Terrestrial runoff is an important source of biological INPs in Arctic marine systems

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Abstract. The accelerated warming of the Arctic manifests in sea ice loss and melting glaciers, significantly altering the dynamics of marine biota. This disruption in marine ecosystems can lead to an increased ~~the~~ emission of biological ice nucleating particles (INPs) from the ocean into the atmosphere. Once airborne, these INPs induce cloud droplet freezing, thereby affecting cloud lifetime and radiative properties. Despite the potential atmospheric impacts of marine INPs, their properties and sources remain poorly understood. Analysing sea bulk water and the sea surface microlayer in two southwest Greenlandic fjords, collected between June and September 2018, and investigating the INPs along with the microbial communities, we could demonstrate a clear seasonal variation in the number of INPs and a notable input from terrestrial runoff. We found the highest INP concentration in June during the late stage of the phytoplankton bloom and active melting processes causing enhanced terrestrial runoff. These highly active INPs were smaller in size and less heat-sensitive than those found later in the summer and those previously identified in Arctic marine systems. A negative correlation between salinity and INP abundance suggests freshwater input as sources of INPs. Stable oxygen isotope analysis, along with the strong correlation between INPs and the presence of terrestrial and freshwater bacteria such as *Aquaspirillum arcticum, Rhodoferax*, and *Glaciimonas*~~the bacterium *Aquaspirillum arcticum*~~, highlighted meteoric water as the primary origin of the freshwater influx, suggesting that the notably active INPs originate from terrestrial sources such as glacial and soil runoff.

1 Introduction

Climate change manifests in a steady rise in the global average temperature (IPCC, 2021b) and the Arctic region is particularly susceptible to its effects, experiencing a four times faster warming than the global average (Rantanen et al., 2022), a phenomenon known as Arctic amplification (Previdi et al., 2021). The consequences of the rise in temperature are severe, as it leads to significant alterations in the energy balance (Letterly et al., 2018), changes that are displaying ~~manifesting~~ in the loss of sea ice, glacial melt, and the thawing of permafrost (Previdi et al., 2021; Box et al., 2019; Chadburn et al., 2017). Enhanced melting processes, e.g. the melting of sea ice and glaciers, lead to a decline in the sea surface salinity (freshening) due to the freshwater input (Ravindran et al., 2021; Fransson et al., 2023). Further, t~~T~~he reduction in sea ice exposes a larger fraction of seawater to the atmosphere, which facilitates the exchange of gases and aerosols between the ocean and the atmosphere. The sea surface microlayer (SML), which is the interface between the ocean and the atmosphere with a thickness of less than a millimeter (Liss and Duce, 1997), plays a particularly important role in the ocean-atmosphere exchange. In the SML, the concentration of organic material is often increased compared to the underlying sea bulk water (SBW) as surface-active compounds preferentially partition into the SML (Wurl et al., 2009). Previous studies have shown that the microbial community of the SML differs from the SBW just a few centimeters beneath the SML (Zäncker et al., 2018; Reunamo et al., 2011) and that specific bacterial taxa (e.g. *Flavobacteriaceae* and *Cryomorphaceae*) are enriched in the SML compared to the SBW (Zäncker et al., 2018). Atmospherically-relevant compounds comprising ice nucleating particles (INPs) have also been found to concentrate in the SML compared to the SBW (Wilson et al., 2015; Hartmann et al., 2021).

INPs are particles that initiate the freezing of water at temperatures higher than the temperature of homogeneous freezing (-38 °C) and are of particular importance in the atmosphere where they impact ice formation in clouds (Kanji et al., 2017). When aerosolized from the ground, INPs can namely be transported ~~to high altitudes~~upwards where they trigger the freezing of cloud droplets and thus affect cloud radiative properties and lifetime. While mineral dust and soot are the numerically dominating atmospheric INPs at temperatures below -15 °C, ~~(Murray et al., 2012),~~ biological INPs are dominating at temperatures above -15 °C and as high as -2 °C (Maki et al., 1974; Vali et al., 1976; Murray et al., 2012). Cloud ice formation has been frequently observed in Arctic mixed-phase clouds at temperatures, where only biological INPs are known to nucleate ice at atmospherically relevant concentrations (Griesche et al., 2021; Creamean et al., 2022). Therefore, there has recently been an increased focus on quantifying biological INPs in both source environments, and the atmosphere in the Arctic (Hartmann et al., 2021; Šantl-Temkiv et al., 2019; Creamean et al., 2022; Pereira Freitas et al., 2023). Especially during summer, when the long-range transport into the Arctic atmosphere is limited, locally sourced biological INPs may play an important role in cloud processes (Griesche et al., 2021). As cloud processes feed into the energy balance in the Arctic, and therefore modulate Arctic amplification (Serreze and Barry, 2011; Tan and Storelvmo, 2019), there is a need to improve our understanding of the sources, controlling factors, and emission rates of cloud-relevant particles such as INPs.

