacterial cells may have been incorrectly included in the unreacted fraction since the samples used for determining the unreacted <sup>35</sup>S-DMSPd were not filtered. The consequence of this is a potential underestimation of the  $k_{\text{DMSPd}}$ , although the fraction of DMSP retained in bacterial cells after several hours is generally only ~5–10% [*Kiene and Linn*, 2000].

[16] This incubation protocol allowed the determination of three parameters: 1) the microbial DMSPd loss rate constant ( $k_{\text{DMSPd}}$ ), calculated as the slope of the ln-transformed activity of unconsumed <sup>35</sup>S-DMSPd during the 3 h time course, 2) the microbial DMS yield, expressed as the percentage of <sup>35</sup>S-DMSPd consumed by bacteria that was recovered as volatile <sup>35</sup>S after 2 h of incubation, and 3) the bacterial DMSP-S assimilation efficiency, expressed as the percentage of <sup>35</sup>S-DMSPd consumed by bacteria that was recovered in TCA-insoluble macromolecules.

## 2.5. DMSP Single-Cell Uptake, MAR-CARD-FISH Experiments

[17] The single-cell DMSP assimilation by several phylogenetic groups was investigated using the microautoradiography (MAR)-CARD-FISH method for <sup>35</sup>S-DMSP developed by *Vila et al.* [2004]. Surface water samples (30 mL) were incubated in the dark at in situ temperature for 24 h with the radioactive substrate <sup>35</sup>S-DMSP (0.112 nmol L<sup>-1</sup>, final concentration). The incubations were stopped by adding 30 mL of 4% paraformaldehyde (2% final concentration) and the samples were stored for 24 h.

Pre-killed samples (2% paraformaldehyde) were used as negative controls to check for adsorption or passive incorporation of <sup>35</sup>S-DMSP into cells. Microautoradiograms were prepared by filtering samples using the same procedure as for CARD-FISH. The resulting filters were rinsed twice with filtered (0.2 μm) MilliQ water to remove unincorporated <sup>35</sup>S-DMSP and stored at -20°C until analysis.

[18] All the microautoradiograms were hybridized with the same HRP-tagged probes according to the CARD-FISH procedure described above. Microautoradiogram sections were mounted onto microscope slides with epoxy glue (UHU plus Sofortfest). All MAR steps were performed in darkness. The slides were first dipped into a melted NTB autoradiography emulsion (46°C; Kodak) diluted 1:1 with 1% agarose. The slides were placed for 7 min on an ice-cold dry metal bar to accelerate the solidification of the emulsion, and exposed at 4°C in the dark for 20 days, according to the optimization tests performed by *Vila et al.* [2004]. After the exposure period, the microautoradiograms were placed for 2 min in Kodak D19 developer at 20°C, for 30 s in MilliQ water to stop the reaction, for 5 min in Kodak Tmax fixer and then rinsed for 10 min in tap water. The slides were dried overnight in a desiccator, stained with DAPI (1 μg mL<sup>-1</sup>) and stored in the dark at -20°C until examined microscopically. The proportion of labeled cells (MAR+ cells) compared with the total hybridized cells (FISH+ cells) for each different HRP-tagged probe was determined using an Olympus BX51 epifluorescence microscope. In order to estimate the variability associated with the MAR procedure, we compared replicate filters from the same seawater sample. Two to five replicate filters per water sample were compared, and we calculated a coefficient of variation from 1 to 20% (mean 10%) for seven sets of replicate seawater samples. There were no labeled cells in the killed controls, reducing the probability of false positives due to adsorption onto the cell, and indicating that the deposition of silver grains around the cells can confidently be interpreted as an active uptake of DMSP-sulfur by the organisms.

[19] The contribution of each phylogenetic group to the total number of <sup>35</sup>S-labeled cells was calculated based on (1) the contribution of each group to the total prokaryote community (% of DAPI-stained cells), and (2) the proportion of labeled cells in the group (MAR+ cells) in relation to the proportion of labeled cells in the total prokaryote community (DAPI MAR+ cells). For example, the contribution of *Gammaproteobacteria* (Gam) to the total number of labeled cells was calculated using the following equation:

$$(\% \text{ Gam} \times \% \text{ Gam MAR+}) / (\% \text{ DAPI MAR+}) \quad (1)$$

where % Gam represents the proportion of prokaryotes identified as *Gammaproteobacteria*, % Gam MAR represents the proportion of *Gammaproteobacteria* that incorporated <sup>35</sup>S-DMSP, and % DAPI MAR + represents the proportion of prokaryote cells that incorporated <sup>35</sup>S-DMSP.

## 2.6. Statistical Analysis

[20] Since the distribution of most variables was not normal, the significance of the relationships between the different variables was calculated using the nonparametric Spearman's rank correlation tests ( $r_s$ ) from JMP® 7.0 software (SAS Institute Inc.). Natural groupings of stations

**Table 1.** Physical, Chemical, and Biological Variables Measured at Different Depths and Stations in Lancaster Sound and Northern Baffin Bay<sup>a</sup>

