



Organic matter distribution in the icy environments of Taylor Valley, Antarctica

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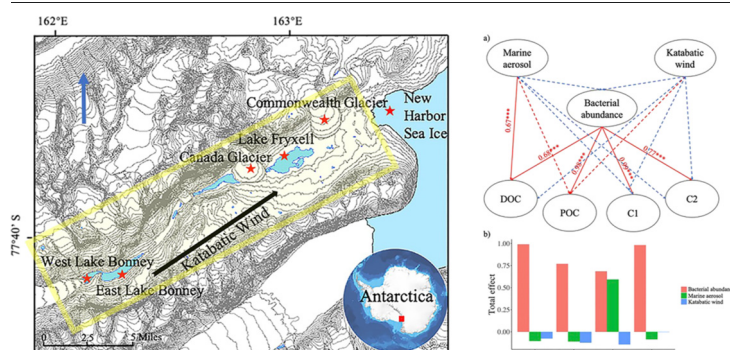
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HIGHLIGHTS

- Both terrestrial and protein-like DOM revealed in Taylor Valley.
- The organic matter showed spatial distribution in Taylor Valley.
- Marine aerosol only influenced the quantity of organic matter.
- Both the quantity and quality of organic matter were modulated by the bacterial abundance.

GRAPHICAL ABSTRACT



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ABSTRACT

Glaciers can accumulate and release organic matter affecting the structure and function of associated terrestrial and aquatic ecosystems. We analyzed 18 ice cores collected from six locations in Taylor Valley (McMurdo Dry Valleys), Antarctica to determine the spatial abundance and quality of organic matter, and the spatial distribution of bacterial density and community structure from the terminus of the Taylor Glacier to the coast (McMurdo Sound). Our results showed that dissolved and particulate organic carbon (DOC and POC) concentrations in the ice core samples increased from the Taylor Glacier to McMurdo Sound, a pattern also shown by bacterial cell density. Fluorescence Excitation Matrices Spectroscopy (EEMs) and multivariate parallel factor (PARAFAC) modeling identified one humic-like (C1) and one protein-like (C2) component in ice cores whose fluorescent intensities all increased from the Polar Plateau to the coast. The fluorescence index showed that the bioavailability of dissolved organic matter (DOM) also decreased from the Polar Plateau to the coast. Partial least squares path modeling analysis revealed that bacterial abundance was the main positive biotic factor influencing both the quantity and quality of organic matter. Marine aerosol influenced the spatial distribution of DOC more than katabatic winds in the ice cores. Certain bacterial taxa showed significant correlations with DOC and POC concentrations. Collectively, our results show the tight connectivity among organic matter spatial distribution, bacterial abundance and meteorology in the McMurdo Dry Valley ecosystem.

1. Introduction

Organic matter is important in the carbon cycle of glacial ecosystems (Antony et al., 2014; Smith et al., 2017). Priscu and Christner (2004) and Priscu et al. (2008) showed that a significant pool of organic matter exists

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in the Greenland and Antarctic ice sheets estimating that the ice sheets alone contained a combined total of approximately 4.4×10^{24} bacterial cells, which equates to 0.95 Pg of bacterial organic carbon. These authors also estimated that together these ice sheets harbor 10.3 Pg of dissolved organic matter (DOM). As global climate change intensifies, the large-scale retreat of glaciers in the Arctic and the Antarctic in concert with the rapid disintegration of ice shelves has accelerated the export of carbon stored in glaciers to downstream aquatic ecosystems affecting their ecological structure and function (Hood et al., 2015; Irvine-Fynn et al., 2021; Smith et al., 2017). Collectively, these studies emphasize the importance of icy environments to local and potentially global carbon transformations.

The character of organic matter in icy environments is not only a consequence of atmospheric processes, but also *in situ* microbial activities (D'Andrilli et al., 2017; Kellerman et al., 2020). Atmospheric deposition can also transport soil, vegetation and anthropogenic organic matter to glacial environments (Fellman et al., 2015; O'Donnell et al., 2016; Stubbins et al., 2012; Santibáñez et al., 2018). Conversely, microorganisms produce labile organic matter from photosynthesis near the surface or chemolithoautotrophic carbon fixation in icy environments feeding heterotrophic microbial communities (Smith et al., 2018; Smith et al., 2017; Zhou et al., 2019). Thus, glacier DOM is a heterogeneous mixture of various organic molecules owing to distinctly diverse sources and it usually consists of low carbon to nitrogen ratio and highly biodegradable substances (e.g., proteins-like compounds) (Antony et al., 2014; D'Andrilli et al., 2017; Feng et al., 2016; Musilova et al., 2017; Spencer et al., 2014). Therefore, organic matter released from glacial and subglacial meltwater can stimulate microbial activity in downstream aquatic ecosystems (Dubnick et al., 2017; Vick-Majors et al., 2020).

Studies have shown that the highly variable DOM in the icy environments of Antarctica is controlled by the allochthonous inputs (Antony et al., 2011; Calace et al., 2001) and microbial activity (Foreman et al., 2007; Priscu et al., 2007; Sanyal et al., 2018). To our knowledge, no studies have focused on the role of katabatic winds and marine aerosols in ice cores in the ice-free McMurdo Dry Valleys (MDV) where seaward katabatic winds originating on the Polar Plateau are a significant climatic feature (Nylen et al., 2004; Streten, 1968; Obryk et al., 2017). The MDV is a microbially dominated ecosystem strongly controlled by climate processes (Fountain et al., 2014; Priscu et al., 1998). Given the profound impacts of climate change in the region (Fountain et al., 2016b; Gooseff et al., 2017), it is particularly important to understand the connectivity between environmental factors, distribution of organic matter and microbial characteristics (Lyons et al., 2007; Šabacká et al., 2012).

We hypothesized that the quality and quantity of organic matter will increase from the Polar Plateau to the coast as the result of wind, aerosols, and microbial activity. To test this hypothesis, we collected ice core samples within Taylor Valley, MDV, Antarctica from glacier and lake ice sites along a spatial gradient from the Taylor Glacier, an outlet glacier draining the Polar Plateau, to the coast. We also collected an ice core sample from sea ice adjacent to the coastal terminus of Taylor Valley. The quantity and quality of dissolved and particulate organic carbon, ions, bacterial abundance and microbial community structure along with a host of physical and chemical parameters were measured within each ice core sample to biogeophysically characterize these individual sites with respect to their geographical location within Taylor Valley.

2. Materials and methods

2.1. Study sites and sample collection

Taylor Valley (Fig. 1), located in the MDV of Southern Victoria Land, Antarctica has been intensively studied since 1993 as part of the MDV Long-Term Ecological Research (LTER) program (Gooseff et al., 2017; Priscu, 2016; Priscu et al., 1999). Taylor Valley extends from Taylor Glacier, an outlet glacier draining the Polar Plateau, to New Harbor, a sea ice dominated environment in McMurdo Sound. Taylor Valley is ~ 34 km long and ~ 12 km wide with an area of ~ 400 km² (Bagshaw et al.,

2013; Fortner et al., 2011) and is one of several valleys that form the 4000 km² MDV region (Fountain et al., 2017; Levy, 2013). The MDV is characterized by a mosaic of gravelly sandy soil, glaciers, ice-covered lakes, and ephemeral melt streams that flow from the glaciers (Priscu, 1998). Permafrost is ubiquitous, with active layers up to 75 cm deep (Bockheim et al., 2007), abundant cyanobacterial mats inhabit the streams, the lakes host microbially dominated communities within the permanent ice covers and underlying water column, and biologically rich cryoconite holes occur on the surface of all glaciers (Priscu, 1998; Priscu et al., 2007). Katabatic winds draining the East Antarctic Ice Sheet significantly impact the climate of Taylor Valley (Nylen et al., 2004; Porazinska et al., 2004; Fountain et al., 2016b). These winds are major transporters of snow, sediment and biological material across the valley which moves allochthonous organic carbon through the region (Porazinska et al., 2004; Šabacká et al., 2012; Lancaster, 2002).