Seawater, and in particular the SML, may act as a source of biological aerosols (bioaerosols) and INPs as wave breaking and bubble bursting can inject a significant amount of biological material and INPs into the atmosphere (Ickes et al., 2020; Wilson et al., 2015). So far it is unknown which types of INPs are responsible for the ice nucleation activity in seawater, but the sources may be linked to indigenous processes performed by marine microorganisms or to external inputs of terrestrial material into marine systems. Therefore, both marine and terrestrial ice nucleation active (INA) organisms may play a role when it comes to marine emissions of INPs. There is also an interplay between these two factors, as terrestrial runoff of nutrients has been shown to enhance the activity of marine microbes (Arrigo et al., 2017). Biological INPs can stem from a variety of sources such as different bacterial (Joly et al., 2013; Maki et al., 1974; Šantl-Temkiv et al., 2015), microalgal (Tesson and Šantl-Temkiv, 2018), and fungal species (Fröhlich-Nowoisky et al., 2015; Kunert et al., 2019), as well as lichen (Eufemio et al., 2023; Kieft and Ruscetti, 1990), viruses (Adams et al., 2021), pollen (Gute and Abbatt, 2020) and subpollen particles (Burkart et al., 2021), which inhabit marine and terrestrial environments. While we have substantial knowledge of bacterial ice nucleation proteins (Hartmann et al., 2022a; Roeters et al., 2021; Garnham et al., 2011; Govindarajan and Lindow, 1988), our understanding of INA material excreted by other microorganisms, i.e. microalgae and fungi, is limited. In addition, the quantitative contribution of different biologically-sources INPs remains to be determined.

Recent studies have shown a correlation between biological INPs in Arctic seawater and the phytoplanktonic growth season (Creamean et al., 2019; Zeppenfeld et al., 2019). If the INPs originate from microorganisms associated with phytoplanktonic blooms their impact on atmospheric processes could become more pronounced with ongoing climate change as e.g. primary productivity is stimulated by higher temperatures and increased CO_2 levels. In addition, the melting of sea ice prolongs the phytoplankton growth season due to increased penetration of shortwave radiation into the water column (Park et al., 2015). This leads to more planktonic biomass and affects the marine ecosystem. Arrigo et al. (2008) observed an increase in annual primary production by marine algae of 35 Tg C yr^{-1} between 2006 and 2007 due to decreasing sea ice coverage and a longer phytoplankton growth season. Consequently, the increased primary production induced by warming could impact the number of biogenic INPs released from the seawater and their ~~c~~affect on atmospheric processes. Further, terrestrial ice melt and runoff have been increasing over time (IPCC, 2021a). Studies have shown that glacial outwash sediment (Tobo et al., 2019; Xi et al., 2022), rivers (Knackstedt et al., 2018), thawing permafrost, and thermokarst lakes (Creamean et al., 2020; Barry et al., 2023) contain high concentrations of INPs active at high sub-zero temperatures. As the runoff processes are enhanced, this will lead to increased inputs of highly active terrestrial INPs into the marine environments. Due to our poor understanding of biological INPs found in marine environments, it remains unclear whether it is indigenous microbial processes or external ~~terrestrial~~ inputs that dominate the pool of INPs in seawater.

Although prior studies have examined the concentrations of INPs in both bulk water and the microlayer, along with the influence of phytoplankton blooms on atmospheric INPs and INP concentrations in bulk water, the complete understanding of

the dynamics and origins of marine INPs remains elusive. Hence, our research delved into the concentrations and properties of INPs within both the bulk water and the microlayer of southwest Greenland during the late bloom and post-bloom seasons. We chose to work on fjord systems to address the roles of indigenous processes versus external inputs such as terrestrial runoff or sea ice melt water as fjords are semi-closed systems where water circulation and therefore dilution of freshwater inputs is restricted. We correlated INP concentrations with chlorophyll a alongside the assessments of microbial composition, diversity, and abundance to understand whether INPs are linked to the abundance of specific microbes, indicating either their indigenous production or acting as tracers for their source environments. Finally, we correlated INP concentrations with salinity and δO^{18} analysis to pinpoint the contribution of terrestrial inputs to the marine INP pool. This holistic approach aims to enhance our understanding of the dynamics and characteristics of biological marine INPs in the low Arctic.