Station	Sampling Depth (m)	Temperature (°C)	Salinity	Chl <i>a</i> <sup>b</sup> ( $\mu\text{g L}^{-1}$ )	Peuk <sup>c</sup> (cells mL <sup>-1</sup> )	Neuk <sup>c</sup> (cells mL <sup>-1</sup> )	Peuk <sup>d</sup> (%)	DMSPp <sup>e</sup> (nmol L <sup>-1</sup> )	DMSPp:Chl <i>a</i> <sup>f</sup> (nmol $\mu\text{g}^{-1}$ )	DMSPd <sup>g</sup> (nmol L <sup>-1</sup> )	DMS <sup>g</sup> (nmol L <sup>-1</sup> )
<i>Arctic Surface Water</i>											
301	3	1.0	30.33	0.31	139 ± 11	190 ± 1	42 ± 2	70 ± 4	229	1.7	1.8
303	2	0.3	30.98	0.80	421 ± 53	563 ± 41	43 ± 5	12 ± 1	15	1.6	4.8 ± 0.4
101	4	-0.6	28.94	0.12	328 ± 34	461 ± 14	41.5 ± 3.3	5 ± 1	45	0.5	0.8 ± 0.1
202	3	-1.0	28.55	0.24	745 ± 48	655 ± 9	53 ± 2	7 ± 2	29	0.0	0.8 ± 0.1
108	2	1.4	30.82	0.71	1030 ± 8	930 ± 93	53 ± 3	36 ± 24	51	1.0 ± 1	1.8 ± 0.1
141	3	1.3	31.55	0.27	808 ± 59	292 ± 10	73.4 ± 0.8	8 ± 3	29	1.2	0.6 ± 0.1
118	3	-1.3	28.93	0.37	644 ± 1	1332 ± 1	32.58 ± 0.05	12 ± 3	34	1.0 ± 1	0.6 ± 0.5
Mean AS		0.2	30.01	0.40	588	632	48	21	62	1.0	1.6
<i>Baffin Bay Surface Water</i>											
Gibbs2	4	1.4	30.10	0.49	1451 ± 130	635 ± 50	70 ± 4	11 ± 1	23	1.5	0.6 ± 0.1
233	4	3.0	31.17	0.52	6863 ± 110	631 ± 32	91.6 ± 0.5	23 ± 5	43	0.0	0.8 ± 0.2
136	4	3.3	32.07	0.18	7096 ± 150	417 ± 36	94.5 ± 0.4	18	97	2.1	0.5 ± 0.1
140	3	3.6	30.88	0.15	3646 ± 21	265 ± 13	93.2 ± 0.4	10 ± 1	67	1.3	1.6 ± 0.1
115	3	3.5	31.27	0.21	6447 ± 280	436 ± 30	93.7 ± 0.7	16 ± 3	77	0.0	0.9 ± 0.1
111	2	3.8	31.50	0.31	3674 ± 230	490 ± 54	88.3 ± 0.5	14	47	0.0	1.8
126	4	3.1	31.59	0.31	5943 ± 550	610 ± 38	90.7 ± 0.3	18 ± 4	60	0.0	1.1 ± 0.3
134	2	3.2	32.13	0.15	6403 ± 200	358 ± 6	94.71 ± 0.08	12 ± 1	77	0.7	0.5 ± 0.1
Mean BBS		3.1	31.34	0.29	5190	480	90	15	61	0.7	1.0

<sup>a</sup>See Figure 1 for station locations. Data are grouped according to the different water masses AS (Arctic surface water) and BBS (Baffin Bay surface water).

<sup>b</sup>Chlorophyll *a* concentrations (Chl *a*).

<sup>c</sup>Abundances ( $\pm$ range) of photosynthetic picoeukaryotes (peuk) and nanoeukaryote (neuk).

<sup>d</sup>Contribution of picoeukaryote cells to total photosynthetic eukaryotes  $<20 \mu\text{m}$ .

<sup>e</sup>Concentrations ( $\pm$ standard deviation) of particulate dimethylsulfoniopropionate.

<sup>f</sup>Ratio of DMSPp to chlorophyll *a*.

<sup>g</sup>Concentrations ( $\pm$ standard deviation) of dissolved dimethylsulfoniopropionate (DMSPd) and dimethylsulfide (DMS).

based on the similarity in the specific abundance of each targeted bacterial phylogenetic group from CARDFISH results were determined by a cluster analysis using the un-weighted pair-group method with arithmetic mean (UPGMA) and the Bray-Curtis similarity index, using the PRIMER 5 software (PRIMER-E Ltd.). Student's *t*-test was used to explore statistical differences between water masses and between bacterial clusters, using SigmaPlot 11.0 (Systat Software Inc.). The Mann-Whitney rank sum test was used as nonparametric alternative test for variables that failed the normality and equal variance tests.

### 3. Results

#### 3.1. Oceanographic Setting

[21] Water temperatures varied between  $-1.3$  and  $3.8^\circ\text{C}$ , with coldest waters found near Ellesmere Island and in Lancaster Sound (Table 1). Surface water salinity ranged from 28.55 to 32.13 psu (Table 1). The lowest salinity values were measured in the northwest part of the study area, associated with the coldest temperatures in Arctic-derived water (mean  $0.2^\circ\text{C}$ ), while the highest salinity values were associated with warmer (mean  $3.1^\circ\text{C}$ ) Atlantic-derived waters in the southern part of the sampling region. We used published hydrographic descriptions of the North Water (northern Baffin Bay) [Melling *et al.*, 2001; Bâcle *et al.*, 2002; Hamilton *et al.*, 2008] to identify the different water masses according to their physical characteristics (Figure S1 in the auxiliary material).<sup>1</sup> Based on