We selected six permanent ice sites in Taylor Valley including lake ice covers (West and East Lake Bonney and Lake Fryxell), and two glaciers (Canada and Commonwealth Glaciers). A seasonal sea ice site was also sampled in New Harbor, several hundred meters from the coastline of the Taylor Valley (see Fig. 1). Lake Bonney abuts the Taylor Glacier and consists of an east (3.5 km²) and west (1.3 km²) basin. Each of the basins is approximately 40 m deep and permanently covered by approximately 4 m of ice (Patriarche et al., 2021; Priscu et al., 1999; Spigel et al., 2018). Lake Fryxell has a permanent ice cover of ~ 5 m thick, a water depth of ~ 20 m and a surface area of about 7 km² (Howard-Williams et al., 1998; Obryk et al., 2016; Santibáñez et al., 2019; Spigel and Priscu, 1998). The Canada and Commonwealth Glaciers are alpine glaciers flanking Taylor Valley on the north with areas of 33.8 km² and 52.2 km², respectively (Fortner et al., 2011; Fountain et al., 2016a). New Harbor is located at the mouth of Taylor Valley in the western part of McMurdo Sound (Hall et al., 2000; Stuiver et al., 1976). The sea ice in New Harbor consisted of multi-year ice (> 3 years) when sampled.

Ice cores were collected from the upper 2 m of West Lake Bonney (WLB) in January 2008 and from New Harbor (3 m, NH), Commonwealth Glacier (1.5 m, CW), and East lobe of Lake Bonney (2 m, ELB) between November and December in 2016. Canada Glacier (3 m, CG) and Lake Fryxell (2 m, FRX) cores were obtained in January 2017. A 10 cm diameter SIPRE or a Kovacs coring device was used to collect the samples near the lake centers. Ice core samples were shipped in the dark at -20 °C to Montana State University (MSU) and stored at -30 °C before final analysis.

Three different core depths were chosen for analysis from each sampling site to represent locations containing clean and sediment-laden ice (Adams et al., 1998; Fritsen et al., 1998; Priscu et al., 1998). The ice core sample depth ranges at each site were: WLB = 1.05–1.20 m, 1.60–1.75 m and 1.80–2.0 m; ELB = 0.70–0.80 m; 1.40–1.80 m and 2.20–2.25 m; FRX = 0.22–0.27 m, 0.47–0.55 m and 1.60–2.1 m; CW = 0.04–0.08 m, 0.18–0.22 m; 0.60–0.70 m; CG = 0.14–0.19 m; 0.28–0.33 m and 0.52–0.57 m; NH = 2.20–2.25 m, and 2.80–2.85 m and 3.00–3.05 m. Because most of our core samples were within the upper part of the lake and sea ice locations, they are free from accretion of organic matter at the ice water interface. Ice cores were handled in a clean cold room (class 1000, ISO 4/5) including a clean bench (class 100) at -10 °C in the Sub-zero Research Facility at MSU. All surfaces which contacted the ice samples were pre-cleaned with ultrapure Milli-Q water and UV irradiated overnight before transferring the cores to the clean cold room. Surface decontamination of the ice samples was performed following the protocol described in Christner et al. (2005). Briefly, the exterior portion (~ 1 cm) of the ice core (contaminated exterior of the sample) was physically removed using a band saw, and all surfaces of the inner core were rinsed with 0.2 µm filtered Milli-Q water to further remove any contaminants from the cutting procedure. Cleaned inner ice samples were then melted in pre-cleaned glass beakers in a laminar flow hood at room temperature. All glassware was soaked in 1 M hydrochloric acid for 48 h, rinsed three times with Milli-Q water and combusted at 450 °C for 5 h before use. The bench surfaces of the laminar flow hood were sterilized with 3 % H₂O₂ and ultraviolet irradiation for at least 2 h before the experiment.

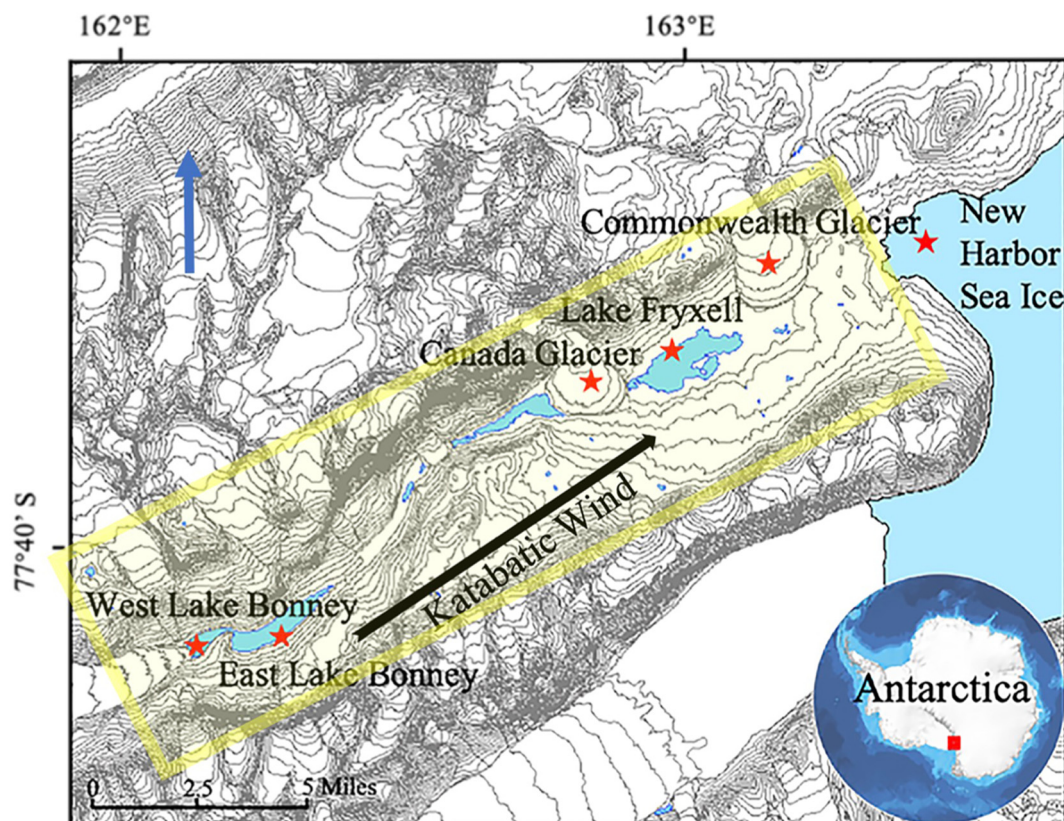


Fig. 1. Map showing the locations (red stars) of our ice core samples within Taylor Valley, Antarctica (the yellow highlighted area). The black arrow shows the down valley direction of the katabatic wind. Blue arrow indicates north.

2.2. Total dissolved carbon and particulate organic carbon analysis

Forty mL of ice melt from the core samples were filtered through a pre-combusted GF/F filter (Whatman, UK) into glass amber vials that had been acid-leached (1 M HCl for 24 h), Milli-Q water rinsed, and pre-combusted (450 °C for 5 h). The filtrate was analyzed immediately for dissolved organic carbon (DOC) concentration using a Shimadzu TOC-L analyzer equipped with a high sensitivity platinum catalyst and represent non-acid purgeable dissolved carbon. Milli-Q water was measured as an instrumental blank.

