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RESEARCH ARTICLE

Bacterial diversity and lipid biomarkers in sea ice and sinking particulate organic material during the melt season in the Canadian Arctic

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The estimation of important carbon fluxes in a changing Arctic environment remains a challenge, one that could benefit from the development of biomarkers that distinguish between sympagic (ice-associated) and pelagic organic material. Products of 10*S*-DOX-like lipoxygenase and fatty acid *cis-trans* isomerase (CTI) activity of bacteria attached to sympagic particulate organic matter (POM) were proposed previously as potential biomarkers of the contribution of sympagic biota to carbon fluxes to the seafloor. To date, neither the bacteria involved in such enzymatic activities nor the detection of these potential biomarkers at their presumed source (i.e., sea ice) has been investigated. Here, we determined and compared the diversity of prokaryotic communities (based on operational taxonomic units) attached to sea ice POM and under-ice sinking particles during an early stage of ice melt (brine drainage) in Baffin Bay (Canadian Arctic). Based on a time series of biodiversity analyses and the quantification of lipid tracers of these two bacterial enzymatic activities, we suggest that CTI-active bacteria, exposed to hypersaline stress, are attached to algal POM just above bottom sea ice and released into the water column following brine drainage. In contrast, bacteria attached to sinking particles and exhibiting 10*S*-DOX-like lipoxygenase activity are suggested to come from the bottommost layer of sea ice, where they may play a role in the detoxification of algae-produce free fatty acids. These results provide a refined view of the potential use of products of CTI activity as specific biomarkers of sympagic organic matter.

Keywords: Bacterial community, Bacterial stress, Biomarkers, *Cis/trans* isomerase, 10*S*-DOX-like lipoxygenase, Ice biota, Arctic environment

1. Introduction

Dense algal populations concentrated in the bottommost centimeters of sea ice (Smith et al., 1990) are ubiquitous features beneath sea ice in polar regions during the springtime. In the high Arctic, these microalgae are concentrated largely at the ice-water interface within the skeletal layer of the congelation ice. Estimates of ice-associated (sympagic) primary production range from 3% to 25% of the total primary production within Arctic marine systems (Rao and Platt, 1984; Legendre et al., 1992) to as high as 50% to 57% in high Arctic regions (Gosselin et al., 1997; Fernández-Méndez et al., 2015). The high production of extracellular polymeric substances (EPS) by sympagic algae (Krembs et al., 2002; Meiners et al., 2003) can favor the formation of dense aggregates (Riebesell et al., 1991; Boetius et al., 2013) and therefore their fall to the bottom and contribution to sediments.

Remineralization of algal material in the water column during sedimentation depends on zooplankton grazing (Forest et al., 2011) and the activity of bacteria associated with the sinking particles (Kellogg et al., 2011) which may have been colonized in the ice (Rapp et al., 2018) or the water column (Balmonte et al., 2018). In general, the exchange of metabolites and infochemicals within the phycosphere (region immediately surrounding an individual algal cell) drives algae–bacteria relationships, which span mutualism, commensalism, antagonism, parasitism, and competition (Amin et al., 2012; Seymour et al., 2017). In perenially cold environments of the Arctic, the activities of both bacterioplankton (Howard-Jones et al., 2002) and particle-associated bacteria (Balmonte et al., 2018) have been considered weaker than in warmer environments. Although often attributed to low temperature constraints, weaker activity in the Arctic could also be the result of other stress factors, particularly salinity stress. During the early stage of ice melting in spring, sea ice brine inclusions (where practical salinity may reach 135; Not et al., 2012) become interconnected and form channels that allow

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brine drainage into underlying seawater (Wadhams, 2000). Sympagic biota, including bacteria, tend to grow in the bottommost centimeters of sea ice where environmental conditions are relatively moderate and stable, yet hypersaline brine drainage and the ensuing downward percolation of hyposaline meltwater as the ice continues to melt can present osmotic challenges to algae (Gosselin et al., 1986; Ralph et al., 2007) and to bacteria (reviewed by Deming, 2010), as also concluded by Amiraux et al. (2017).

In general, prokaryotic cells subjected to extremes in osmotic pressure have developed mechanisms to live under such conditions, including in sea ice (Firth et al., 2016). Various general strategies are possible: (1) implementation of active Na^+ and K^+ ion transport systems (Thompson and MacLeod, 1971), (2) accumulation of osmocompatible compounds such as glycine betaine or proline (Piuri et al., 2003), and (3) production of EPS which can act as a diffusion barrier (Kim and Chong, 2017). Another major adaptive response of many microorganisms, including bacteria, is to maintain membrane fluidity under stressful conditions through "homeoviscous adaptation" (Sinensky, 1974). Peroxidation of membrane lipids by lipoxygenases (LOXs) can constitute an important mechanism to modify membrane fluidity (Bhattacharjee, 2014). Lipoxygenases were long considered eukaryotic-specific but have been detected in some Gram-negative bacteria (Hansen et al., 2013). In particular, activity of the LOX-like enzyme, 10*S*-DOX-like lipoxygenase, has been observed in *Pseudomonas* 42A2 (Guerrero et al., 1997; Busquets et al., 2004) and more recently in members of the genera *Pseudoalteromonas*, *Shewanella*, and *Aeromonas* (Shoja Chaghervand, 2019), although the exact role of this enzyme remains unclear. Another possibility for microorganisms to maintain the fluidity of their membranes is by enzymatic conversion of *cis*- to *trans*-unsaturated fatty acids through the activity of *cis-trans* isomerases (CTI) (Loffeld and Keweloh, 1996; Heipieper et al., 2003).

Previous analyses of sinking particles of high sympagic algal content, collected in the water column under sea ice during Arctic vernal melting periods, showed strong CTI and 10*S*-DOX-like lipoxygenase activity (Amiraux et al., 2017). These enzymatic activities were hypothesized to have been triggered in bacteria associated with the sinking algal material by salinity stress experienced earlier during sea ice brine drainage. CTI activity is only used by bacteria as an acute response to permit survival (under continuous stress, its activation is substituted by other mechanisms; Fischer et al., 2010). In the absence of osmotic stress (in this case, following release into a salinity-stable water column), the *trans/cis* ratio of previously stressed bacteria can be expected to decrease to the basic level, a process dependent on growth (de novo synthesis of *cis* fatty acids; Fischer et al., 2010). Because the *trans/cis* ratios observed in sinking particles beneath sea ice (at 25-m depth) and in underlying surface sediment (350 m) were similarly high, the sinking particle-associated bacteria were considered to be in a non-growing state, with limited potential to attenuate the flux of sympagic particulate organic matter (POM) toward the seafloor (Amiraux et al., 2017).

Here, we investigated microbial diversity, based on the 16S rRNA gene, and lipid biomarkers for the activity of CTI and 10*S*-DOX-like lipoxygenase enzymes in both sea ice and sinking particles collected during the 2015 fieldwork at the ice camp of the Green Edge project in Baffin Bay. Our aims were (1) to examine the proposed link between bacterial communities attached to sympagic POM and those associated with sinking particles during the early stage of a sea ice melt season and (2) to further consider the potential sea ice origin of the fatty acid CTI and 10S-DOX-like lipoxygenase activity previously hypothesized to result, respectively, from exposure to hypersaline brine and algal bactericidal free fatty acids produced in the bottommost layer of sea ice.

2. Materials and methods

2.1. Study site and sampling

Samples of sea ice and sinking particles were obtained for this study between May 2 and June 4, 2015, at a landfast ice station located near Broughton Island (67°28.766′N; 63°47.579′W) in Baffin Bay (**Figure 1**) as part of the Green Edge project. Samples for both bacterial diversity and lipid analyses were collected for both sample types on the same dates for a total of 7 sampling dates in the time series: May 4, May 8, May 12, May 14, May 22, May 27, and June 2, 2015. Samples were designated as sea ice particulate organic matter (SIPOM) and sinking particulate organic matter (SPOM) and numbered 1–7, corresponding to the sampling date.