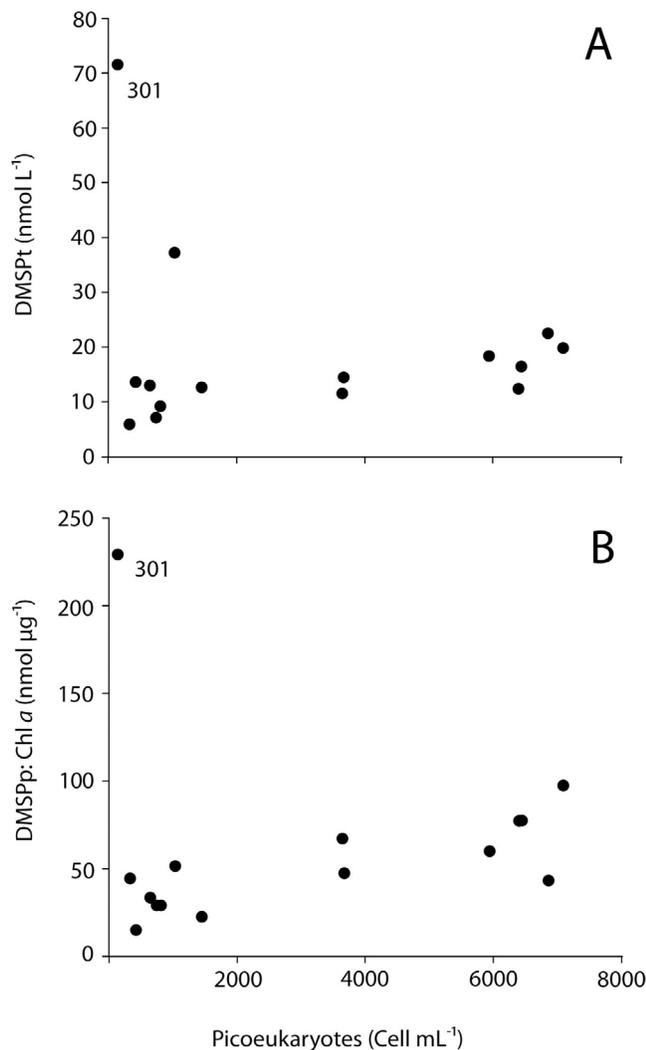
these criteria, stations 301, 303, 101, 202, 108, 141 and 118 were classified as Arctic surface water mass (AS), and stations Gibbs2, 233, 136, 140, 115, 111, 126 and 134 as Baffin Bay surface water mass (BBS). Intermediate stations (301, 108, 141 and Gibbs2) were assigned to one of the two water masses based on the specific composition of their bacterial assemblage as discussed below.

[22] Surface Chl *a* concentrations estimated from in situ fluorescence varied between 0.12 and  $0.80 \mu\text{g L}^{-1}$ , with the highest value being measured in Lancaster Sound (Table 1). The mean Chl *a* concentration for the whole area was  $0.34 \mu\text{g L}^{-1}$ , and we found no significant difference between the two water masses (*t*-test  $p = 0.3$ ). The abundance of the photosynthetic nanoeukaryotes was also not different between the two water masses (Table 1; Mann-Whitney rank sum test,  $p = 0.54$ ). Photosynthetic picoeukaryotes were however ten times more abundant in BBS (mean  $5190 \text{ cells mL}^{-1}$ ) than in AS (mean  $588 \text{ cells mL}^{-1}$ ; *t*-test  $p < 0.001$ ). Accordingly, the contribution of picoeukaryote cells to the total photosynthetic eukaryote ( $<20 \mu\text{m}$ ) community varied significantly (*t*-test  $p < 0.001$ ) between AS (mean 48%) and BBS (mean 90%). The abundance of photosynthetic picoeukaryotes in the whole region was positively correlated with water temperature ( $r_s = 0.77$ ,  $p < 0.001$ ).

#### 3.2. Dimethylated Sulfur Compound Pools

[23] Concentrations of DMSPp varied from 5 to  $70 \text{ nmol L}^{-1}$  with a mean value of  $18.2 \text{ nmol L}^{-1}$  (Table 1). DMSPp:Chl *a* ratios averaged  $62 \text{ nmol } \mu\text{g}^{-1}$  and showed a single peak value of  $229 \text{ nmol } \mu\text{g}^{-1}$  at Station 301 in Lancaster Sound (Table 1). As shown in Figure 2, both

<sup>1</sup>Auxiliary materials are available in the HTML. doi:10.1029/2011JC007330.



**Figure 2.** Scatterplots of (a) DMSPt concentrations and (b) DMSPP:Chl *a* ratios versus the abundance of picoeukaryotes. The number indicates station 301.

DMSPt concentrations and DMSPP:Chl *a* ratios tend to increase with the abundance of photosynthetic picoeukaryote cells, but the correlations are only significant ( $r_s = 0.591$ ,  $p \leq 0.05$  and  $r_s = 0.697$ ,  $p \leq 0.01$  for DMSPt and DMSPP:Chl *a* respectively) when station 301 is excluded from the analysis. DMSPt concentrations ranged between  $<0.3 \text{ nmol L}^{-1}$  (limit of quantification) and  $2.1 \text{ nmol L}^{-1}$  (Table 1) with a mean of  $0.8 \text{ nmol L}^{-1}$ . DMS concentration was maximal at Station 303 in Lancaster Sound ( $4.8 \text{ nmol L}^{-1}$ ), a value more than twofold higher than the second highest value found at Station 301 ( $1.8 \text{ nmol L}^{-1}$ ), also located in Lancaster Sound (Table 1). The mean DMS concentration for the whole area was  $1.3 \text{ nmol L}^{-1}$ . The mean concentrations of the dimethylated sulfur compounds and DMSPP:Chl *a* ratios were not statistically different between the two water masses (Mann-Whitney rank sum test,  $p > 0.1$ ). However, when Station 301 is excluded from the analysis, the average DMSPP:Chl *a* ratio is significantly higher ( $t$ -test,  $p < 0.05$ ) in BBS (62) than in AS (34).