Samples (150–200 mL) for particulate organic carbon (POC) and nitrogen (PON) determination were filtered onto pre-combusted (450 °C for 5 h) 25 mm GF/F filters under low vacuum (< 0.3 atm). After drying at 70 °C, the samples were acidified in a HCl (12 N) chamber for 48 h to remove inorganic carbon. The acidified filters were analyzed with a CE Instruments Flash EA 1112 elemental analyzer using acetanilide as the standard.

2.3. Dissolved organic matter quality

Three-dimensional fluorescence excitation–emission matrices (EEMs) of DOM were obtained with an Aqualog fluorescence spectrofluorometer (Horiba, Japan) using excitation wavelengths (Ex) ranging from 240 to 450 nm at 5 nm increments and emission wavelength (Em) every 5 nm from 250 to 600 nm. The Aqualog system automatically corrects Rayleigh-Tyndall and Raman scatter. Fluorescence intensities of all spectra were normalized by the area of the Raman peak and expressed in Raman units (R.U.) (Murphy et al., 2010). Because EEMs specifically represent chromophoric DOM, a PARAFAC analysis was conducted to decompose the EEMs data into individual fluorescent chemical components of organic matter with MATLAB R2020b (Mathwork, Natick, MA) using the DOMFluor toolbox (www.models.life.ku.dk) (Barker et al., 2013). Samples with abnormal fluorescence signals were removed from the data as outlier

samples using outlier tests and leverage values. Using published protocols (Murphy et al., 2013), PARAFAC modeled 2 DOM components, which were verified using a split-half analysis combining with an examination of the model's residuals.

Three indexes were further derived from the EEMs fluorescence data including fluorescence index (FIX), humification index (HIX) and biological Indices (BIX) (Huguet et al., 2009; McKnight et al., 2001; Zsolnay et al., 1999; Zabłocka et al., 2020).

FIX was calculated as the ratio of fluorescence at emission 450 nm and 500 nm, at fixed excitation of 370 nm:

$$\text{FIX} = \frac{F_{370,450}}{F_{370,500}} \quad (1)$$

BIX was calculated by dividing the fluorescence intensity emitted at emission 380 nm and 430 nm, at fixed excitation of 310 nm:

$$\text{BIX} = \frac{F_{310,380}}{F_{310,430}} \quad (2)$$

HIX was calculated as the ratio of the sum of the fluorescence emission between 435 and 480 nm and between 300 and 345 nm, at fixed excitation of 254 nm:

$$\text{HIX} = \frac{\sum_{\text{em}435}^{\text{em}480} F_{254}}{\sum_{\text{em}300}^{\text{em}345} F_{254}} \quad (3)$$

2.4. Major ion concentration

Ions were determined using a Metrohm ionic chromatography (Riverview, FL) using Metrosep columns (Metrohm). For cations (Na^+ ,

K⁺, Mg²⁺, Ca²⁺), the system was equipped with a Metrosep A C4 column with a 13 μL sample injection volume. For anions (Cl⁻, SO₄²⁻), the system was equipped with a 25 mm Metrosep A Supp 5 column with 20 μL sample injection volumes. Corresponding anion and cation concentration detection limits for samples were 6, 8, 13, 47, 2, and 0.4 $\mu\text{g L}^{-1}$ for Cl⁻, SO₄²⁻, Na⁺, K⁺, Mg²⁺, and Ca²⁺, respectively.

2.5. Cell enumeration

Cell abundance of the samples was determined following the procedure described by Lisle and Priscu (2004). Briefly, ~ 40 mL samples were fixed in 1 % formalin and stained with SYBR Gold (1 $\times$ final concentration) for 10 min in the dark. The stained sample was then gently filtered through a 0.2 μm pore size black polycarbonate filter (Whatman, UK) with a syringe. Filters were mounted on glass microscope slides with ProLong® Diamond Antifade (ThermoFisher Scientific, MA). Cells were enumerated using a Nikon Eclipse 80i microscope equipped with a QIMAGING Retiga 2000R camera (QIMAGING, Canada) at an excitation wavelength of 450–490 nm and emission wavelength of 515–550 nm. For each sample, images of at least 15 random views were recorded with a 100 $\times$ objective lens and the cell concentrations were calculated using ImageJ software (V1.47, National Institutes of Health, US).

2.6. DNA extraction, PCR amplification, and 16S rRNA gene sequencing

DNA of ice melt samples was extracted using a FastDNA™ Spin kit (MP Biomedicals, CA) following the manufacturer's instructions. The region V4 of the 16S rRNA gene was amplified using the primer set 515F (5'-GTGCCA GCMGCCGCGGTAA-3') and 806R (5'-GGACTACHVGGGTWTCTAAT-3'), including the barcodes and linkers. More details on PCR and MiSeq sequencing reactions can be obtained in protocols provided by the Earth Microbiome Project (Caporaso et al., 2012). Sample sequencing was performed on an Illumina MiSeq platform using a 300-cycle MiSeq Reagent Kit v2 (Illumina, CA, United States) with a 2 $\times$ 150 bp paired-end run in the presence of 25 % PhiX sequencing control DNA. Raw data generated on the MiSeq were demultiplexed with the Quantitative Insights Into Microbial Ecology (QIIME) pipeline (v1.8.0) (Caporaso et al., 2010). Briefly, reads were truncated at any site containing more than three consecutive bases with quality score below 20, and any read containing one or more ambiguous base calls was deleted. The truncated reads <75 % (of the raw read length) consecutive high-quality base calls were discarded. Then, the sequences were clustered into operational taxonomic units (OTUs) at 97 % pairwise identity with the UCLUST algorithm (Edgar, 2013). Bacterial alpha diversity diversities including Chao1-richness, Simpson and Shannon index were quantified using the QIIME script (Kuczynski et al., 2012). Bacterial sequences from each OTU were aligned using PyNAST (Caporaso et al., 2010). After taxonomies had been assigned, the taxonomic identity of each representative sequence was clustered with a similarity cutoff of 97 % pairwise identity against the SILVA (version 132 NR) database (Pruesse et al., 2007). OTUs that were affiliated with chloroplast and archaeal were removed because of the bias of universal 16S primers (Baker et al., 2003).

2.7. Wind data

Wind data was retrieved from twelve year-round meteorological stations in Taylor Valley (Doran and Fountain, 2021; Doran et al., 1995). Wind frequency and speed were monitored 3 m above ground level every 30 s (4 s for wind speed) which were averaged and recorded by a Campbell Scientific solid-state data logger every 15 min (Nylen et al., 2004).

2.8. Statistical analyses

Unless otherwise indicated, all statistical analyses were made with Rstudio v1.2.1335 (<http://cran.r-project.org/>) (Wickham, 2016). The correlation and stepwise regression analysis was conducted by IBM SPSS

Statistics version 24 for Windows (IBM Corporation) which revealed the distribution of organic carbon, bacterial abundance, ion concentrations and the correlations between bacteria taxa and organic carbon. In the PAST software (version 3.24, Oslo, Norway), non-metric multidimensional scale (NMDS) was used to assess the relationship between microbial communities. Partial least squares path modeling (PLS-PM) was used to further reveal the possible pathways of the environmental predictor variables on the DOC, POC and DOM composition along the spatial gradients by using the “plsmp” package in Rstudio. The observed variables in our PLS-PM modeling contained marine aerosol, katabatic wind speed and frequency and bacterial abundance. Ion data were used to represent the effects of marine aerosols. Path coefficients estimate the strength of the linear relationships between variables.