2 Materials and methods

2.1 Sample collection

Sea surface microlayer and sea bulk water samples were collected at Kobbefjord (KF, N64°09.228, W51°25.906) and Godthåbsfjord (GF, N64°20.794, W51°42.709) in southwest Greenland (Fig. 1) in June, July, and September 2018. Approximately 100 mL of SML were collected per sample using a glass plate sampler (Harvey and Burzell, 1972). The glass plate sampler was immersed vertically and retracted at approximately 5 cm s^{-1}. The seawater was allowed to run off before the adherent SML samples were scrapped of into a sterile bottle using a neoprene wiper.

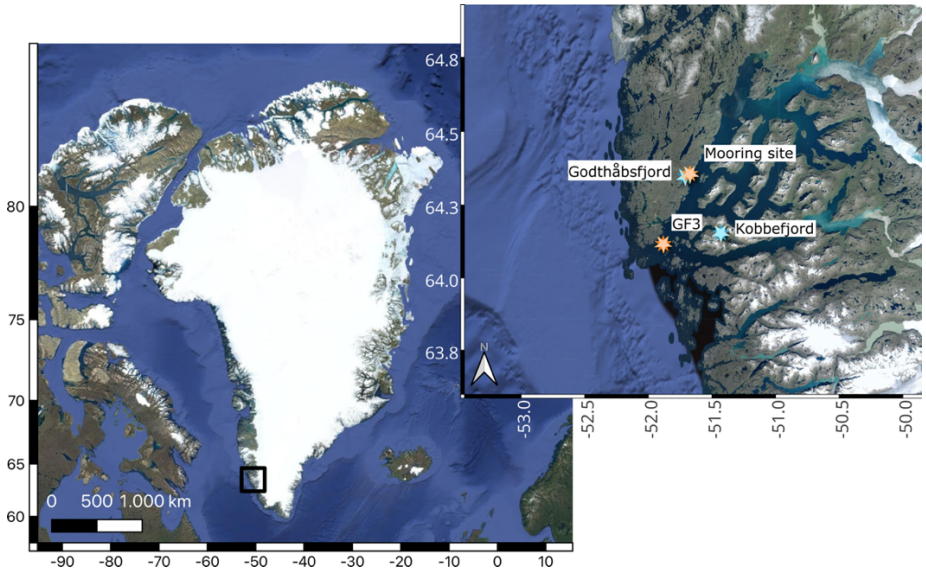

Figure 1: Map of Greenland with a zoomed in view on the region around Nuuk. The sampling stations for SBW and SML samples Kobbefjord and Godthåbsfjord (blue) as well as the two stations for the chlorophyll and nutrient measurements GF3 and the

mooring station (orange) are indicated by stars. The map was produced in QGIS using the publicly available © Google Maps Satellite data layer.

SBW samples were collected simultaneously by lowering a sterile bottle below the SML. Care was taken that the bottle was opened below the SML and closed before retrieving it back onto the boat. Samples for microbial community analysis were immediately mixed 1:1 with a high-salt solution containing 25 mM sodium citrate, 10 mM EDTA, 450 g l^{-1} ammonium sulphate, pH 5.2, (Lever et al., 2015) for the preservation of RNA. The samples were taken back to the lab immediately after sampling where they were concentrated onto Sterivex filters (0.22 µm), fixed in the presence of 1 ml of RNA later (Sigma Aldrich, US), and frozen at – 20 °C until the analysis.