Two sets of SIPOM samples were collected. For the first set, the bottommost 10-cm sections of sea ice were sampled with a Kovacs Mark V 14-cm diameter corer (Smith et al., 1990) for biological analyses. To compensate for biomass heterogeneity, common in sea ice (Gosselin et al., 1986), three equivalent core sections were pooled in isothermal containers. Pooled sea ice sections were then melted in the dark with 0.2-µm filtered seawater (FSW; 3:1 v:v) to minimize osmotic stress to the microbial community during melting (Bates and Cota, 1986; Garrison and Buck, 1986), with 400 mL dedicated to the analysis of prokaryotic communities. This pooled sea ice sampling was performed in duplicate. For the second set, a Kovacs Mark II 9-cm diameter corer was used to collect samples dedicated to lipid analyses. The bottommost 10 cm of sea ice were sliced into five subsections: 0–1, 1–2, 2–5, 5–7, and 7–10 cm. Two additional entire sea ice cores were collected to measure sea ice temperature and salinity, thus allowing calculation of brine salinity and volume (Cox and Weeks, 1983). Sea ice internal core temperatures were measured using a Testo 720 temperature probe inserted into a hole drilled to the center of the core every 10 cm, while practical salinity was measured in melted (10-cm) sea ice sections using a conductivity meter (Orion portable salinometer model WP-84TPS, Thermo Fisher Scientific, Waltham, MA, USA) calibrated against 15N KCL solution at 20 °C.

For SPOM samples, short-term sediment traps were deployed unfilled and without preservative on a mooring

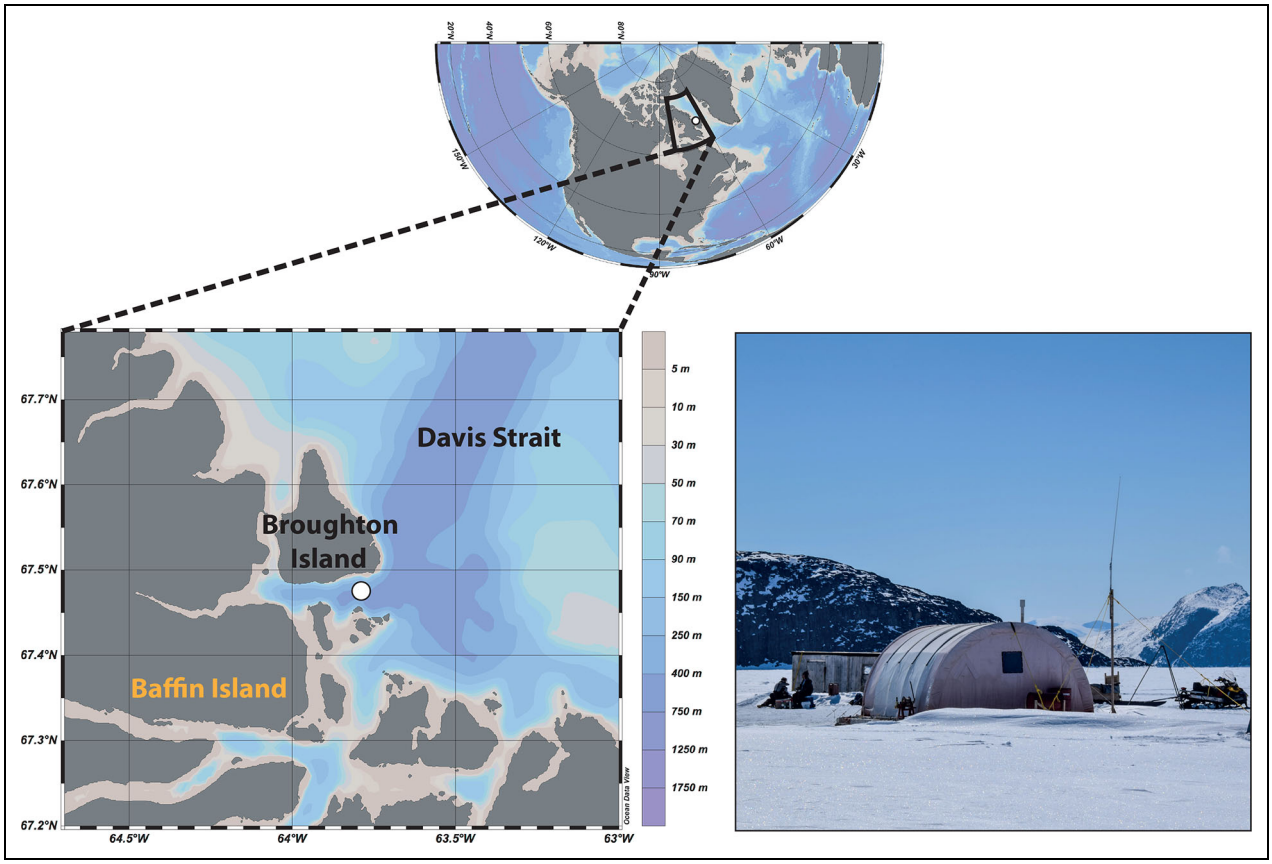

Figure 1. Map and photo of the study area with location of the station investigated in Baffin Bay. White circle on the enlarged map of western Baffin Bay indicates the sampling location. DOI: https://doi.org/10.1525/elementa.2021.040.f1

line to collect sinking particles at 2 m and 25 m below the sea ice. Sediment traps were built in-house of polyvinyl chloride with an aperture diameter of 15 cm for a height-to-diameter ratio of 6.7 and a collection cup at the base. The two traps were deployed on the same line through a large hole (75 cm × 75 cm) made previously in the ice. Sediment traps were immersed at depth for approximately 48 h and recovered at the same frequency as the sea ice sampling sets. The ice hole was covered during deployment with a wooden plate and snow. After recovery, sample cups were removed from the traps, closed and kept at near in situ temperature in the dark (in insulated containers) until further analyses at the shore laboratory. Selected lipid data (CTI and 10S-DOX-like lipoxygenase signals) were published previously for both sediment trap depths by Amiraux et al. (2017); only the 25-m sediment traps, however, were available for the bacterial diversity analyses and new lipid analyses of this study.

For both sea ice and sinking particles, lipid samples were obtained by filtration through pre-weighed Whatman glass fiber filters (Buckinghamshire, UK; porosity 0.7 µm, 47 mm, combusted 4 h at 450 °C) and kept frozen (< –20 °C), while diversity samples were obtained by filtration in duplicate on 0.8 µm Whatman nuclepore filters (24 mm, autoclaved 1 h at 110 °C) and kept frozen (< –80 °C) prior to DNA extraction. Given the pore size of the filters, these analyses were considered to involve primarily algae and their attached bacteria (Bidle and Azam, 1999; Ghiglione et al., 2007), though a potential contribution of grazers and their attached bacteria cannot be excluded.

2.2. Lipid analyses

Samples for lipid analyses were reduced with excess sodium borohydride (Sigma Aldrich, Saint-Louis, Missouri, USA) after addition of methanol (25 mL, 30 min; Rathburn, Walkerburn, Scotland) to reduce labile hydroperoxides to alcohols, which are more amenable to analysis using gas chromatography–mass spectrometry (GC–MS). Water (25 mL) and potassium hydroxide (2.8 g; Riedel de Haen, Seelze, Germany) were then added and the resulting mixture saponified by refluxing (2 h). After cooling, the mixture was acidified (hydrochloric acid, 2N; Chem lab, Zedelgem, Belgium) to pH 1 and extracted with dichloromethane (DCM; 3 × 20 mL; Rathburn). The combined DCM extracts were dried over anhydrous sodium sulfate, filtered and concentrated via rotary evaporation at 40 °C to give total lipid extracts (TLEs). Aliquots of TLEs were either silylated and analyzed by gas chromatography–electron impact quadrupole time-of-flight mass spectrometry (GC–QTOF; Agilent, Les Ulis, France) for monounsaturated fatty acid oxidation product quantification, or methylated, then treated with dimethyldisulfide (DMDS; Sigma Aldrich) and analyzed by GC–MS/MS for the determination of double bond stereochemistry. *Cis* and *trans* isomers of monounsaturated fatty acid methyl esters react with DMDS stereospecifically to form *threo*

and *erythro* adducts, which exhibit similar mass spectra but are well separated by gas chromatography, allowing unambiguous double bond stereochemistry determination (Buser et al., 1983). A detailed protocol of lipid analyses, including GC–MS/MS and GC–QTOF analyses and determination of the lipid degradation products employed for estimating potential salinity stress, is provided by Amiraux et al. (2017) and Galeron et al. (2018). Here, we focused on quantifying the *trans/cis* vaccenic acid ratio and the oxidation products of palmitoleic acid, particularly 10-hydroxyhexadec-8(*trans*)-enoic acid, as respective indicators of bacterial fatty acid CTI and 10S-DOX-like lipoxygenase activity, as proposed by Amiraux et al. (2017). We also determined the desmosterol/brassicasterol ratio as a relative indicator of sympagic algae versus phytoplankton and zooplankton in our samples.