3. Results

3.1. Organic matter distribution

DOC concentrations across all 18 ice core samples ranged from 114.7 to 1479 $\mu\text{g L}^{-1}$, with a grand average ($\pm$ SD) concentration of 425.7 $\pm$ 450.6 $\mu\text{g L}^{-1}$ (Table S1). Mean DOC levels were lowest in the Lake Bonney ice covers and increased towards the coast (New Harbor). A one-way analysis of variance (ANOVA) revealed a statistically significant difference among sites ($p = 0.027$). Tukey's multi-comparison test further revealed that a statistically significant difference between pairs occurred only between New Harbor and the ice covers from ELB and WLB ($p < 0.05$). High variances from the mean in certain samples caused by the heterogeneous distribution of sediments in many of the sites, in concert with a low sample size ($n = 3$), greatly increased within sample variance leading to insignificant differences between means of many pair-wise comparisons.

POC concentrations varied widely among samples (range = 0.5–21,732.9 $\mu\text{g L}^{-1}$) with a grand average of 1480.6 $\mu\text{g L}^{-1}$ (Table S1). The higher POC concentrations were observed in sediment-rich samples from CG, FRX CW and NH. A one-way ANOVA revealed no significant differences ($p = 0.47$) among POC levels within the locations sampled. High variability within samples influenced this outcome. Despite the high within sample variations, DOC and POC concentrations all exhibited spatial patterns (spearman correlation, $r = 0.47$, $p = 0.002$ and $r = 0.49$, $p = 0.038$, respectively) with increasing values occurring in closer proximity to the coast (Fig. 2a, b).

3.2. DOM quality

PARAFAC analysis of the EEMs data from the 18 ice core samples revealed that fluorophores explained 29.3 % of the variation within the dataset. Two components were identified with unique spectral series (Fig. 3). Component 1 (C1) had a primary fluorescence excitation peak at 240 nm with 444 nm emission wavelengths, which was similar to peak A and related to terrestrial humic-like substances (Coble, 1996; Coble et al., 1998; Murphy et al., 2008) (Table 1). Component 2 (C2) had a fluorescence excitation peak at 240 nm and emission maxima at 320 nm, which has been identified as a protein-like fluorophore (Coble, 1996; Coble et al., 1998). Fluorescence intensity (F_{max}) was used to correspond to the concentrations of each component (Li et al., 2015). The F_{max} of C1 component ranged from 0.004 to 0.198 whereas C2 scores ranged from 0.013 to 0.143. The F_{max} of C2 was higher than C1 in the ice core samples. The F_{max} of C1 and C2 components all increased from the Polar Plateau to the coast (Fig. 4). In addition, repeated-measured ANOVA indicated that the F_{max} of C1 showed a significant difference between Lake Bonney and the New Harbor ($p < 0.05$), while the F_{max} of C2 was significantly different between west Lake Bonney and the Canada Glacier ($p < 0.05$, Fig. 4). The scores of C1 and C2 ranged from 0.06 to 2.93 and 0.10 to 1.14, respectively. Their spatial distributions were consistent with the results of the values of F_{max} (Fig. S1).

The indexes FIX, BIX and HIX can reveal the characteristics and sources of DOM in the natural aquatic environments (McKnight et al., 2001; Birdwell and Engel, 2010; Huguet et al., 2009) (Fig. S2). The FIX index in

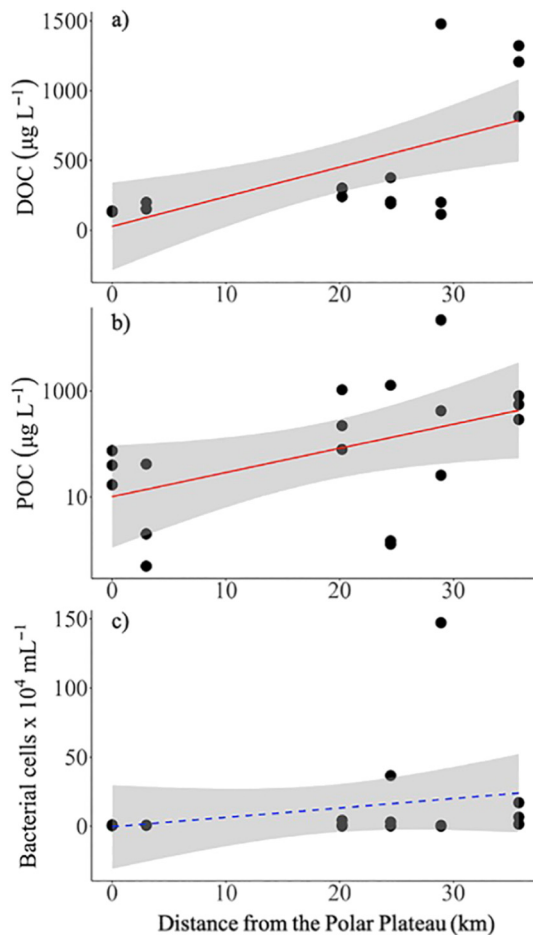


Fig. 2. Linear regression of normalized a) DOC concentration, b) POC concentration and c) bacterial cell abundance with distance from the coast along 6 sampling sites. Red line indicated statistically significant relationships ($p < 0.05$). The grey shaded area is the 95% confidence interval for the regression line.

all ice core samples ranged from 1.05 to 2.41 (average 1.62 ± 0.37) and decreased towards the coast (Fig. S2). HIX index values ranged from 0.12 to 0.69 and, although variable within each site, showed an increasing trend to the coastal site (Fig. S2). BIX was higher in the ELB and CG than in other sampling sites. BIX values were higher in the Lake Bonney (WLB and ELB) and Canada Glacier (CG) ice cores (range = 1.39 to 2.21, 0.98 to 5.44, and 1.26 to 3.45 for WLB, ELB and CG, respectively) relative to the FRX, CW and NH cores (range = 0.89 to 1.67, 1.32 to 1.71 and 1.07 to 1.42, respectively).

3.3. Bacterial cell abundance

The bacterial abundances in WLB (0.3×10^4 to 0.9×10^4 cells mL^{-1} , average (SD) $0.6 \pm 0.3 \times 10^4$ cells mL^{-1}) were similar to ELB (0.6×10^4 to 0.7×10^4 cells mL^{-1} , average (SD) $0.6 \pm 0.07 \times 10^4$ cells mL^{-1}) (Table S1). Cores from the Lake Bonney ice cover had the lowest bacterial abundances among our samples. The bacterial abundances in CG (4.2×10^4 cells mL^{-1} , average (SD) $1.7 \pm 2.2 \times 10^4$ cells mL^{-1}) were higher than CW (0.03×10^4 to 0.6×10^4 cells mL^{-1} , average (SD) $0.3 \pm 0.4 \times 10^4$ cells mL^{-1}) except for samples from CW with elevated sediment (147.2×10^4 cells mL^{-1}). The average bacteria abundance in FRX ($13.3 \pm 20.2 \times 10^4$ cells mL^{-1}) was greater than in other sampling sites. The range of bacteria abundance in the NH sea ice cores ranged from 1.4×10^4 to 17.1×10^4 cells mL^{-1} (average, SD = $8.4 \pm 8.0 \times 10^4$ cells mL^{-1}) (Table S1). Although Spearman correlation analysis showed that the spatial distribution of bacterial abundance across the landscape was not statistically significant,

there was a general increasing trend of cell abundances closest to the coast (Fig. 2c).