### 3.3. Total Prokaryotic Cell Abundance, Production and Taxonomic Composition

[24] The total abundance of prokaryotes (DAPI-stained cells) ranged from  $0.27$  to  $2.1 \times 10^6 \text{ cells mL}^{-1}$  (Table 2) and was positively correlated with temperature ( $r_s = 0.84$ ,  $p < 0.01$ ). Results from a cluster analysis based on the composition of the bacterial assemblages at the 11 stations reveal the presence of two distinct groups at the 54% similarity level (Figure 3). Apart from the few stations (301, 108, 141 and Gibbs2) which exhibited intermediate temperature and salinity characteristics, these groups coincided well with the two main water masses, AS and BBS, identified previously based on their physical properties. The two clusters varied in terms of both bacterial cell abundance and taxonomic composition (Table 2). The total abundance of prokaryotes was higher in BBS (mean  $1.5 \times 10^6 \text{ cells mL}^{-1}$ ) compared to AS (mean  $0.49 \times 10^6 \text{ cells mL}^{-1}$ , Mann-Whitney rank sum test,  $p < 0.01$ ). Bacterial production (BP) varied between  $0.07$  and  $2.5 \mu\text{g C L}^{-1} \text{ d}^{-1}$ , with a mean value of  $1.03 \mu\text{g C L}^{-1} \text{ d}^{-1}$  (Table 2), and showed no difference between the two clusters ( $t$ -test;  $p = 0.2$ ). The average relative contributions of Eub, Gam, Bet and Ros to the total prokaryotic abundance were significantly higher in the AS cluster compared to the BBS cluster ( $t$ -tests,  $p < 0.01$ ), while conversely, the contributions of Alf<sub>R</sub> and unidentified prokaryotes (100% - %Eub) were lower in the AS than in the BBS cluster ( $t$ -test  $p < 0.01$ ; Table 2).

### 3.4. <sup>35</sup>S-DMSP Single-Cell Uptake

[25] Between 40 and 65% of the total DAPI-positive prokaryotic cells incorporated sulfur from <sup>35</sup>S-DMSP during our study (Table 3). The Gam and Alf exhibited the highest fractions of labeled cells, with 65 to 96% and 60 to 94% of MAR positive (MAR+) cells, respectively. The proportion of Ros cells that were labeled was lower, ranging from 46 to 65%. There was no significant difference between the two bacterial clusters in the proportion of DMSP-assimilating cells within each ( $t$ -test  $p > 0.4$ ). As shown in Figure 4, Alf and Gam accounted for 36–50% and 15–48% of the total labeled prokaryotes, respectively, while Ros and Bet accounted for only 6–16% and 2–9%, respectively.

### 3.5. DMS(P) Microbial Metabolism

[26] The microbial DMSPd loss rate constant ( $k_{\text{DMSPd}}$ ) ranged from  $0.0285$  to  $0.112 \text{ h}^{-1}$ , with a mean value of  $0.064 \text{ h}^{-1}$  (Table 4). The  $k_{\text{DMSPd}}$  was 78% higher ( $t$ -test  $p < 0.01$ ) in the BBS cluster ( $0.082 \text{ h}^{-1}$ ) than in the AS cluster ( $0.046 \text{ h}^{-1}$ ). When all stations were pooled,  $k_{\text{DMSPd}}$  was positively correlated with the total abundance of both bacteria ( $r_s = 0.71$ ,  $p < 0.05$ ) and photosynthetic picoeukaryotes ( $r_s = 0.83$ ,  $p < 0.01$ ). The bacterial DMS yield ranged from 12 to 30.8% (Table 4), with a mean value of 20%. There was no significant difference in the bacterial DMS yields between the two bacterial clusters ( $t$ -test  $p = 0.2$ ). The bacterial DMSP-S assimilation efficiency, which represents the proportion of <sup>35</sup>S-DMSP assimilated into macromolecules after 2 h, was relatively uniform over the study area, ranging from 11.4% to 17.79%

**Table 2.** Abundance of Prokaryotes and Percentages of Bacteria, *Gammaproteobacteria*, *Betaproteobacteria*, *Alphaproteobacteria*, and *Roseobacter* Calculated From DAPI-Stained Cells After CARD-FISH Treatment With the Probes EUB338, ALF968, BET42a, GAM42a and ROS537, Respectively<sup>a</sup>

Station	Prokaryotes <sup>b</sup> ( $10^6$ cells mL <sup>-1</sup> )	Eub (%)	Gam (%)	Bet (%)	Alf (%)	Ros (%)	Alf <sub>R</sub> <sup>c</sup> (%)	BP <sup>d</sup> ( $\mu\text{g C L}^{-1} \text{d}^{-1}$ )
<i>Arctic Surface Water</i>								
301	0.27 ± 0.02	89 ± 8	24 ± 6	4 ± 2	23 ± 5	17 ± 7	6 ± 8	1.2 ± 0.4
303	0.38 ± 0.03	73 ± 10	27 ± 5	4 ± 1	29 ± 6	12 ± 5	17 ± 8	0.19 ± 0.04
202	0.54 ± 0.05	75 ± 7	19 ± 4	4 ± 1	25 ± 5	6 ± 2	19 ± 5	1.7 ± 0.8
108	0.45 ± 0.02	80 ± 10	29 ± 7	6 ± 4	33 ± 10	14 ± 4	19 ± 11	1.3 ± 0.5
141	0.68 ± 0.06	68 ± 10	15 ± 4	4 ± 2	31 ± 6	13 ± 3	18 ± 7	0.6 ± 0.1
118	0.64 ± 0.01	70 ± 9	26 ± 6	6 ± 3	31 ± 10	10 ± 3	21 ± 11	2.5 ± 0.7
Mean AS	0.49	76	23	5	28	12	16	1.2
<i>Baffin Bay Surface Water</i>								
Gibbs2	1.24 ± 0.01	68 ± 6	13 ± 3	2 ± 1	31 ± 8	7 ± 2	24 ± 8	0.7 ± 0.1
233	1.2 ± 0.3	58 ± 10	13 ± 3	1 ± 1	32 ± 8	5 ± 1	26 ± 9	1.8 ± 0.2
140	1.3 ± 0.4	56 ± 7	11 ± 3	3 ± 3	36 ± 6	6 ± 1	30 ± 6	0.3 ± 0.2
126	1.5 ± 0.3	66 ± 8	17 ± 6	1.2 ± 0.4	27 ± 7	7 ± 2	20 ± 8	1.0 ± 0.4
134	2.1 ± 0.1	43 ± 6	8 ± 2	2 ± 1	31 ± 8	5 ± 2	26 ± 8	0.07 ± 0.05
Mean BBS	1.5	58	12	2	31	6	25	0.8