2.3. Analysis of the bacterial communities associated with SIPOM and SPOM

2.3.1. DNA extraction and PCR amplification

Genomic DNA was obtained from the filters by treatment with lysozyme-sodium dodecyl sulfate (Thermo Fisher Scientific, Waltham, MA, USA) followed by phenol-chloroform extraction and subsequent precipitation using ethanol (Rathburn). The concentration of DNA was determined spectrophotometrically following treatment with RNase (Sigma Aldrich; Sambrook, 1989). For ribosomal diversity analysis, the V4 region of the bacterial and archaeal 16S rDNA genes (16S) was amplified using universal primer set, 515F (5′-GTGYCAGCMGCCGCGGTAAA-3′) and 806R (5′-GGACTANVSGGGTATCTAA-3′; Caporaso et al., 2012), and using 1U Pfu DNA polymerase (Promega; Madison, Wisconsin, USA). The 16S amplicons were sequenced by the MiSeq Illumina (paired end 2* 250) platform Get of Genotoul (INRA, Narbonne France, https://get.genotoul.fr).

2.3.2. Sequences analysis

The paired-end raw reads were first overlapped and merged using the FLASH assembly software (Magoč and Salzberg, 2011). Analysis of the 16S-assembled data relied on the use of the QIIME package and its recommendations (Kuczynski et al., 2012). Removal of low-quality bases and chimera sequences was performed by QIIME script and UCHIME (Edgar et al., 2011), respectively. The high-quality sequences were next clustered into operational taxonomic units (OTUs) using a 97% sequence identity threshold and the UCLUST algorithm (Edgar, 2010). The OTU table was filtered for low abundance OTUs (Bokulich et al., 2013) followed by a subsampling-based normalization implemented in QIIME (Kuczynski et al., 2012). The full taxonomic hierarchy classification was performed by UCLUST taxonomy querying the Greengenes database (DeSantis et al., 2006). We removed all OTUs classified as chloroplasts or mitochondria.

Finally, alpha diversity (within each sampling site), reported as the Simpson, Shannon index, and beta diversity (differences in OTU composition and abudance among sites) were characterized by the core_diversity_analyses.py script (Kuczynski et al., 2012). Phyloseq, an open-source software package project for R (www.r-project.org) was used for representation (McMurdie and Holmes, 2013).

The raw data have been deposited to the short-read archive (NCBI SRA) and are available under the bioproject PRJNA591440.

3. Results

3.1. Sampling site characteristics

During the sampling period, sea ice thickness was relatively constant (mean $\pm$ standard deviation of 122 $\pm$ 7 m, $n = 19$) with a thick snow cover (mean of 28 $\pm$ 7 cm, $n = 19$; Oziel et al., 2019, their **Figure 2G**), which resulted in under-ice transmitted photochemically active radiation falling mostly below 0.1 mol m^{-2} d^{-1} (Massicotte et al., 2020). The increase in daily air temperature throughout the sampling period (mean of –7.3°C in May to –3.2 °C in June 2015) likely caused the decrease in sea ice brine salinity (mean salinity in the whole ice core: 70.9 on May 4, 51.1 on June 2) as well as the increase in brine volume (8.7% on May 4, 11.5% on June 2), as published earlier (Oziel et al., 2019, their **Figure 3**). During the sampling period, chlorophyll-*a* concentration increased from 12.7 to 39.4 mg m^{-2} within the bottommost 3 cm of sea ice, while its concentration in the 3- to 10-cm section was steady (0.8 $\pm$ 0.25 mg m^{-2}; Oziel et al., 2019, their Figure 9E).

3.2. Bacterial diversity

The 16S rRNA sequencing generated 36,234 sequences per sample after the trimming process and sampling normalization. The global species richness, which represents the total number of non-redundant OTUs found in a sample group, was similar between the sea ice and sinking particle groups with 497 and 524 observed OTUs, respectively. Both sample groups presented variability in species richness (Figure **2A**), but this variability was more pronounced for the SPOM group (Mann–Whitney test, $n = 25$, $P = 0.0010 < 0.05$). Although a significantly higher number of OTUs was observed in SPOM than SIPOM (Mann–Whitney test, $n = 13$, $P = 0.0001 < 0.05$; Figure **2A**), species diversity in SPOM by both Shannon (H′) and Simpson (D1) indices (mean $\pm$ *SD*, $n = 13$: $H' = 3.39 \pm 0.61$; $D1 = 0.86 \pm 0.13$) did not differ significantly from that observed in SIPOM ($H' = 3.65 \pm 0.34$, $D1 = 0.93 \pm 0.03$, $n = 12$; Figure **2B** and **C**). When OTU composition was compared between sample types recovered on the same day, a considerable fraction of shared OTUs was observed, ranging from 52% (SIPOM2/SPOM2) to 80% (SIPOM4/SPOM4). The SPOM communities included more unique OTUs than SIPOM communities (Table **S1**).

At the phylum level, the bacterial composition consisted mainly of *Proteobacteria* (76%–92% and 83%–91% for sea ice and sinking particles, respectively), *Bacteroidetes* (7%–20% and 6%–13% for SIPOM and SPOM, respectively) and *Actinobacteria* (0.4%–1% and 0.5%–3.7% for SIPOM and SPOM, respectively; **Figure 3**). Among the Proteobacteria, about 65% belonged to Gammaproteobacteria and 30% to Alphaproteobacteria. An apparent increase in *Bacteroidetes* at the expense of *Proteobacteria* was observed in sea ice on May 8 and in sinking particles on May 12 (**Figure 3**). The archaeal fraction of

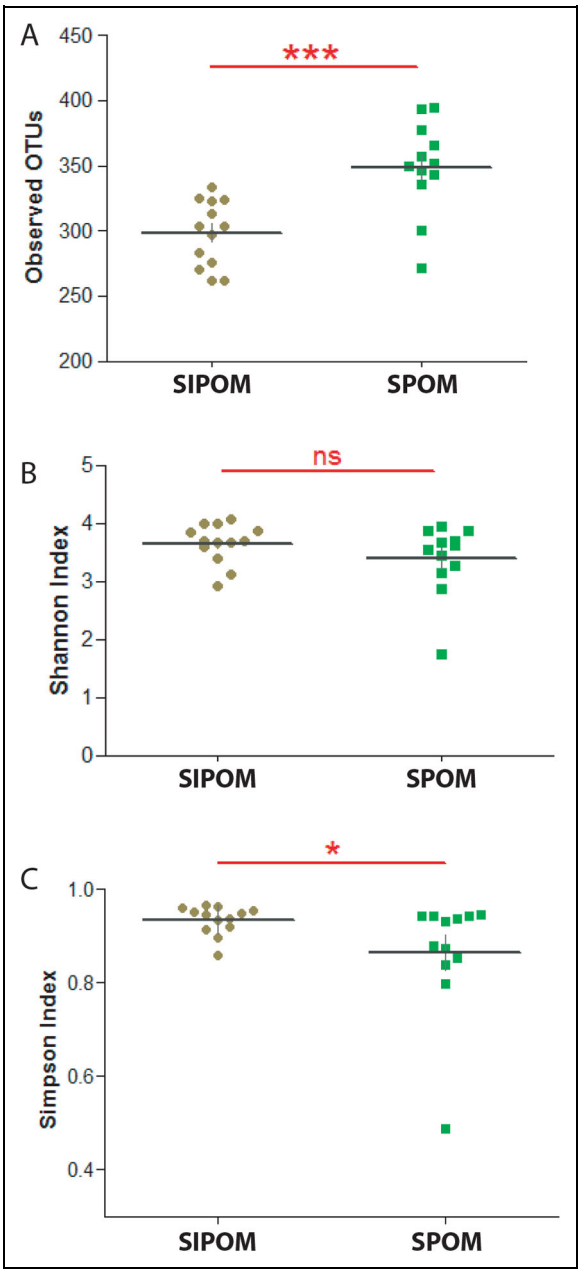

Figure 2. Biodiversity indices of the prokaryotic community in sea ice and sinking particles. (A) Observed number of OTUs, (B) alpha diversity (Shannon index), and (C) beta diversity (Simpson index) for prokaryotic communities from sea ice particulate organic matter (SIPOM) and sinking POM (SPOM) collected from May 2 to June 4, 2015, at the sampling location in Baffin Bay (Figure 1; Mann–Whitney test, $P > 0.05$ ns nonsignificant, $^{*}P < 0.05$. $^{**}P < 0.01$. $^{***}P < 0.001$). DOI: https://doi.org/10.1525/elementa.2021.040.f2