3.4. Major ion concentration

The chloride (Cl^-) and sulfate (SO_4^{2-}) concentrations in the ice core samples ranged from below detection to $2770.89 \text{ mg L}^{-1}$ and 0.04 to 380.58 mg L^{-1} , respectively (Table S1). Concentrations of major cations were in the ranges of 0.02 – $1209.34 \text{ mg L}^{-1}$ for sodium (Na^+), 0 – 45.15 mg L^{-1} for potassium (K^+), 0.16 – 18.44 mg L^{-1} for calcium (Ca^{2+}) and 0.008 – 128.40 mg L^{-1} for magnesium (Mg^{2+}), respectively (Table S1). ANOVA analysis revealed that all ions showed significant differences ($p < 0.05$) except Ca^{2+} . In addition, a statistically significant difference occurred only between New Harbor and other sites ($p < 0.05$) according to Tukey's multi-comparison test. Results from these analyses infer that the parameters have high variation in terms of their spatial distribution in the study area. Aeolian dust transport plays an important role in the deposition of Ca^{2+} in the Taylor Valley (Witherow et al., 2006). Weathering of Ca-rich aluminosilicates and windblown CaCO_3 also contribute to the concentrations of Ca^{2+} in the ice core samples of the Taylor Valley (Nezat et al., 2001; Gooseff et al., 2003; Fortner et al., 2005). The significantly higher ion concentrations in NH are likely due to its marine location; up valley winds are required to transport this marine derived matter into the Taylor Valley. Spearman correlation showed the ions were all significantly positively correlated with each other (Table S2) and significantly decreased with increasing distance from the Polar Plateau (Pearson correlation, $r = 0.65$, $p = 0.004$; Na^+ , $r = 0.469$, $p = 0.05$; Cl^- , $r = 0.55$, $p = 0.02$; SO_4^{2-} , $r = 0.698$, $p = 0.01$; K^+ , $r = 0.732$, $p = 0.01$; Mg^{2+} , $r = 0.54$, $p = 0.02$, Ca^{2+}) (Fig. S3). Ca^{2+} and SO_4^{2-} to Cl^- ratios were calculated to differentiate marine and terrestrial effects (Bergh and Compton, 2015). Due to high Cl^- contents of seawater, relative changes in ratios of $\text{Ca}^{2+}/\text{Cl}^-$ or $\text{SO}_4^{2-}/\text{Cl}^-$ indicate ion sources from marine or terrestrial environments in the ice core. Although $\text{Ca}^{2+}/\text{Cl}^-$ and $\text{SO}_4^{2-}/\text{Cl}^-$ both showed a decreasing trend from the Polar Plateau to the coast, only the values of $\text{Ca}^{2+}/\text{Cl}^-$ were negatively correlated with the distance from the Polar Plateau significantly (Pearson correlation, $r = -0.66$, $p = 0.004$) (Fig. S4).

3.5. Bacterial community composition

A total of 5700 OTUs were obtained in the ice core samples and classified into 62 phyla. According to the result of PERMANOVA analysis, there were no significant differences in bacterial communities among the six site locations. The Shannon Index, which measures the diversity within individual samples (Bryant et al., 2016), was between 0.95 and 5.85 (mean 4.20 ± 1.37) among all ice core samples. Bacterial alpha diversity from the terminus of the Taylor Glacier to the coast exhibited significant differences between sampling sites (Kruskal-Wallis test, $p < 0.05$), with the highest mean values in FRX and the lowest mean values in NH (Fig. S5). The result of NMDS indicated that there was no significant similarity between bacteria communities among different samples (Fig. S6).

There were eleven major phyla (average relative abundance $> 1\%$). The top four phyla were (average $\pm$ SD): Proteobacteria ($42.31\% \pm 21.02\%$), Bacteroidetes ($16.83\% \pm 11.03\%$), Cyanobacteria ($10.62\% \pm 16.42\%$), and Firmicutes ($5.95\% \pm 15.14\%$) (Fig. S7a). The top three major classes across all samples were average $\pm$ SD): Gammaproteobacteria ($17.35\% \pm 24.46\%$), Betaproteobacteria ($11.81\% \pm 8.64\%$) and Deltaproteobacteria ($7.63\% \pm 7.76\%$) (Fig. S7b). The proportions of these taxa in the ice core samples varied among the six sites. For example, Proteobacteria showed a significantly increasing trend from the Polar Plateau to the coast (spearman correlation, $r = 0.52$, $p = 0.026$, Fig. S8a), comprising 26.42%–73.33% of the bacterial reads in all samples. The second and third most abundant group was Bacteroidetes and Cyanobacteria, which showed the same distributional pattern to Proteobacteria. However, Firmicutes showed the opposite spatial pattern to the other three major taxa, the proportion of Firmicutes decreased significantly from the Polar Plateau to the coast

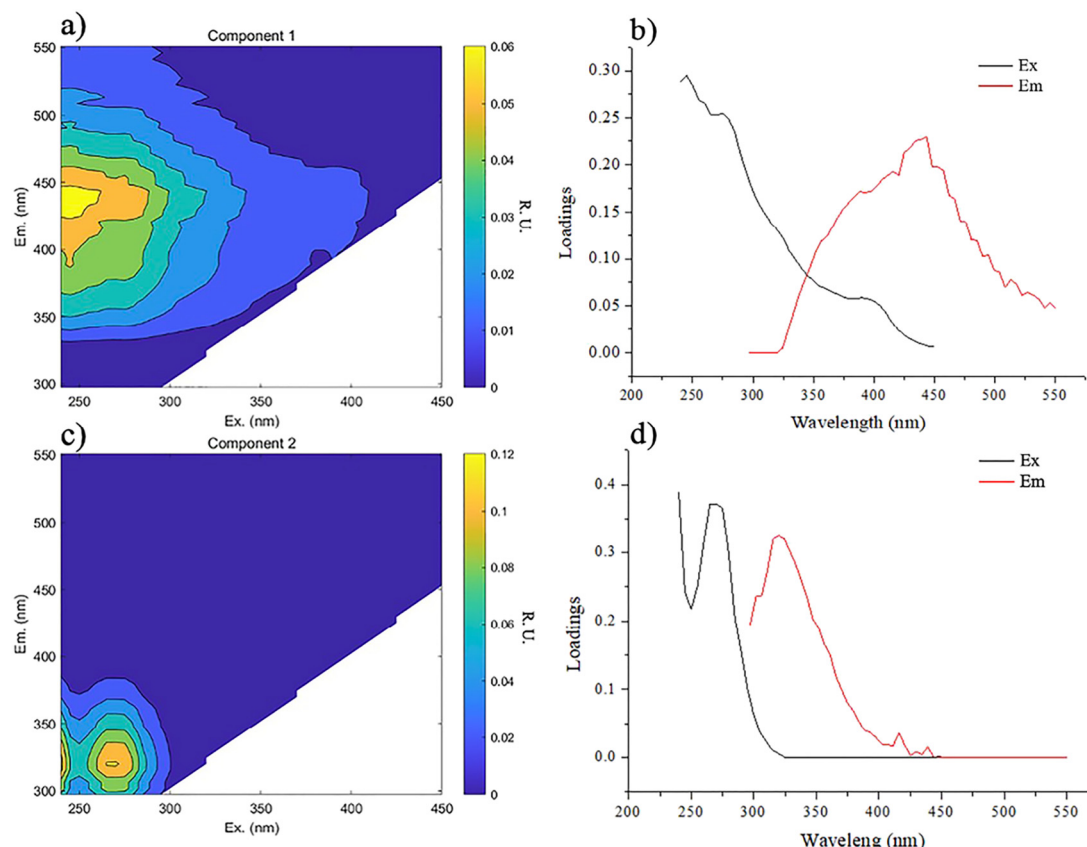


Fig. 3. EEM contours and Ex/Em loadings of C1 (a, b) and C2 (c, d) fluorescent components derived by the PARAFAC model. R.U. = Raman Units. See text for details.