2.2 Measurement of ice nucleation activity

Ice nucleation analysis was conducted using the micro-PINGIUN instrument (Wieber et al., 2024). Micro-PINGUIN is an instrument that allows droplet freezing assays using 384-well PCR plates. To ensure optimal thermal contact between the PCR plate and the cooling unit, a gallium bath is heated to 40 °C, and the PCR plate is immersed in the liquid gallium. The instrument is then cooled to 10 °C until the gallium solidifies, creating effective contact between the PCR plate and the surrounding cooling unit. Once the plate is mounted, the samples are added to the wells to prevent sample heating during the melting process of the gallium, which could negatively impact the ice nucleating activity. For each sample, 80 wells of the 384-well PCR plates were filled with 30 µl of the sample each using an automatic 8-channel pipette (PIPETMAN P300, Gilson, US). The remaining 64 wells were filled with MilliQ water filtered through a 0.22 µm PES filter, serving as a negative control. The system is then cooled at a rate of 1 °C min^{-1} until reaching -30 °C, while the freezing processes are recorded by an infrared camera (FLIR A655sc/25° Lens; Teledyne FLIR, US).

The salt concentration for each sample was measured using a refractometer (WZ201, Frederiksen scientific, Denmark) and the freezing curves were corrected for the freezing point depression ΔT_f using the theoretical formula for sodium chloride solutions:

$$\Delta T_f = n\, c\, E_f = n\, c\, \left(-1.86\ \frac{\mathrm{K*kg}}{\mathrm{mol}}\right),$$

c is the molarity of the salt, n is the number of ions of the dissociated salt (n = 2 for NaCl), and E_f is the cryoscopic constant of water (Schwidetzky et al., 2021). The contribution of other components such as sulfate, magnesium, and calcium to the freezing point depression was considered minor and therefore neglected. 10-fold serial dilutions for the ice nucleation measurements were prepared using autoclaved sodium chloride solutions closest to the salinity of the original seawater samples (5, 10, 15, 20, 25, 30, or 35 g kg^{-1}).

2.2.1 Heat treatment of the INP samples

Heat treatments were performed using a water bath. Following the initial ice nucleation test, PCR plates from the ice nucleation assay were covered with adhesive plastic foil to prevent cross-contamination of the samples during removal as well as evaporation of water during the heat treatment. The plates were then placed in a preheated water bath at 48 °C for 30 minutes. Subsequently, the plastic foil was removed, and ice nucleation activity was measured. The heat treatment was repeated the same way at 88 °C for 30 minutes and ice nucleation activity was remeasured a final time.

2.2.2 Filtration of the water samples

During the sampling campaign, filtrates for all samples were prepared with a 0.22 µm PES filter. Ice nucleation tests were conducted on all these samples. Selected samples (one of the duplicates) underwent a detailed investigation of ice nucleation activity across different size ranges. Thus, prefiltered samples were loaded into Vivaspin filters (Vivaspin 20, Sartorius, Germany) with molecular weight cut-offs (MWCO) ranging from 1000 kDa to 100 kDa. Prior to use, Vivaspin filters were prewashed with 5 ml of MilliQ water to remove observed salt residues.

2.3 The fraction of meteoric water derived from stable oxygen isotopes

The fraction of stable oxygen isotopes $\delta^{18}O$ can be used to determine the contributions of sea ice meltwater (SIM) and meteoric water (MW), originating from precipitation e.g. rivers and glacial melt water, within a sample. This approach has previously been used and proven valuable to distinguish between SIM and MW in the Arctic Ocean (Burgers et al., 2017; Irish et al., 2019; Alkire et al., 2015; Yamamoto-Kawai et al., 2005). Following the approach used by Irish et al. (2019) and Burgers et al. (2017) the water volume fractions of sea ice melt water (f_{SIM}), meteoric water (f_{MW}), and seawater (f_{SW}) were calculated using the following equations:

$$f_{SIM} S_{SIM} + f_{MW} S_{MW} + f_{SW} S_{SW} = S_{obs}$$
$$f_{SIM}\, \delta^{18}O_{SIM} + f_{MW}\, \delta^{18}O_{MW} + f_{SW}\, \delta^{18}O_{SW} = \delta^{18}O_{obs}$$
$$f_{SIM} + f_{MW} + f_{SW} = 1,$$

where S is the corresponding salinity of the sample and $\delta^{18}O$ the ratio between ^{18}O and ^{16}O in water molecules. These equations assume that each sample consists of sea ice melt water, meteoric water, and a seawater reference and are derived from the