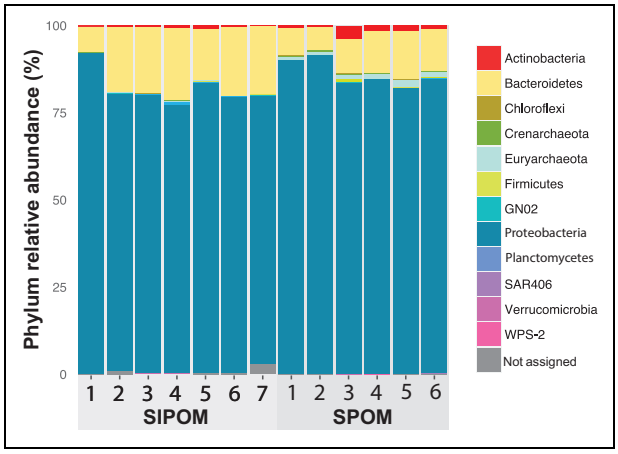

Figure 3. Relative abundance of prokaryotic phyla in sea ice (SIPOM) and sinking particles (SPOM). Percentage of prokaryotic phyla abundance in both sea ice particulate organic matter (SIPOM) and sinking POM (SPOM) collected from May 2 to June 4, 2015, at the sampling location in Baffin Bay (Figure 1). DOI: https://doi.org/10.1525/elementa.2021.040.f3

the prokaryotic communities in both SIPOM and SPOM was always less than 2% (**Figure 3**).

Among the three main bacterial phyla, different clusters based on genus abundance could be identified (**Figure 4**). These clusters gathered either the genera abundant in both SIPOM and SPOM or the genera scarce in both sample types, and either the genera relatively well represented in both sample types and constant over time or the genera poorly represented in SIPOM while present in SPOM.

Among the main phyla investigated, the most abundant genera in both SIPOM and SPOM were *Candidatus Endobugula*, *Alcanivorax*, *Alteromonas*, *Pseudoalteromonas, Oleispira*, *Psychrobacter*, *Pseudomonas*, *Marinobacter*, and *Erythrobacter* of the Proteobacteria (Figure **4A**); *Maribacter* and *Polaribacter* of the Bacteroidetes (Figure 4B); and *Propionibacterium* of the Actinobacteria (Figure **4C**). In contrast, *Glaciecola* (Proteobacteria) was strongly abundant in SIPOM while less abundant in SPOM (Figure **4A**). Although the two environments share a very similar bacterial composition, the relative abundances of their genera differ. Thus, the relative abundances of *Candidatus Endobugula*, *Polaribacter*, *Ulvibacter*, and *Glaciecola* genera were higher in SIPOM and, conversely, lower in SPOM (**Figure 4**). In contrast, the relative abundances of *Alteromonas*, *Pseudoalteromonas*, and *Salinibacter* were higher in SPOM but lower in SIPOM (**Figure 4**).

To examine how the relative abundance of the most abundant genera present in the three main phyla changed with sampling time and sample types, we performed a biplot principal component analysis (PCA; **Figure 5**). The first principal component (Dim1 in **Figure 5**) accounts for the environment (SIPOM vs. SPOM), with the genera (variables) displayed according to their contribution (in %) to the dimensions of the biplot. The quality of the contribution is color-scaled in the figure, with good contribution considered to be above 4 (orange, indicator length of arrows). This analysis showed that the genera *Candidatus Endobugula*, *Polaribacter*, *Ulvibacter*, and *Glaciecola* were the main contributors in the sea ice samples and, conversely, were less represented in the sinking particles. In contrast, *Pseudoalteromonas*, *Alteromonas*, and *Salinibacter* (followed closely by others) were major contributors to

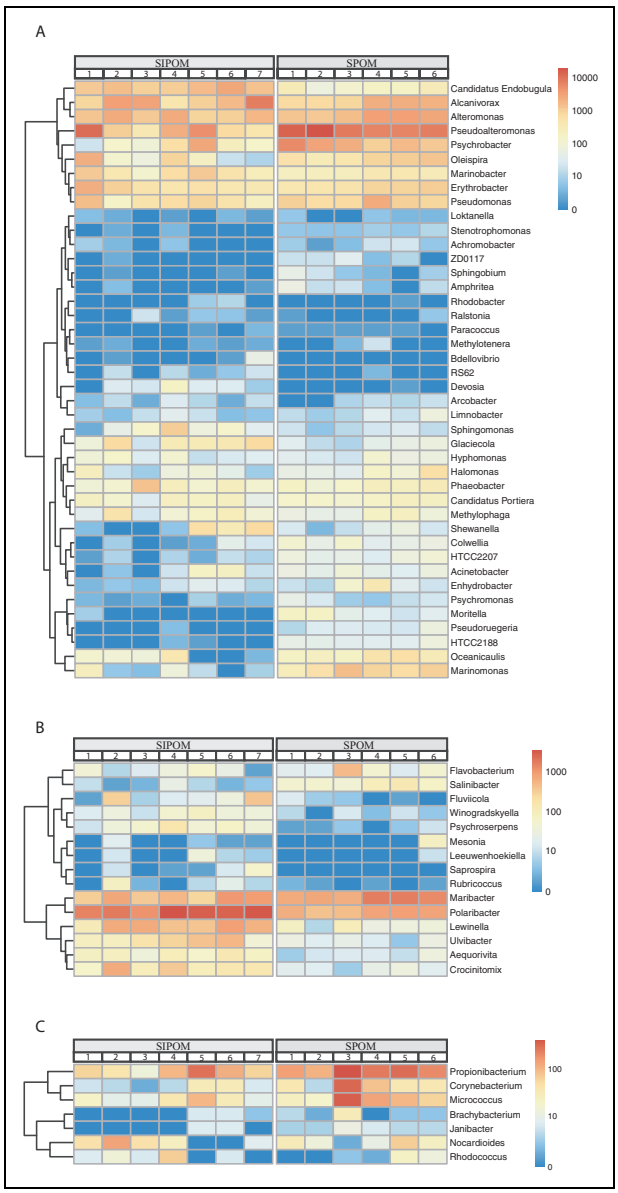

Figure 4. Relative abundance of Proteobacteria and Bacteroidetes genera in sea ice and sinking particles. Heat map presenting the relative abundance of all genera of the phyla (A) Proteobacteria, (B) Bacteroidetes, and (C) Actinobacteria detected in samples of sea ice particulate organic matter (SIPOM) and sinking POM (SPOM) collected from May 2 to June 4, 2015, at the sampling location in Baffin Bay (Figure 1). The color bar is relative to the subsampling-based normalized count. DOI: https://doi.org/10.1525/elementa.2021.040.f4

sinking particles but minor ones within sea ice. The second principal component (Dim2 in **Figure 5**) separates the samples according to sampling time. No temporal pattern was evident for the SIPOM samples, but the first sampling times for the sinking particles (SPOM1, SPOM2, SPOM3) associated positively with *Psychrobacter*, *Moritella*, and *Pseudoalteromonas* genera, while the last three (SPOM4, SPOM5, SPOM6) were more affected by *Alteromonas*, *Maribacter*, *Oceanocaulis*, and *Salinobacter*.