(spearman correlation, $r = -0.54$, $p = 0.026$, Fig. S8b). The spatial distribution of Chloroflexi and Verrucomicrobia was similar to Firmicutes. The relative abundances of other major taxa did not have clear spatial patterns in the six sites. On class level, the relative abundances of Gammaproteobacteria in the phyla Proteobacteria increased significantly from WL to NH (spearman correlation, $r = 0.66$, $p = 0.003$), while Bacilli in the phyla Firmicutes showed the opposite distribution trend (spearman correlation, $r = -0.49$, $p = 0.035$) (Fig. S8c and d).

3.6. Correlation between environmental factors, bacterial community and organic matter

We used PLS-PM modeling to determine and present the complex networks including the direct and indirect impacts between environmental variables and organic matter (Fang et al., 2021; Zhao et al., 2018) (Fig. 5). The model exhibited a reasonable fit based on our hypothesis (GOF = 0.81) and explained 92.29 % of the variance of DOC, 96.32 % of the variance of POC, and 98.26 % and 59.98 % of the variances in the C1 and C2 fluorescence components, respectively. The total effects are the sum of both the direct and indirect effects. Marine aerosol showed a positive direct influence on the DOC content which the total effects were

0.81. Bacterial abundance was significantly positively correlated with DOC concentration (total effects were 0.68), POC concentration (total effects were 0.98), C1 component (total effects were 0.99) and C2 component (total effects were 0.77). Katabatic winds showed no significant correlations with organic matter.

Stepwise regression analysis was performed to assess the quantity and quality of organic carbon with major taxa on phylum, class and order levels. At the phylum level, only the relative abundance of Cyanobacteria was significantly positively correlated with POC concentrations ($r^2 = 0.81$, $p < 0.001$) and Chlorobi negatively correlated with DOC concentration ($r^2 = 0.28$, $p = 0.029$). The relative abundances of Gammaproteobacteria showed a significant positive relationship with DOC concentration ($r^2 = 0.28$, $p = 0.017$), while Betaproteobacteria was negatively correlated with DOC concentration ($r^2 = 0.26$, $p = 0.021$) at the class level. The relative abundances of Synechococcophycideae and Oscillatoriohyphycideae showed significant positive correlations with POC concentrations ($r^2 = 0.32$, $p = 0.011$ and $r^2 = 0.82$, $p < 0.001$, respectively). At the order level, Alteromonadales were positively correlated with DOC concentrations ($r^2 = 0.27$, $p = 0.02$) and Rhizobiales were negatively correlated with DOC concentrations ($r^2 = 0.21$, $p = 0.04$). Oscillatoriales, Synechococcales, and Chroococcales had positive relationships with POC concentrations ($r^2 =$

Table 1

Spectral characteristics of excitation and emission maxima of two fluorescent components identified by PARAFAC modeling compared with previously identified sources. Ex_{max}: peak excitation wavelength; Em_{max}: peak emission wavelength.

Component	Ex _{max} (nm)	Em _{max} (nm)	Tradition peak according to Coble (1996)	Description and probable origin
C1	240	444	Peak A: 230–260/380–460	Terrestrial humic materials ^a
C2	240	320	Peak T: 225–230 (275)/340–350	Protein-like fluorophore (tyrosine and tryptophan compounds) ^b

^a Murphy et al. (2008).

^b Abdelradly et al. (2018).

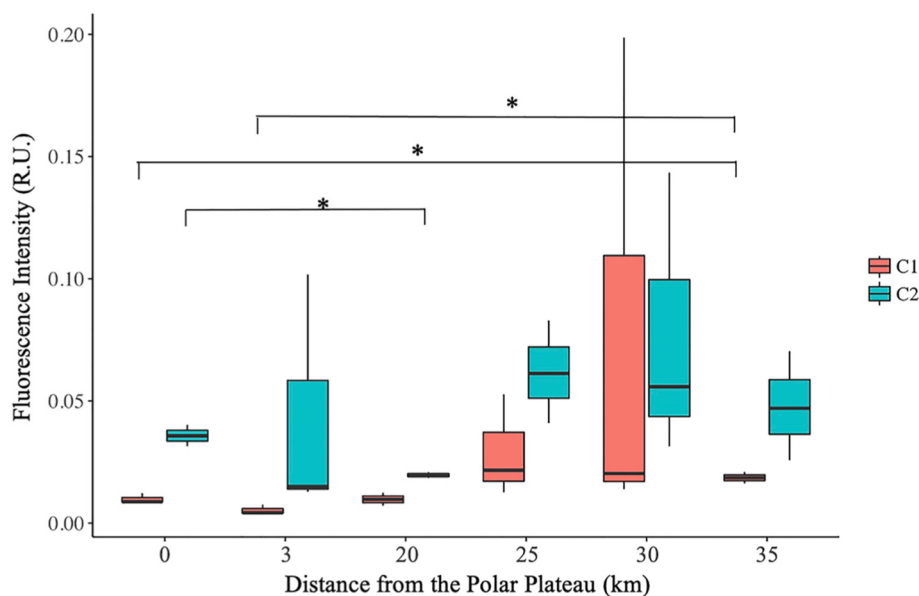


Fig. 4. Boxplot diagram of the fluorescence intensity of the fluorescence components C1 and C2 in ice cores collected from the Polar Plateau to the coast. ANOVA revealed the significant differences of DOM components among six sampling sites. Only the relationships with significant differences are shown within the horizontal brackets: * $p < 0.05$. The lower and upper vertical lines of box plots show the first and third quartiles; central horizontal lines indicate median values.

0.90, $p < 0.001$; $r^2 = 0.69$, $p < 0.001$; $r^2 = 0.57$, $p < 0.001$, respectively) (Fig. 6).

4. Discussion

4.1. Characteristics of organic matter in Taylor Valley

The concentrations of organic carbon increased from the Polar Plateau to the coast (Fig. 2). Two DOM components best described the variance in the EEM data set including one humic-like component (C1) and one protein-like component (C2). C1 has been commonly observed in many freshwater environments and regarded as terrestrial origin composition (Hiriart-Baer, 2013; Singh et al., 2017). C1 likely represents degraded and/or “aged” organic matter such as terrestrial-derived humic-like organic matter and is more refractory than protein-like components (Burdige et al., 2004; Hedges, 1988; Komada et al., 2002; Stedmon et al., 2003). The significant differences of C1 components between the Polar Plateau and the coast infers that the bioavailability of DOM decreased from the Polar Plateau to the coast. This result is also consistent with the distribution of fluorescence indices. The FIX value provides insight into the DOM source (DeVilbiss et al., 2016; McKnight et al., 2001). A FIX value of 1.2 or less corresponds to a terrestrial origin humic-like DOM, while a value of 1.8 or higher indicated a microbe-derived protein-like material (McKnight et al., 2001). HIX values compare the humification levels of different DOM samples and the humification degree of DOM can be used as an indicator of DOM recalcitrance in a natural system (Birdwell and Engel, 2010; Ohno, 2002; Zsolnay et al., 1999). High values of BIX (>0.8) correspond to a freshly produced liability DOM of biological or microbial origin (Birdwell and Engel, 2010; Huguet et al., 2009). Based on this information, the decreased FIX and BIX with the increased HIX in our study showed the DOM was more labile near the Polar Plateau. Overall, the concentration of organic matter and the bio-liability of the organic matter in Taylor Valley were inversely related with distance from the Polar Plateau to the coast.