conservation equations. Net sea ice formation results in negative f_{SIM} values (Alkire et al., 2015). For the sea ice melt water, we assume a salinity of 4 g kg^{-1} and a $\delta^{18}O$ of 0.5 ‰ and for the meteoric water values of 0 g kg^{-1} and -20 ‰, respectively (Irish et al., 2019; Burgers et al., 2017). Further, we assume that our samples are mainly influenced by the west Greenland current waters and thus we chose the values for the reference seawater as S_{SW} = 33.5 g kg^{-1} and $\delta^{18}O_{SW}$ = -1.27 ‰ (Burgers et al., 2017). $\delta^{18}O$ values were measured with PICARRO Li-1102 (18O). $\delta^{18}O$ values correspond to the deviation from the Vienna Standard Mean Ocean Water (V-SMOW) in permille (‰). Measurements were calibrated using three internal reference water samples (-55.5 ‰, -33.4 ‰, and -8.72 ‰) and the average value of 5 to 6 replicate injections was taken for the calculations. Standard deviations between replicate measurements are ranging between 0.004 ‰ to 0.12 ‰.

2.4 Nutrient and chlorophyll a concentrations

Nutrient concentrations were extracted from the database of the Greenland Ecosystem Monitoring (GEM) Project (https://data.g-e-m.dk). Measurements were carried out at the MarineBasis in Nuuk (location GF3 in Fig.1). Nitrate and nitrite concentrations were measured by vanadium chloride reduction (Greenland Ecosystem Monitoring, 2020c), phosphate (Greenland Ecosystem Monitoring, 2020b) and silicate (Greenland Ecosystem Monitoring, 2020a) concentrations were measured spectrophotometrically. Additionally, chlorophyll a measurements from 1 m depth were extracted from the GEM database. After collection, the seawater samples were filtered, and the filters were stored frozen in 10 ml 96% ethanol until analysis with a Turner TD-700 Fluorometer. The same method was applied for seawater sampled at 12 m depth in Kobbefjord during the sampling dates of this study. For chlorophyll measurements from the mooring site (Fig. 1) a fluorescence sensor (Cyclops-7 Logger, PME) was deployed at 5 m depth from March to October 2018. The sensor was calibrated with chlorophyll standards (Turner Design). To prevent biofouling, the instruments were wrapped with copper tape. Upon retrieval, data was read out and despiked using the OCE package (Kelley et al., 2022) and chlorophyll a concentrations were calculated as a 3-day average.

2.5 DNA Extraction, Quantitative Polymerase Chain Reaction (qPCR) and amplicon sequencing

As freezing of the Sterivex filters, containing the high-salt solution, lysed some microbial cells and thus released their nucleic acids (data not shown), we used two different protocols for DNA extraction, one for the DNA in solution and one for the DNA which was still within the intact cells on the filter. In brief, the high-salt solution was extracted from the Sterivex filter into a separate tube. Then, DNA was purified using the CleanAll RNA/DNA Clean-up and concentration Kit (Norgen Biotek) following the manufacturers protocol. A combination of chemical and physical lysis was used on the Sterivex filters for simultaneously extraction of DNA as described by Lever et al. (2015). Last, the purified DNA from the Norgen Purification was pooled with the corresponding DNA from the Lever et al. (2015) extraction. qPCR was performed to quantify the amount

of bacterial 16S rRNA gene copies (DNA) as described earlier (Jensen et al., 2022), while 18S rRNA gene copies were quantified using primers Euk345F (5'- AAGGAAGGCAGCAGGCG-3') and Euk499R (5'- CACCAGACTTGCCCTCYAAT-'3) (Zhu et al., 2005). 16S rRNA library preparation of DNA was performed as described in Jensen et al. (2022). ~~while~~ 18S rRNA library preparation was performed with slight modification. ~~:~~ Primers TareukFWD1 (5'- CCAGCASCYGCGGTAATTCC-3') and TAReukREV3 (5'- ACTTTCGTTCTTGATYRA-3') were used to amplify the V4 region of the small subunit (18S) ribosomal RNA targeting primarily the marine microalgae (Stoeck et al., 2010). The PCR mixture contained 4 µl template DNA instead of 2 µl. The thermal cycling was run with touchdown PCR approach with an initial denaturation step at 95 °C for 3 minutes, 10 cycles with denaturation at 95 °C for 30 seconds, annealing at 57 °C for 30 seconds, elongation at 72 °C for 30 seconds, followed by 15 cycles with denaturation at 95 °C for 30 seconds, annealing at 47 °C for 30 seconds, elongation at 72 and a final elongation at 72 °C for 5 minutes. PCR clean-up was performed as for the 16S rRNA PCR products. The second round of PCR was run for 10 cycles to incorporate overhang adapters and was run with the same conditions as the previous PCR with an annealing temperature of 57 °C. Products were cleaned, and the Nextera XT Index primers were incorporated in a third PCR reaction which was run for 8 cycles following the previous condition and an annealing temperature of 55 °C. The PCR products were quantified using a Quant-iT™ dsDNA BR assay kit on a FLUOstar Omega fluorometric microplate reader (BMG LABTECH, Ortenberg, Germany), diluted and pooled together in equimolar ratios. The pool was quantified using the Quant-iT™ dsDNA BR assay kit on a Qubit fluorometer (Thermo Fisher Scientific, Waltham MA) and then sequenced on the Illumina MiSeq platform (Illumina, San Diego, CA) which produces two 300-bp long paired-end reads.