3.3. Lipid markers of CTI and 10S-DOX-like lipoxygenase activity

The *trans/cis* ratio of vaccenic acid, considered a typical biomarker for bacteria (Marchand and Rontani, 2003; Rontani et al., 2003), was determined after DMDS treatment of the different sea ice and sediment trap samples (**Table 1**; **Figure 6A**). This ratio did not exceed 0.09 in the bottommost layers of ice (0–1 and 1–2 cm) and in most cases was lower (range of 0.02–0.09), while in layers higher in the ice (2–5, 5–7, and 7–10 cm) numerous values (8 of 21) were above the stress threshold of 0.1 (reaching 0.25; **Table 1**). In the sediment trap samples, all but 3 of the 13 ratios fell above 0.1 (reaching 0.33; **Table 1**).

The fatty acid 10-Hydroperoxyhexadec-8(*trans*)-enoic acid produced during the oxidation of palmitoleic acid by 10*S*-DOX-like lipoxygenase was quantified in sea ice and sediment trap samples after $NaBH_4$-reduction to the corresponding hydroxyacid (more amenable to analysis using GC–MS). This compound was present mainly in the 0–2 cm layer of the first samples in the time series, SIPOM1–SIPOM5, and not detected in any layer of the final samples, SIPOM6 and SIPOM7 (**Table 1**; Figure **6B**). In the sediment traps (including the 2-m traps; Amiraux et al., 2017), non-negligible amounts were not detected until halfway through the time series, in SPOM4–SPOM6 (**Table 1**).

Sterols, which have been employed to evaluate algal diversity (Rampen et al., 2010), allowed an estimate of the relative proportions of sympagic algae versus phytoplankton and zooplankton in the sinking particle samples. Based on desmosterol/brassicasterol ratios in the sea ice samples, which ranged from 0.19 to 0.40, the contribution of sympagic algae appeared to be minimal in SPOM1–SPOM4, where the ratios ranged from 8.75 to 18.78, and more important in SPOM5 and SPOM6, where the ratios were 3.65 and 1.90, respectively (**Table 1**).

4. Discussion

4.1. Bacterial diversity in SIPOM and SPOM during a melting season

In springtime sea ice in the Arctic, bacteria tend to be concentrated along with other biota in the lowermost centimeters of the ice, where they remain active at subzero temperature (Deming, 2010). These ice-inhabiting organisms are adapted to grow within a labyrinth of interconnected pores and channels that permeate the ice. The challenges of low temperature, salinity fluctuation as overlying snow and the ice begin to melt, and possible resource limitation appear to have been met by many types of microorganisms, including diatoms, other microalgae, protozoa, bacteria, and archaea, as well as their viruses (Maranger et al., 1994; von Quillfeldt et al., 2003; Junge et al., 2004; Collins et al., 2010; Torstenssen et al., 2015). Bacterial diversity in Arctic sea ice is well known from short-term studies, primarily in spring and summer (reviewed by Deming and Collins, 2017), but to the best of our knowledge has only been tracked through a full season in wintertime (Collins et al., 2010; see Kaartokallio et al., 2008, for full bacterial succession in sub-Arctic sea ice). Our work is unique in the use of high

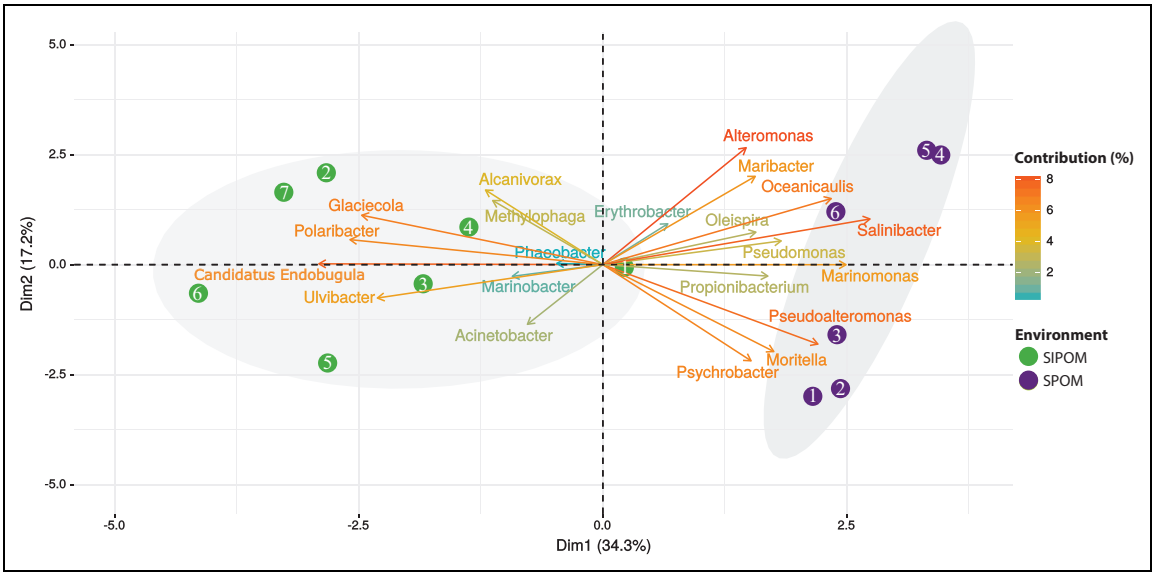

Figure 5. Principal component analysis (PCA) of sea ice and sinking particles according to most representative bacterial genera. PCA correlation biplot showing 13 samples (colored points) and the 21 most representative bacterial genera (arrows) from the three primary phyla. The analysis accounts for 51.5% of the total variation among sites (Axis 1: 34.3% and Axis 2: 17.2%). Green indicates samples of sea ice particulate organic matter and blue, sinking POM, numbered from 1 to 7 corresponding to sampling date: May 4, May 8, May 12, May 14, May 22, May 27, and June 2, 2015. The genera (variables) are displayed according to their contribution (%) to the dimensions of the biplot. The quality of the contribution is colored, with good contribution considered above 4 (orange, indicator length of arrow). DOI: https://doi.org/10.1525/elementa.2021.040.f5

throughput sequencing to assess the temporal succession of bacterial diversity in Arctic sea ice during the melting season and in sinking particulate organic matter under the ice at the same time.

Our analysis of the attached prokaryotes in sea ice (SIPOM) and sinking particles under the ice (SPOM) showed a similar global richness and composition between the two environments (**Figures 2** and **3**), including when the main bacterial phyla were examined separately (**Figure 4**). Prokaryotic diversity measured by the Shannon index (**Figure 2**) compares well to similar measures reported previously for both seasonal and multiyear Arctic sea ice (Bowman et al., 2012; Hatam et al., 2016), as well as for seasonal Antarctic pack ice (Torstensson et al., 2015). Diversity by the Simpson index was higher in our samples, which may be due to the time-series nature of our study compared to other short-term evaluations. Our PCA analysis indicated that day of sampling was associated with diversity in the sinking particle samples, though not in the sea ice samples (**Figure 5**). Other factors may pertain, but divergence over time in sinking material is consistent with our lipid analyses (as discussed in Section 4.2). Amiraux et al. (2017) had concluded earlier, based on high CTI signals in 2-m and 25-m sediment trap materials, that sinking particles had not been colonized by ambient seawater bacteria. Preliminary data on prokaryotic communities associated with suspended material in ambient seawater (included in a nonmetric multidimensional scaling or NMDS analysis of SIPOM and SPOM samples; Figure S1) tended to support this conclusion. Both our PCA and the limited NMDS analysis, however, also indicated a separation between sea ice and sinking particle communities despite their global similarities.

As in previous studies of sea ice bacterial composition, members of the *Proteobacteria* and *Bacteroidetes* were overwhelmingly dominant across our data sets, with the *Actinobacteria* a distant third phylum (**Figure 3**; Brown and Bowman, 2001; Brinkmeyer et al., 2003). Many *Proteobacteria* associated with sea ice, including members of the genera *Psychrobacter* and *Glaciecola*, are known to be associated with sympagic algae (Bowman et al., 1997; Staley and Gosink, 1999; Brown and Bowman, 2001). In the *Bacteroidetes*, the abundance of most of these genera as found in sea ice tended to be lower in sinking particles, with the exception of the predominant *Polaribacter* and *Maribacter* genera (Figure 4B). *Bacteroidetes* are notable for their close physical association with pelagic (Schäfer et al., 2002; Jasti et al., 2005) and sympagic algae (Brown and Bowman, 2001). If this genus-level difference in community composition between SIPOM and SPOM is due to differences in environmental conditions during the melt season (cold temperature but fluctuating salinity in SIPOM, more stable conditions for SPOM in the water column), then some members of the Bacteroidetes appear to be more competitive after fluctuating salinities have stabilized. The compositional shift in favor of Bacteroidetes observed early in the time series (**Figure 3**) may be associated with the drop in salinity of that same period (**Table 1**).