<sup>a</sup>Abbreviations: Eub, bacteria; Gam, *Gammaproteobacteria*; Bet, *Betaproteobacteria*; Alf, *Alphaproteobacteria*; Ros, *Roseobacter*. Average from fields counted ± standard deviation. Data are grouped according to the different clusters AS and BBS.

<sup>b</sup>DAPI-stained cells; average from two replicate filters ± standard deviation.

<sup>c</sup>Non-*Roseobacter Alphaproteobacteria* (Alf<sub>R</sub>) contribution is calculated from the difference in averaged contributions of Alf and Ros ± standard deviation.

<sup>d</sup>BP is bacterial production (average from triplicates ± standard deviation).

and did not vary significantly between the AS and BBS clusters ( $t$ -test  $p = 0.6$ , Table 4).

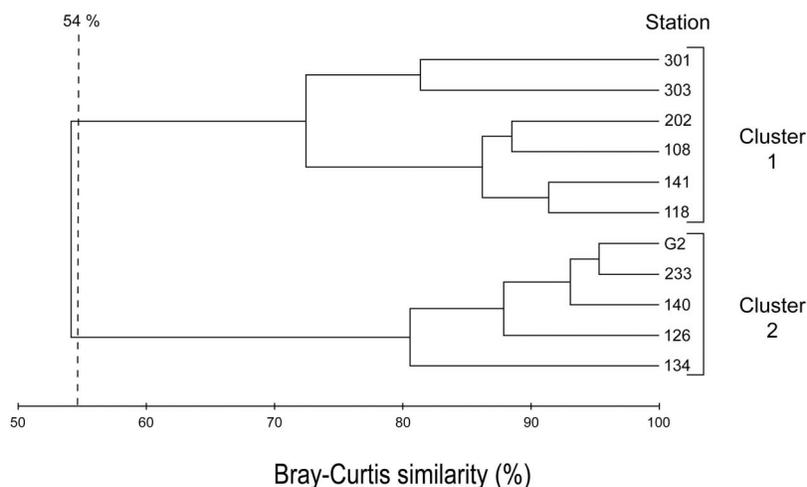
## 4. Discussion

### 4.1. General Oceanographic Conditions and Distribution of the Sulfur Pools

[27] The Arctic surface water mass (AS) and the Baffin Bay surface water mass (BBS) were identified in the study area and their general geographical locations were consistent with a previous identifications based on silicic acid:nitrate ratios [Tremblay *et al.*, 2002]. The two water masses, which

coincided roughly with bacterial taxonomic clusters (Figure 1), were also characterized by distinct picoeukaryote abundance and microbial DMSP loss rate constants.

[28] Despite the low Chl *a* concentrations prevailing during the cruise (mean  $0.34 \mu\text{g L}^{-1}$ ), DMSPp concentrations and DMSPp:Chl *a* ratios were relatively high, suggesting the presence of strong DMSP producers. Our DMSPp concentrations ( $5\text{--}70 \text{ nmol L}^{-1}$ ) were higher than those measured by Luce *et al.* [2011] in the same region in 2007 and by Matrai *et al.* [2008] in August 2001 in a lead of the ice-covered central Arctic Ocean. The DMSPp: Chl *a* ratio is a common metric used as an indicator of the



**Figure 3.** Dendrogram showing similarity of prokaryote assemblages at 11 stations from Lancaster Sound and northern Baffin Bay. The dendrogram was derived from the abundance of total prokaryote cells (DAPI-stained cells) and the abundance of 5 bacterial phylogenetic groups (*Eubacteria*, *Gammaproteobacteria*, *Betaproteobacteria*, *Alphaproteobacteria*, *Roseobacter*), using the UPGMA linkage method performed on a Bray-Curtis similarity matrix.