The autochthonous fluorescence signature of DOM was important in the ice cores of Taylor Valley. The protein-like C2 component showed higher $F_{\max}$ in the fluorescence spectra of DOM than humic-like C1 component in most ice core samples. Protein-like compounds represent fresh and easily biodegradable organic matter that is generally associated with autochthonous organic matter (Fellman et al., 2009; Wang et al., 2018). A viable

microbial assemblage dominated by cyanobacterial biomass in Taylor Valley contributes significantly to the primary productivity (Barrett et al., 2006; Fritsen and Priscu, 1998; Michaud et al., 2012; Priscu et al., 1998, 2005). The C2 component can therefore indicate active microbial communities in the ice cores of the Taylor Valley. The average FIX in our ice core samples indicated that microbially-derived DOC contributed significantly to the DOC in Taylor Valley. The low range of HIX (0.13–2.01) in our samples represents fresher and more labile DOC derived from biological activities (Birdwell and Engel, 2010). The BIX values in ice core samples were all higher than 0.8, suggesting elevated levels of autochthonous contribution of the DOC (Huguet et al., 2009). However, bacteria are likely not the only contributor to DOC in the ice environment across Taylor Valley.

4.2. Directly effects of environmental factors on the spatial distribution of organic matter

The significant spatial distribution of DOC and POC concentration in Taylor Valley may be influenced by marine aerosol. Previous studies have indicated the importance of marine aerosols in the transport of organic carbon to the terrestrial environment (Antony et al., 2011; Calace et al., 2005). The concentrations of DOC in ice cores of Taylor Valley were within the range of Antarctica surface snow samples (88 to 928 $\mu\text{g L}^{-1}$) and Antarctica sea ice (781 to 10,990 $\mu\text{g L}^{-1}$) (Antony et al., 2011; Ma et al., 2013) which may indicate the same sources. The dominant ions in our ice core samples were SO_4^{2-} , Cl^- and Na^+ . SO_4^{2-} from acidic sulphate and sulphate in sea-salt aerosol are significant in other Antarctic ices (Mulvaney and Wolff, 1994). According to Witherow et al. (2006), the dominant contributor of Cl^- in the snow of the McMurdo Dry Valleys is the adjacent McMurdo Sound and associated Ross Sea. Na^+ in MDV ice has also been shown to reflect marine influence (Williamson et al., 2007; Lyons et al., 2003). In addition, concentrations of all ions significantly correlated with each other and showed significantly increasing trends to the coast further corroborating their marine source. The decreasing $\text{Ca}^{2+}/\text{Cl}^-$ and $\text{SO}_4^{2-}/\text{Cl}^-$ ratios from the Polar Plateau to the coast specifically showed the increasing marine effects from the Polar Plateau to the coast. The standardized total effects from PLS-PM modeling indicates that marine aerosols have a significant positive on the DOC concentration and bacterial abundance (Fig. 5). The effects of marine aerosols decreased from the coast to

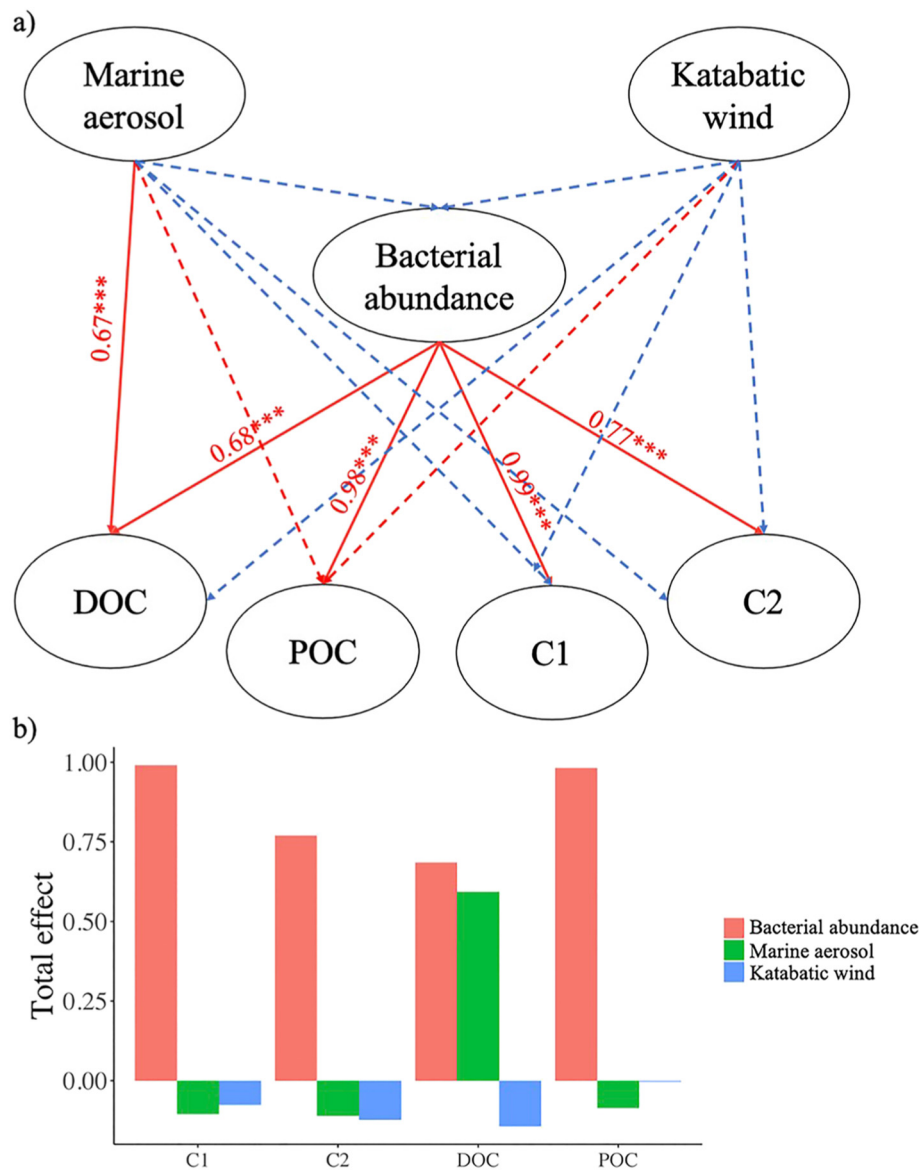


Fig. 5. a) Results of the PLS-PM models for the organic matter in ice samples from Taylor Valley. Solid arrows indicate notable effect sizes ($p < 0.05$, dashed lines $p > 0.05$), where the colour of the arrow represents the relationship (blue indicates negative and red indicates positive relationships). b) The total effects of marine aerosol (green), katabatic wind (blue) and bacterial abundance (red) on the organic matter.

the Polar Plateau, which presumably led to the down valley decreasing trend of DOC concentrations.

Katabatic wind was not a significant factor influencing the distribution of organic matter in our ice core samples. The correlations between katabatic wind and organic matter were all opposite that of marine aerosol and not statistically significant. Although the down valley katabatic wind is one of the principal environmental factors for transporting sediment in Taylor Valley (Moorhead et al., 1999; Porazinska et al., 2004; Šabacká et al., 2012), it can hinder the up-valley deposition of organic matter brought by marine aerosol.

Other possible sources of organic matter to the surface of the lake and marine icy environments we sampled may be related to potential concentrating factors related to ice dynamics (ablation at the surface and accretion of new ice at the bottom), and emissions from fossil burning by research teams. Our own research has shown that organic matter in Taylor Valley lake ice is primarily associated with aeolian sources and little or no organic matter accumulates due to accretion of new ice at the ice lake water interface (e.g., Priscu et al., 1998; Šabacká et al., 2012; Priscu et al., 1998;

Santibáñez et al., 2019). Lyons et al. (2018) and Diaz et al. (2018) identified the potential for anthropogenic input of organic carbon throughout the dry valley ecosystem (soils, glaciers, lakes). However, their estimates of fossil fuel emissions of particulate organic carbon from is $\sim 1 \text{ kg y}^{-1}$, which would likely be diluted and transported from the ecosystem by the high and persistent winds that exist in the Taylor Valley. Lyons et al. (2018) conclude that, although POC fluxes remain very low, the recent finding of black carbon in the Taylor Valley landscape indicates more on-going monitoring of the source of this material is merited.