Heterotrophic bacteria represented the major group in our analyses of microbial communities, which likely reflects elevated concentrations of organic matter in both

Table 1. Lipid biomarkers measured in samples of sea ice particulate organic matter, with corresponding brine salinities, and sinking particulate organic matter collected in spring 2015 in Davis Strait. DOI: https://doi.org/10.1525/elementa.2021.040.t1

		Sample Number (Collection Date in 2015)						
Parameter	**Depth (cm)**	**SIPOM1 (May 4)**	**SIPOM2 (May 8)**	**SIPOM3 (May 12)**	**SIPOM4 (May 14)**	**SIPOM5 (May 22)**	**SIPOM6 (May 27)**	**SIPOM7 (June 2)**
Sea ice								
Brine salinity	0–10	70	70	63	58	53	53	51
Desmosterol/brassicasterol ratio	0–10	0.31	0.36	0.29	0.35	0.19	0.33	0.40
10*S*-DOX-like lipoxygenase product[a] (ng ml^{-1})	0–1	0.04	2.29	12.07	4.16	1.40	nd[b]	nd
	1–2	0.65	nd	0.74	28.29	29.70	nd	nd
	2–5	nd	nd	nd	3.53	nd	nd	nd
	5–7	nd	nd	nd	nd	nd	nd	nd
	7–10	nd	nd	nd	nd	nd	nd	nd
Trans/cis vaccenic acid ratio	0–1	0.04	0.04	0.02	0.08	0.04	0.02	0.04
	1–2	0.09	0.08	0.03	0.03	0.03	0.03	0.05
	2–5	0.14	0.05	0.02	0.06	0.02	0.03	0.04
	5–7	0.16	0.17	0.04	0.12	0.06	0.05	0.05
	7–10	0.19	0.18	0.03	0.12	0.25	0.04	0.06
		Sample Number (Collection Date in 2015)						
Parameter	**Depth (m)**	**SPOM1 (May 4)**	**SPOM2 (May 8)**	**SPOM3 (May 12)**	**SPOM4 (May 14)**	**SPOM5 (May 22)**	**SPOM6 (May 27)**	**SPOM7[d] (June 2)**
Sinking particles[c]								
Desmosterol/brassicasterol ratio	25	8.75	11.71	17.28	17.01	3.65	1.90	na[d]
10*S*-DOX-like lipoxygenase product[a] (μg m^{-2} d^{-1})	25	nd	nd	nd	3.20	0.28	1.11	na
Trans/cis vaccenic acid ratio	2[e]	0.13	0.07	0.17	0.04	0.23	0.28	na
	25	0.16	0.15	0.20	0.29	0.23	0.33	0.22

[a]10-Hydroxyhexadec-8(*trans*)-enoic acid.

[b]Not detected.

[c]Mean values ($n = 2$) for sinking particulate organic matter (SPOM) collected in sediment traps at 2 and 25 m below ice; seawater salinity was constant at 32.5 at both trap depths during the study period (Oziel et al., 2019, their Figure 5E).

[d]Not available.

[e]Data from the 2-m sediment trap samples are from Amiraux et al. (2017).

sea ice and sinking particles relative to surrounding seawater, as expected for these environments. Sympagic algae were blooming during the sampling period investigated (Oziel et al., 2019; Massicotte et al., 2020), and most of the dominant bacterial genera we found in the sea ice have been reported in literature as associated with algal blooms. For example, the increase in relative abundance of *Polaribacter* and *Ulvibacter* during the sampling period agrees with previous documentation of their predominance during an algal bloom in the North Sea, where these genera were presumed to be fast-growing opportunists specializing in the use of high molecular weight compounds derived from the algae (Teeling et al., 2012). Members of the Gammaproteobacterial genus *Pseudoalteromonas* which were, particularly abundant in both environments throughout the sampling period (**Figures 4** and **5**), are also known to play major roles in the transformation of complex organic compounds that are too large for direct uptake by marine bacteria (Chrost, 1991). For this purpose, they produce a variety of extracellular enzymes (protease, lipase, amylase, chitinase, β-galactosidase, cellulase) which may contribute to their

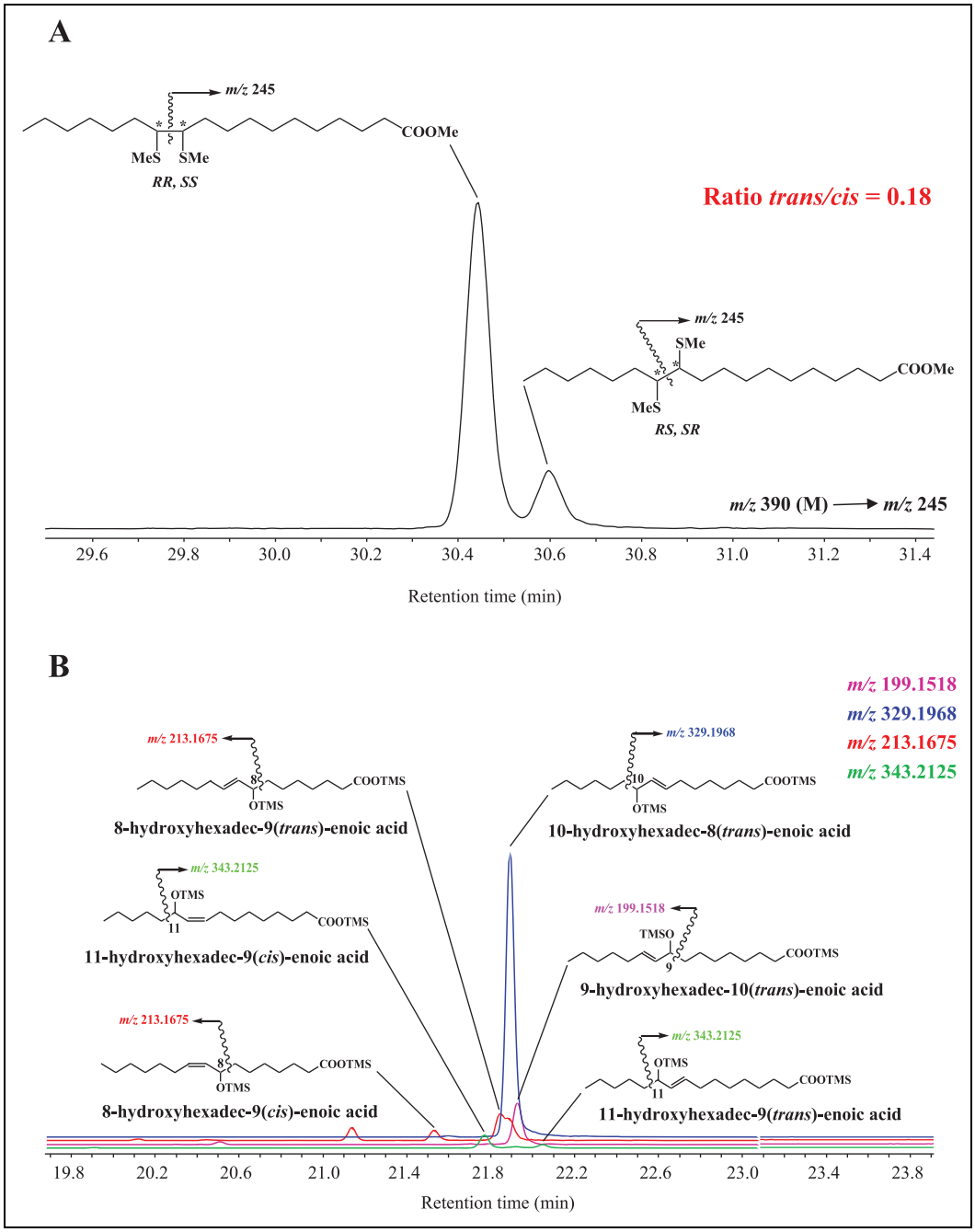

Figure 6. Lipid markers of fatty acid cis-trans isomerase and 10S-DOX-like lipoxygenase activity. (A) Multiple reaction monitoring chromatogram (m/z 390 → 245) of DMDS adducts showing an example of cis-vaccenic isomerization (trans/cis ratio of 0.18) in the 7–10 cm layer of sea ice collected May 8, 2005, and (B) time of flight ion chromatograms (at m/z 199.1518, 213.1675, 329.1968, and 343.2125) showing an example of the predominance of 10-trans isomer (blue line) in palmitoleic oxidation profiles of the bottommost centimeter of sea ice collected June 2, 2015, at the sampling location in Baffin Bay (Figure 1). DOI: https://doi.org/10.1525/elementa.2021.040.f6