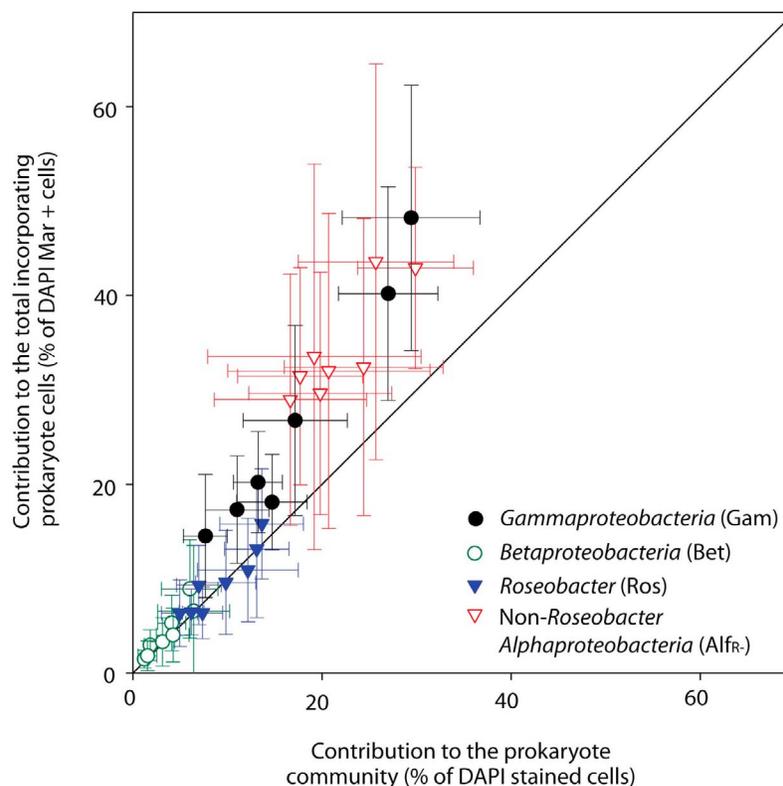
**Table 3.** Percentage of Cells Incorporating  $^{35}\text{S}$ -DMSP in Each Group<sup>a</sup>

Station	Prokaryotes Incorporating DMSP (%)	Eub (%)	Gam (%)	Bet (%)	Alf (%)	Ros (%)
<i>Arctic Surface Water</i>						
303	65 ± 13	69 ± 9	96 ± 6	84 ± 32	90 ± 9	58 ± 9
108	40 ± 1	40 ± 8	65 ± 10	41 ± 36	60 ± 14	46 ± 8
141	65 ± 4	79 ± 9	80 ± 8	62 ± 36	94 ± 5	65 ± 4
118	59 ± 9	77 ± 6	-	89 ± 22	81 ± 7	58 ± 11
Mean AS	57	66	80	69	81	57
<i>Baffin Bay Surface Water</i>						
Gibbs2	45 ± 6	59 ± 10	69 ± 8	53 ± 31	60 ± 13	61 ± 12
140	58 ± 4	63 ± 5	91 ± 9	61 ± 40	79 ± 8	60 ± 18
126	60 ± 11	74 ± 7	94 ± 5	73 ± 38	80 ± 10	52 ± 9
134	47 ± 14	73 ± 10	89 ± 11	77 ± 22	77 ± 7	61 ± 16
Mean BBS	53	67	86	66	74	59

<sup>a</sup>Mean from fields counted ± standard deviation. Total prokaryotes (DAPI-stained cells), Bacteria (Eub), *Gammaproteobacteria* (Gam), *Betaproteobacteria* (Bet), *Alphaproteobacteria* (Alf), *Roseobacter* (Ros). Data are grouped according to the different bacterial clusters AS and BBS. Dash indicates no data available.

relative importance of autotrophic DMSP producers. During our study, DMSPp:Chl *a* ratios varied between 15 and 97 nmol  $\mu\text{g}^{-1}$ , with a single peak value of 229 nmol  $\mu\text{g}^{-1}$  measured at station 301 in Lancaster Sound. These values are generally higher than previously measured in the Canadian Arctic later in the season by *Luce et al.* [2011] (39 nmol  $\mu\text{g}^{-1}$ ). Low DMSPp:Chl *a* ratios have also been reported in the Barents Sea during spring and summer (0.7–17 nmol  $\mu\text{g}^{-1}$ ) by *Matrai et al.* [2007] and *Matrai and Vernet* [1997]. Diatoms are known to have low intracellular concentrations of DMSP, and thus very

low DMSPp:Chl *a* ratios (see review by *Yoch* [2002]). The higher contribution of diatoms during early summer and spring blooms may explain the low DMSPp:Chl *a* values measured during these studies. However, ratios similar to those reported here have been measured in several environments, including the Subarctic Pacific (171 nmol  $\mu\text{g}^{-1}$  [*Royer et al.*, 2010]), in Antarctic waters (up to 60 nmol  $\mu\text{g}^{-1}$  [*Turner et al.*, 1995]), and in the northwest Atlantic (between 100 and 300 nmol  $\mu\text{g}^{-1}$  [*Scarratt et al.*, 2002]). Values as high as 905 nmol  $\mu\text{g}^{-1}$  were reported in the Barents Sea in March by *Matrai et al.* [2007]. During our



**Figure 4.** Percent contribution of each bacterial phylogenetic group to  $^{35}\text{S}$ -DMSP incorporating cells versus their contribution to total prokaryote abundance. Symbols and lines represent mean and standard deviation, respectively. Data on the 1:1 line indicate an equal contribution to the DMSP-incorporating cells and to the total community.

**Table 4.** Bacterial DMSP Loss Rate Constant, Bacterial DMS Yield, and DMSP-S Assimilation Efficiency Mean From Two Replicates  $\pm$  Range<sup>a</sup>