4.3. Roles of the bacterial community in the spatial distribution of organic carbon in Taylor Valley

Except for marine aerosol, biotic factors like bacteria also regulate the quantity and quality of organic matter. Bacteria represent a substantial reservoir of organic matter in Antarctica (Priscu and Christner, 2004; Priscu et al., 2008). Previous studies showed bacterial abundance was significantly correlated with the accumulation of semi-labile DOC in Antarctic

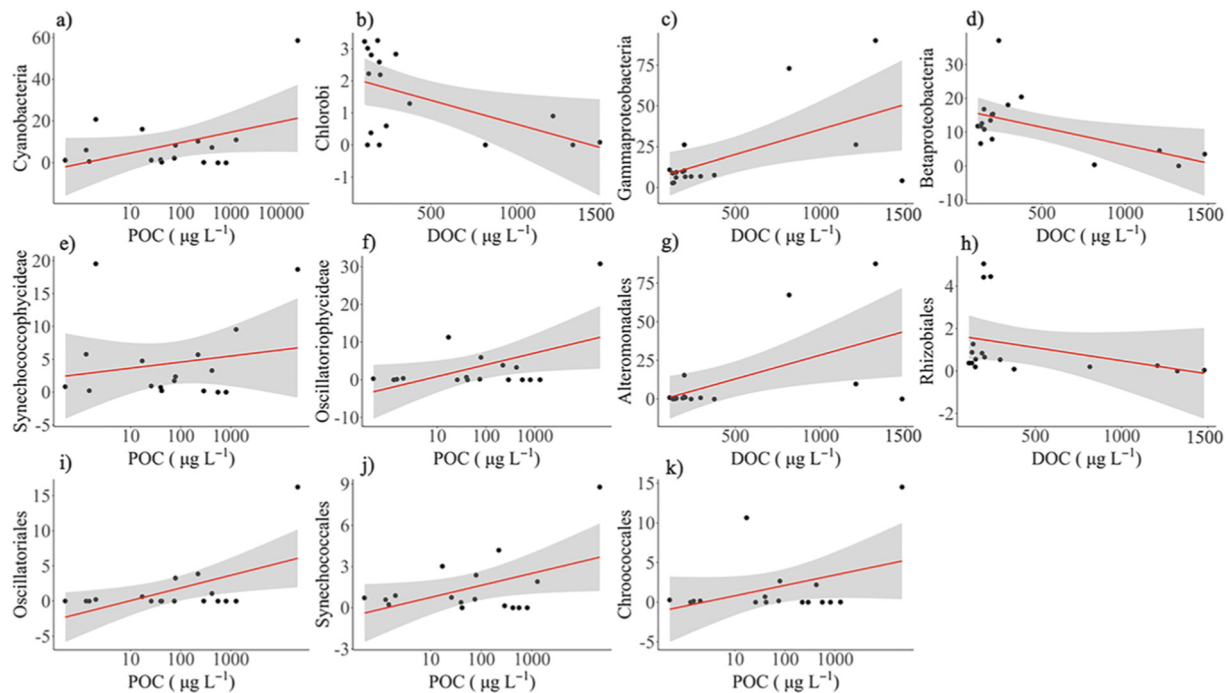


Fig. 6. Linear correlations (red line) between selected environmental variables and relative abundance of dominant bacterial groups on the (a-b) phylum level, (c-f) class level and (g-k) order level. Only the statistically significant relationships ($p < 0.05$) are shown. The grey shaded area denotes standard deviation 95 % confidence interval.

aquatic environments (Ducklow, 2003; Priscu et al., 2005) and specifically within the lake ice cover of Lake Bonney (Priscu et al., 1998; Fritsen and Priscu, 1998). Our data reveal similar positive correlations between bacteria abundance and DOC concentration in the icy environments we sampled. The high correlation between bacterial abundance and DOC concentration suggests that heterotrophic bacteria (including cyanobacteria, Paerl and Priscu (1998) strongly influenced DOC in our samples, particular in lake ice (see also Priscu et al., 1998; Priscu et al., 2005). Based on these publications, microbial activity should have a key role in the spatial distribution of organic carbon in Taylor Valley. The C2 composition, regarded as labile DOM produced by microbial activities, showed significant positive correlations with bacteria abundance. A previous study found that microbial transformations of DOM can lead to the production of the C1 component (Amaral et al., 2016). Since the fresh DOM could be rapidly transformed, the C2 component could be used immediately by heterotrophic production after they are released in Antarctic glacial environments (Smith et al., 2017). Thus, with the increasing bacteria abundance, the relative concentration of the C1 component increased accordingly. The total effect of bacterial abundance on C1 was higher than C2, revealing a stronger effect on the C1 component. The decreased bioavailability of DOM from the Polar Plateau to the coast could result from the stronger effect of bacterial abundance on the C1 component. Therefore, bacterial abundance and associated activity are affected both the quantity and quality of organic matter in our Taylor Valley ice core sampling sites.

Bacteria community structure was strongly correlated with both DOC and POC concentration. The major cyanobacterial orders in the ice cores consisted of Oscillatoriales and Synechococcales, results consistent with previous studies in the MDV regions (Paerl and Priscu, 1998; Priscu et al., 2005; Priscu et al., 1998). The positive correlations between cyanobacterial abundance and POC concentration underlines the potential contribution of the organic matter to the ice environments by *in situ* activities of photosynthetic organisms (Fritsen and Priscu, 1998; Paerl and Priscu, 1998). The negative correlations between Chlorobi, Betaproteobacteria, Rhizobiales (Alphaproteobacteria) and DOC is likely caused by the degradation of DOC by heterotrophic bacteria in the ice. Conversely, the relative abundances of Gammaproteobacteria and Alteromonadales (Gammaproteobacteria) can

increase as the result of DOC input in the ice cores. Since there was no significant change of bacteria communities from the Polar Plateau to the coast according to the results of NMDS and ANOSIM analysis, indicating that distinct bacteria communities have a small role on the spatial distribution of the quality of organic matter in the ice cores of Taylor Valley. Collectively, our results show the roles of both environmental factors and the bacteria community in the transformation of DOM.

5. Conclusions

Our study represented a comprehensive spatial scale organic matter investigation in lake and glacier ice cores of Taylor Valley, Antarctica. The quantity of organic matter showed a significant increase from the Polar Plateau to the coast. One terrestrial humic-like component and one protein-like component were identified by EEM-PARAFAC, and the fluorescence intensities of these two components both increased from the Polar Plateau to the coast. The fluorescence indices indicated that the lability of DOM decreased from the Polar Plateau to the coast. The distributions of organic matter were controlled largely by bacterial abundance, while specific bacterial communities were significantly correlated with DOC and POC concentrations. In addition, marine aerosol had an impact on DOC concentrations in the ice cores. Our results are some of the first to define the role of allochthonous and autochthonous sources on the spatial distribution of the organic matter from the Polar Plateau through the Transantarctic Mountains to the regional coastline of Antarctica.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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CRediT authorship contribution statement

Bixi Guo: Conceptualization, Investigation, Methodology, Data curation, Writing - original draft. **Wei Li:** Data processing, Supervision, Writing - review & editing. **Pamela Santibáñez:** Methodology. **John C. Priscu:** Conceptualization, Supervision, Funding acquisition, Writing - review & editing. **Yongqin Liu:** Supervision, Funding acquisition. **Keshao Liu:** Data processing, Writing - review & editing.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2022.156639>.

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