dominance in a bacterial community. In a study of a total of 338 aerobic heterotrophic bacterial strains isolated from sea ice samples in the Arctic, more than 56% were cold-tolerant *Pseudoalteromonas* spp., each of which produced a variety of extracellular enzymes (Yu et al., 2009). Members of the genus *Glaciecola*, also relatively abundant in our SIPOM samples (Figure 4A), are known for their dominant role in consuming dissolved organic matter during a cold-water diatom bloom (von Scheibner et al., 2017). Most members of this genus are considered psychrophilic, with experimental work showing *Glaciecola* to be the dominant consumers of algal material in low-temperature environments (von Scheibner et al., 2017). The relative abundances in some of our samples of other genera known to contain primarily psychrophilic or psychrotolerant and halophilic bacteria, such as *Psychrobacter*, *Colwellia*, *and Moritella*, is not surprising (Figure 4A).

4.2. Origin of production and potential bacterial source of CTI and 10S-DOX-like lipoxygenase activity

A major adaptive response of microorganisms to rapid increases in salinity is the conversion of *cis*- to *trans*-unsaturated fatty acids in order to retain membrane fluidity (Loffeld and Keweloh, 1996; Heipieper et al., 2003). *Trans/cis* ratios > 0.1 in environmental samples have previously been suggested to indicate bacterial stress (Guckert et al., 1986), with isomerization induced by the action of the CTI enzyme (Heipieper et al., 2003). In the ice cores collected at the beginning of our time series, we found *trans/cis* vaccenic acid ratios > 0.1, which we attribute to the presence of salinity-stressed bacteria (**Table 1**; Figure 6A). These elevated ratios were observed only in the upper layers of the investigated sea ice section (2–5, 5–7, and 7–10 cm above the ice-water interface; **Table 1**). Indeed, when upper portions of sea ice are colder, the corresponding brines are more hypersaline, relegating many organisms to the more moderate conditions of bottom ice (Grant and Horner, 1976), where our *trans/cis* ratios were below the stress threshold. *Trans/cis* ratios of vaccenic acid above the stress threshold were also measured in the sinking particle samples of this 2015 field campaign (**Table 1**). We suggest that these high values point to an origin in the upper portions of the sea ice examined, that is, that a flush of material with high *trans/cis* ratio from the upper sections of the sea ice through brine drainage accounts for the high values observed in sinking material below the ice. The low *trans/cis* ratios observed in the uppermost sections of ice by the end of the time series (SIPOM6, SIPOM7; **Table 1**) support a previous drainage of stressed organisms through brine channels.

The presence of the specific tracer of ice diatoms, IP_{25} (Belt and Müller, 2013; Belt, 2018), in particles collected at 25 m during our time series (though not on exactly the same dates), where values ranged from 14 pg mL^{-1} for May 2 to 71 pg mL^{-1} for May 31 (L Smik, personal communication), attests to an increasing contribution of sympagic algae to the sinking particles investigated. Unexpectedly, the *trans/cis* ratio measured in sinking particles did not parallel brine salinity in the corresponding sea ice (**Table 1**), remaining high even as brine salinity dropped over time. We considered that this lack of correlation derived from a dilution of the high *trans/cis* ratios of stressed bacteria initially flushed from upper brines by unstressed (low ratio) pelagic bacteria associated with phytoplankton or zooplankton. The latter contribution was estimated from sterol ratios. During the sampling period, sympagic algae appeared to be dominated by pennate diatoms (Massicotte et al., 2020), which are characterized by a high content of brassicasterol and 24-methylenecholesterol (Rampen et al., 2010). In contrast, the sediment trap samples contained a high proportion of desmosterol, which is present in some centric diatoms (Rampen et al., 2010) and produced by zooplankton during the conversion of algal sterols to cholesterol (Harvey et al., 1987). A temporal comparison of the ratio desmosterol/brassicasterol (**Table 1**) suggests a strong contribution of either phytoplankton or zooplankton in the initial samples (SPOM1through SPOM4), but not in the later ones (SPOM5 and SPOM6). The low values of the *trans/cis* ratio of vaccenic acid observed in sinking particle samples at the beginning of the time series (when sea ice brine salinity was highest; **Table 1**), thus appears to be consistent with a dilution of stressed bacteria associated with sympagic algae by unstressed bacteria associated with pelagic algae or zooplankton. However, despite this potential dilution effect, the *trans/cis* ratios remained high (above the stress threshold value of 0.1; Guckert et al., 1986) in nearly all of the sinking particle samples (**Table 1**). A potential contributing factor here may be the number of epiphytic bacteria per algal cell, which is generally an order of magnitude higher for sea ice diatoms than for phytoplankton (Smith et al., 1989; Kaczmarska et al., 2005).

The taxa specifically responsible for the CTI activity measured during this time series (and thus allowing for evaluations by *tran/cis* ratio) are not known and may be numerous, but CTI activity has been demonstrated experimentally only in bacteria of the orders Vibrionales and Pseudomonadales (Okuyama et al., 1991; Heipieper et al., 2003; Mrozik et al., 2005; Fischer et al., 2010). As the Vibrionales contributed weakly to SPOM (**Figure 4**) where CTI activity was highest, much of the observed CTI activity may be attributed to the Pseudomonadales. Bacteria belonging to Pseudomonadales contain high amounts of vaccenic acid (Holstrom et al., 1998; Rontani et al., 2005), which also makes them good candidates for the isomerization of this acid in sea ice and in sinking particles. The *Alcanivorax*, also abundant in SPOM samples (**Figure 4**) and known to contain vaccenic acid (Liu and Shao, 2005) and the CTI gene (Eberlein et al., 2018), may have been involved as well. Following this line of reasoning, the low abundance of Pseudomonadales observed in SIPOM6 and SIPOM7 samples (**Figure 4**) where the lowest *trans/cis* ratios were also observed (**Table 1**) suggests the efficiency of brine channel discharge at the end of the time series.

CTI activity does not represent a reliable proxy for prolonged stress in the environment because bacteria may substitute its action (used only as an acute response to permit survival) by other mechanisms (Fischer et al., 2010). Once flushed into the pelagic system, where acute hyperosmotic stress is typically lacking, the *trans/cis* ratio of salinity-stressed bacteria should thus decrease (Fischer et al., 2010). However, recovery of the typically low *trans/cis* ratio requires de novo synthesis of *cis* fatty acids, as the conversion of *tran*s to *cis* fatty acids is not catalyzed (Eberlein et al., 2018). This recovery mechanism is thus dependent on bacterial growth rates. Consequently, the high values of *trans/cis* ratios previously observed in sinking particles collected at 2 and 25 m and in the underlying surficial sediment in Baffin Bay (Rontani et al., 2018) were considered indicative of non-growing attached bacteria (Amiraux et al., 2017; Amiraux et al., 2020).

To estimate the role of 10*S*-DOX-like lipoxygenase, a potentially important biomarker, in the degradation process of SIPOM, we examined oxidation products of palmitoleic acid known to be present in some bacteria (de Carvalho and Caramujo, 2014) and dominant in sympagic

algae (Leu et al., 2010). Among the different oxidation products of palmitoleic acid detected in our sea ice samples (Figure 6B), we observed a strong predominance of the 10-hydroxyhexadec-8(*trans*)-enoic acid (Figure 6B). The presence of an unusual abundance of this isomer was previously attributed to the involvement of a specific enzymatic oxidation process and, more specifically, to a bacterial 10*S*-DOX-like lipoxygenase enzyme (Amiraux et al., 2017). The selective conversion of oleic acid to 10(*S*)-hydroperoxyoctadec-8(*trans*)-enoic acid by *Pseudomonas aeruginosa* 42A2 had been observed previously (Guerrero et al., 1997; Busquets et al., 2004; Vidal-Mas et al., 2005) and attributed to a lipoxygenase-like enzyme, subsequently called 10*S*-DOX (Martínez et al., 2010; Estupiñán et al., 2014; Estupiñán et al., 2015). Such an enzyme, which is particularly active on free monounsaturated fatty acids containing double bonds in position Δ^9 (Brash et al., 2014), converts palmitoleic acid to 10(*S*)-hydroperoxyhexadec-8(*trans*)-enoic acid (hereafter referred to as 10-*trans*; Brash et al., 2014), which could be then reduced to the corresponding hydroxyacid during sample treatment.