Station	$k_{\text{DMSPd}}$ ( $\text{h}^{-1}$ )	DMSy (%)	Macro (%)
<i>Arctic Surface Water</i>			
301	$0.0285 \pm 0.0022$	$26.7 \pm 2.1$	$14.69 \pm 0.37$
202	$0.048 \pm 0.018$	$30.8 \pm 0.8$	$15.1 \pm 1.2$
108	$0.053 \pm 0.003$	$24.39 \pm 0.43$	$16.1 \pm 0.4$
141	$0.041 \pm 0.003$	$12.8 \pm 0.1$	$17.79 \pm 0.06$
118	$0.0595 \pm 0.0076$	-	$11.4 \pm 1.4$
Mean AS	0.046	23.7	15.0
<i>Baffin Bay Surface Water</i>			
Gibbs2	$0.0894 \pm 0.0038$	$21.3 \pm 1.4$	$17.4 \pm 1.2$
233	$0.112 \pm 0.029$	$12 \pm 1$	$16.6 \pm 0.4$
140	$0.0615 \pm 0.0042$	$15.8 \pm 1.1$	$15.1 \pm 3.8$
126	$0.079 \pm 0.016$	-	$16.3 \pm 2.2$
134	$0.0697 \pm 0.0054$	$17.83 \pm 0.43$	$13.1 \pm 1.4$
Mean BBS	0.082	17	15.7

<sup>a</sup>Bacterial DMSP loss rate constant ( $k_{\text{DMSPd}}$ ), bacterial DMS yield (DMSy), and DMSP-S assimilation efficiency (Macro). Data are grouped according to the different bacterial clusters AS and BBS. Dash indicates no data available.

study, a large portion of the DMSPp was present in cells smaller than  $2 \mu\text{m}$ , as suggested by the positive correlation found for most of the stations between the abundance of picoeukaryote cells and both the DMSPt concentration and the DMSPp:Chl *a* ratios. Station 301 in Lancaster Sound was the exception, with a very high concentration of DMSP and a high DMSPp:Chl *a* ratio, in spite of a low abundance of picoeukaryotes (Figure 2). Potential causes include a very high proportion of strong DMSP-producers in the phytoplankton community, high DMSP content in zooplankton [Tang et al., 2000; Simó et al., 2002] and/or their fecal pellets [Kwint et al., 1996].

[29] Our DMSPd values are similar to what has been measured previously in the Arctic [Damm et al., 2008] and in other marine environments, and therefore substantiate the conclusion of Kiene and Slezak [2006] that DMSPd concentrations are generally  $<4 \text{ nmol L}^{-1}$  over a wide range of marine environments. DMS concentrations during our study were high ( $0.5$  to  $4.8 \text{ nmol L}^{-1}$ ) compared to the concentrations ranging from  $0.05$  to  $0.80 \text{ nmol L}^{-1}$  measured later in the season by Luce et al. [2011]. Even September measurements from different studies conducted at high latitudes reported lower concentrations, ranging from  $0.03$  to  $1 \text{ nmol L}^{-1}$  in the Greenland Sea [Leck and Persson, 1996] and averaging  $1.53 \text{ nmol L}^{-1}$  in the Bering Sea [Bates et al., 1987]. Overall, these results suggest the presence of a dynamic system in terms of DMSP and DMS cycling during the September period in the Arctic, with picoeukaryote cells representing the major source of DMSP.

#### 4.2. Microbial DMSP Metabolism

[30] The rate at which the microbial community turned over DMSP ( $k_{\text{DMSPd}}$ ) was low at all stations. The  $k_{\text{DMSPd}}$  never exceeded  $0.112 \text{ h}^{-1}$ , a low value in comparison with those of  $0.26 \text{ h}^{-1}$ ,  $0.54 \text{ h}^{-1}$ , and  $0.77 \text{ h}^{-1}$  reported from the Mediterranean sea [Vila-Costa et al., 2008a] the Northwest Atlantic Ocean [Merzouk et al., 2008], and in the NE Subarctic Pacific Ocean [Royer et al., 2010], respectively. Our  $k_{\text{DMSPd}}$  values are however remarkably similar to the ones

reported by Luce et al. [2011] in the same region in October 2007 ( $0$  to  $0.14 \text{ h}^{-1}$ , mean  $0.06 \text{ h}^{-1}$ ). The positive correlation found between  $k_{\text{DMSPd}}$  and the abundance of prokaryotes ( $r_s = 0.83$ ,  $p < 0.01$ ) during our study suggests that a large portion of the bacterial assemblage was incorporating DMSP, a conclusion also supported by results from single cell measurements (see below). Bacteria cleaved a relatively high percentage of the DMSP consumed into DMS ( $12$  to  $30.8\%$ ; mean  $20\%$ ). Using the same technique, Luce et al. [2011] measured DMS yields varying between  $4$  and  $15\%$  (mean  $7.5\%$ ) in the same region in October 2007. Our DMS yields are also high when compared with other environments such as the Gulf of Mexico ( $<3\%$  [Slezak et al., 2007]), the North West Atlantic ( $6$ – $10\%$  [Lizotte, 2010]), and North East Subarctic Pacific ( $3$ – $13\%$  [Royer et al., 2010]). Bacterial DMS yields are believed to vary as a function of the bacterial sulfur demand and the availability of DMSP [Kiene et al., 2000; Pinhassi et al., 2005; Levasseur et al., 2006]. Accordingly, high DMS yields, as measured during this study, could be interpreted as a low bacterial S demand and/or a DMSP-rich environment. Bacterial production was low during our cruise and the dominance of autotrophic DMSP producers in the photosynthetic community (as shown by the relatively high DMSPp:Chl *a* ratio) suggests a sufficient supply of DMSPd, probably through algal exudation and grazing, thereby favoring higher DMS yields from DMSPd.

#### 4.3. Phylogenetic Affiliation of DMSP-Degrading Bacteria

[31] Results from the MAR-CARD-FISH method show that  $40$  to  $65\%$  of the cells were taking up  $^{35}\text{S}$ -DMSP, which is similar to that reported for lower latitudes: ca.  $46\%$  in the Gulf of Mexico, ca.  $57\%$  in the Gulf of Maine,  $44\%$  in the Sargasso Sea,  $61\%$  in North Carolina coastal waters [Malmstrom et al., 2004], and  $5$  to  $42\%$  in the Mediterranean Sea [Vila et al., 2004]. However, our percentages of assimilating cells were considerably higher than the value of  $4\%$  measured by Vila-Costa et al. [2008b] under the sea ice in March and May in the southeast Beaufort Sea. Their low percentage probably reflects the combined effects of the extremely low bacterial activity ( $0.013$ – $0.1 \mu\text{g C L}^{-1} \text{ d}^{-1}$  [Garneau et al., 2008]) and DMSPp concentrations ( $0.7$  to  $4.4 \text{ nmol L}^{-1}$ ) under the ice.

[32] Most of the bacterial groups tested contributed to the  $^{35}\text{S}$ -DMSP-incorporating cells in rough proportion to their relative abundance (close to the 1:1 line; Figure 4), but the contribution of Alf<sub>R</sub> and Gam to DMSP-incorporating cells tended to exceed their share of total abundance. A prominent role in DMSP uptake and metabolism has been attributed to members of the Ros group due to their frequent association with strong DMSP-producing phytoplankters [González et al., 2000; Zubkov et al., 2001]. In the Mediterranean Sea, Vila et al. [2004] found a slightly higher percentage of DMSP-incorporating cells in Ros (not observed in this study), but also in Gam groups as reported here. Tripp et al. [2008] recently suggested that organisms affiliated with the SAR11 sub-group of Alf must obtain their S from reduced compounds like DMSP since they lack assimilatory sulfate reduction genes. The contribution of SAR11 bacteria to the DMSP-incorporating cells was found to be proportional to their overall abundance in the Sargasso Sea [Malmstrom et al., 2004]. During their under-ice winter survey in the

Arctic, *Vila-Costa et al.* [2008b] found that Alf contributed less to DMSP assimilation than their relative abundance in the community would suggest. A SAR11 probe was not used during our study, but since SAR11 represents up to 37% of the total abundance of bacteria in the western Canadian Arctic in summer [*Alonso-Sáez et al.*, 2008], this group was most probably an important contributor to the Alf<sub>R</sub> clade, which showed a high proportion of DMSP assimilating cells (Figure 4). Although the contribution of SAR11 might be higher in the summer than reported in winter, our results highlight the important contribution of the Gam members in the overall assimilation of DMSP. It is important to note that the use of the general subphyla level probes (Eub, Gam, Bet and Alf) and the putative genera specific probe (ROS537) only gives an indication of the taxonomic affinity of DMSP assimilating cells. Although useful for comparing sites within a study region such as during our study, the differences among the studies discussed above could reflect metabolic diversity within larger taxonomic groups.

#### 4.4. Arctic Versus Baffin Bay Surface Water Masses

[33] Our results showed that AS and BBS water masses had distinct microbial communities and DMSP loss rate constants. The abundance of picoeukaryotes (<2 μm) was 10-fold higher in BBS than in AS (Table 1). *Mostajir et al.* [2001] also reported an association between picophytoplankton and the warm and saline surface waters on the Greenland side of Baffin Bay in fall. Since the early loss of sea ice and the associated increase in underwater irradiance can trigger blooms two or three months earlier in the northern part of Baffin Bay than in the Canadian Archipelago [*Mei et al.*, 2002; *Michel et al.*, 2006], the phytoplankton assemblage observed in BBS might represent a more mature stage of phytoplankton succession compared to the assemblage present in the AS.

[34] The BBS and AS water masses also had distinct prokaryote abundances and taxonomic compositions. Results from the cluster analysis highlighted the presence of distinct bacterial assemblages, with a threefold higher cell abundance and a 1.5-times greater contribution of Alf<sub>R</sub> to the total prokaryote community in BBS compared with AS waters. The dominance of <2 μm photosynthetic eukaryotes in BBS and the high number of bacteria suggest the prevalence of a well developed microbial food web, also suggesting a more advanced stage of plankton seasonal succession. The threefold higher bacterial abundances measured in BBS compared with AS waters corresponded to a twofold increase in bacterial k<sub>DMSPd</sub>. However, we found no difference between the two water masses in the bacterial DMS yields from DMSPd consumption. As mentioned above, the relatively high DMS yields measured in both water masses suggest that low bacterial S demand and/or high DMSP supply prevailed in the two water masses during our sampling period.

## 5. Summary

[35] The Canadian Arctic region sampled during this study exhibited post-bloom characteristics, with low levels of Chl *a* in the surface mixed layer. The late summer sampling period revealed the occurrence of a phytoplankton community dominated by DMSP-rich cells and a bacterial

assemblage actively using DMSP. Bacterial production and DMSPd loss rate constants (k<sub>DMSPd</sub>) were low, probably reflecting the low to moderate primary production rates and low release of labile dissolved organic matter. In these conditions, bacteria were probably using DMSP mostly as a carbon source, as suggested by the high DMS yields measured. All bacterial phylogenetic groups tested incorporated DMSP, with two groups (Gam and Alf<sub>R</sub>) tending to contribute proportionally more to the DMSP-incorporating cell abundance than to the total prokaryotic abundance. The two main surface water masses present in the study region, BBS and AS, exhibited distinct plankton assemblages and microbial DMSP loss rate constants. Photosynthetic picoeukaryotes and total prokaryotes were respectively tenfold and threefold more abundant in BBS than in AS, whereas the contribution of Alf<sub>R</sub> to the total prokaryotic community was 50% higher in BBS than in AS. Finally, the bacterial rate constants for DMSPd turnover were 78% higher in BBS than in AS. These results highlight the diversity of the prokaryotic communities and associated affinity for DMSP in the two Arctic water masses studied.

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