As hypothesized, 10*S*-DOX-like lipoxygenase oxidation of palmitoleic acid occurs in sea ice. This activity appears later in the melting season than the CTI activity and was highest in SIPOM4 and SIPOM5 (**Table 1**). Interestingly, 10-*trans* resulting from this enzymatic activity could be only detected in the bottommost (0–2 cm) sea ice layer (**Table 1**), that is, where most of the algal material is assumed to have accumulated (Arrigo and Thomas, 2004) and where salinity variation was limited due the influence of seawater (Oziel et al. 2019, their Figure 3A). Consequently, the induction of this bacterial enzymatic activity does not seem likely to result from salinity stress; instead, we suggest that it derives from the growth of sympagic algae (chlorophyll-*a* concentration in the ice increased from 12.7 mg m^{-2} in the 0–3 cm layer of SIPOM1 to 20.5 mg m^{-2} in the corresponding layer of SIPOM5; Oziel et al., 2019). Bacterial 10*S*-DOX-like lipoxygenase is known to be expressed extracellularly (Kim et al., 2000) and be particularly active on free fatty acids (Martínez et al., 2010), and sympagic algae are known to produce free palmitoleic acid (Fahl and Kattner, 1993; Leu et al., 2010), which can be bactericidal (Amiraux et al., 2020). Enzymatic production of 10-*trans* in sea ice and sinking particles may thus be attributed to the bacterial degradation of algae-produced palmitoleic acid as a defense mechanism. The relative age of organic matter can be deduced from the time-dependent allylic rearrangement state of 10-hydroperoxyhexadec-8(*trans*)-enoic acid, which is produced during the 10*S*-DOX-like lipoxygenase oxidation of palmitoleic acid. The older the degradation reaction, the more this 10-*trans* isomer is rearranged into 8-*trans* isomers (8-hydroperoxyhexadec-9(*trans*)-enoic acid; Porter et al., 1995). As expected, the allylic rearrangement appeared to be low in sea ice (8-*trans*/10-*trans* ratio = 0.12 in SIPOM1 the 02 May; Figure 6B) where the organic matter is produced, while it was high (8-*trans*/10-*trans* ratio = 1.01) in the corresponding sinking particles SPOM1 (Rontani et al., 2018). These results bolster the sea ice origin of the 10*S*-DOX-like lipoxygenase activities and indicate that the sea ice material collected in the sediment traps is older than that present in the corresponding ice sample. This time-dependent lipid analysis is also consistent with the link between bacterial community composition and progressive day of sampling observed in our PCA analysis (**Figure 5**).

Pseudomonas and *Pseudoalteromonas* are well known for their 10*S*-DOX-like lipoxygenase activity (Guerrero et al., 1997; Busquets et al., 2004; Vidal-Mas et al., 2005; Shoja Chaghervand, 2019). The dominance of these two genera in SPOM samples (Figure 4A) suggests that they could be the producers of the 10-hydroxyhexadec-8(*trans*)-enoic acid observed in sinking particles collected at the end of the time series (**Table 1**). Other bacterial sources cannot be excluded, however. The oxidative stress induced by the 10*S*-DOX-like lipoxygenase activity in sinking particles (production of hydroperoxides) could also be linked to the accumulation of members of the genera *Maribacter* and *Erythrobacter* toward the end of the time series (**Figure 4**). Indeed, bacteria associated with phytodetritus containing high amounts of photochemically produced hydroperoxides were predominantly pigmented bacteria, notably *Maribacter* and aerobic anoxygenic photoheterotrophic bacteria, likely due to their high content of antioxidant compounds (carotenoids in the case of the latter; Petit et al., 2015).

5. Conclusions

Overall, we found that bacterial community composition associated with particulate organic matter in sea ice and sinking particles under the ice during our spring time series was dominated by members of the *Proteobacteria* and *Bacteroidetes*. Evidence of community changes over time during this melting season appeared primarily in the sinking particle data set. We considered that CTI and 10*S*-DOX-like lipoxygenase activity arose from bacteria inhabiting the sea ice and attached to sinking particles, the latter originating from the sea ice. We suggest that during the early stages of sea ice melt, brine pockets throughout the sea ice become interconnected and drain sporadically from the ice, imposing hypersaline stress on organisms living in the bottommost centimeters of sea ice. As brine drains from the sea ice, sympagic POM with its attached bacteria flushes from the ice and begins sinking. These bacteria have high CTI activity because of the hypersaline stress they underwent while in the sea ice. In contrast, bacterial 10*S*-DOX-like lipoxygenase activity appeared to be expressed only later in the melting season and then limited to the bottommost chlorophyll-rich layer of sea ice. As previously suggested by Martínez et al. (2010), this bacterial enzyme could play a role in bacterial colonization and survival in environments rich in free fatty acids such as sympagic algae (Falk-Petersen et al., 1998). Additional research is needed to confirm these hypotheses.

In previous works, we suggested that CTI and 10*S*-DOX-like lipoxygenase enzymatic activity could represent useful biomarkers of sea ice biota in the Arctic (Amiraux, 2017; Amiraux et al., 2017; Amiraux et al., 2020). Indeed, the need for source-specific tracers allowing

discrimination between pelagic and sympagic algal material is still clear. In this study, the detection of CTI activity in sea ice, which we argue resulted from osmotic stress to sympagic bacteria upon exposure to hypersaline brines, supports the use of this activity as a tracer of sympagic algal material. As previously expected, bacterial 10*S*-DOX-like lipoxygenase activity was also detected in sea ice. However, its use appeared to be in response to the production of bactericidal free fatty acids by sympagic algae rather than to an osmotic stress, which may limit the use of this activity as a tracer of sea ice biota. Indeed, high amounts of free fatty acids may also be produced by some pelagic diatoms in the presence of copepods (Pohnert, 2002).

Data accessibility statement

The raw sequence data have been deposited to the short-read archive (NCBI SRA) and are available under the bio-project PRJNA591440. All data are accessible at the Green Edge database (http://www.obs-vlfr.fr/proof/php/GREENEDGE/greenedge.php) and will be made public prior to publication.

Supplemental files

The supplemental files for this article can be found as follows:

Table S1. Number of OTUs shared between samples of sea ice particulate organic matter (SIPOM) and sinking POM (SPOM), globally and by same-day sampling pairs, with number of OTUs (defined by 97% sequence similarity) unique to each sample.

Figure S1. Ordination analysis of prokaryotic communities associated with sea ice, sinking particle, and suspended particle samples. Nonmetric multidimensional scaling ordination analysis, using Bray–Curtis dissimilarity distances, of sea ice particulate organic matter (SIPOM), sinking POM (SPOM), and suspended particle (Seawater) samples, where numbers indicate sampling dates (see Materials and Methods). Seawater samples were collected on May 12, 2015, corresponding to SIPOM3 and SPOM3, using 20-L Niskin bottles at an under-ice depth of 20 m, the closest water sampling depth to the 25-m sediment trap deployments. Microorganisms associated with suspended particulate matter in the water samples were obtained by filtration, using 0.8 μm Whatman nuclepore filters. Color is used to visualize sample pairs. Samples closer in ordination space have more similar community composition.

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Competing interests

The authors declare that they have no competing interests.

Author contributions

RA, JFR, and PB led the design of the study, while MB led its insertion within the GreenEdge project.

RA led the sampling, in the framework of the Green-Edge project led by MB.

RA, JFR, and PB led the writing.

RA led the lipid analysis, to which LA contributed.

RA led the bacterial diversity analysis, to which FA and EF contributed in terms of interpretation and figures.

All authors revised the earlier version of the manuscript, helped in the interpretation, and approved the final version for publication.

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