2.6 Bioinformatic analysis

Bioinformatic analyses were performed in RStudio 4.3.3. 16S and 18S sequence reads were processed following the same pipeline. Primer and adapter sequences were trimmed from the raw reads using cutadapt 0.0.1 (Martin, 2011). Forward and reverse read quality were plotted with the plotQualityProfile function from DADA2 1.21.0 (Callahan et al., 2016). Based on the read quality a trimming of 280 bp and 200 bp were set for the forward and reverse reads, respectively, using FilterAndTrim, according to their quality. The fastq files were randomly subsampled to the lowest read number using the ShortRead package 1.48.0 (Morgan et al., 2009), resulting in 42375 reads per sample for the 16S and 63555 reads per sample for the 18S, respectively. The subsampling allows for a more accurate comparison of the richness of the different samples. Error models were built for the forward and reverse reads, followed by dereplication and clustering into amplicon sequence variants (ASVs) (Callahan et al., 2017) with DADA2. The denoised forward and reverse reads were merged using the function mergePairs with default parameters with a minimum overlap of 12 nucleotides, allowing zero mismatches. Sequence tables were made with the function makeSequenceTable. ASVs shorter than 401 and longer than 430 nucleotides were removed from the 16S whereas sequences shorter than 360 and longer than 400 nucleotides were removed for the 18S dataset followed by chimeric sequence

removal using the removeBimeraDenovo function. Taxonomic assignment was accomplished using the naive Bayesian classifier against the SILVA ribosomal RNA gene database v138 (Quast et al., 2012) for the 16S sequences, while the 18S sequences were classified against the Protist Ribosomal Reference (PR2) database v5.0.1 (Guillou et al., 2013) with the assignTaxonomy function from DADA2, and species assignment was performed with the assignSpecies function from DADA2. ASVs mapped to mitochondria, chloroplasts and metazoa were removed from the dataset. Samples were decontaminated using the prevalence method (Threshold = 0.1) from the Decontam package (Davis et al., 2018). Statistical tests and visualization of the data was performed with phyloseq (Mcmurdie and Holmes, 2013), Vegan (Dixon, 2003) and microeco (Liu et al., 2021).

3 Results and Discussion

3.1 Spring bloom and secondary bloom in summer 2018

The chlorophyll a concentration, serving as a proxy for algal biomass (Creamean et al., 2019; Krawczyk et al., 2021; Huot et al., 2007; Hartmann et al., 2021), increased from early April to late May with a brief decline in the end of April (Fig. 2a). In late August, there was a subsequent increase in chlorophyll a concentration lasting for two to three weeks. These periods of increased chlorophyll a concentration align closely with times of nutrient scarcity, particularly a reduction in silicate levels, indicating that the nutrients were likely consumed by phytoplankton, most probably diatoms (Fig. 2b) (Kröger and Poulsen, 2008; Mayzel et al., 2021). The abundance and composition of nutrients, specifically carbon (C), nitrogen (N), and phosphorus (P), determine the activity and composition of the phytoplankton community (Arrigo, 2005). Increased primary production and chlorophyll a concentrations were previously shown to correlate with reduced nutrient concentrations such as nitrates ($NO_3^- + NO_2^-$), silicate (SiO_2), and phosphate (PO_4^{3-}) (Juul-Pedersen et al., 2015). Low levels of these nutrients can limit phytoplankton growth (Harrison and Li, 2007). Silicate is a constituent of diatom cell walls and thus a limiting factor for diatom cell growth (Bidle and Azam, 1999). Based on this data, we conclude the occurrence of a spring bloom (beginning of April to June) followed by a shorter secondary bloom at the end of August in the Nuuk region in 2018.

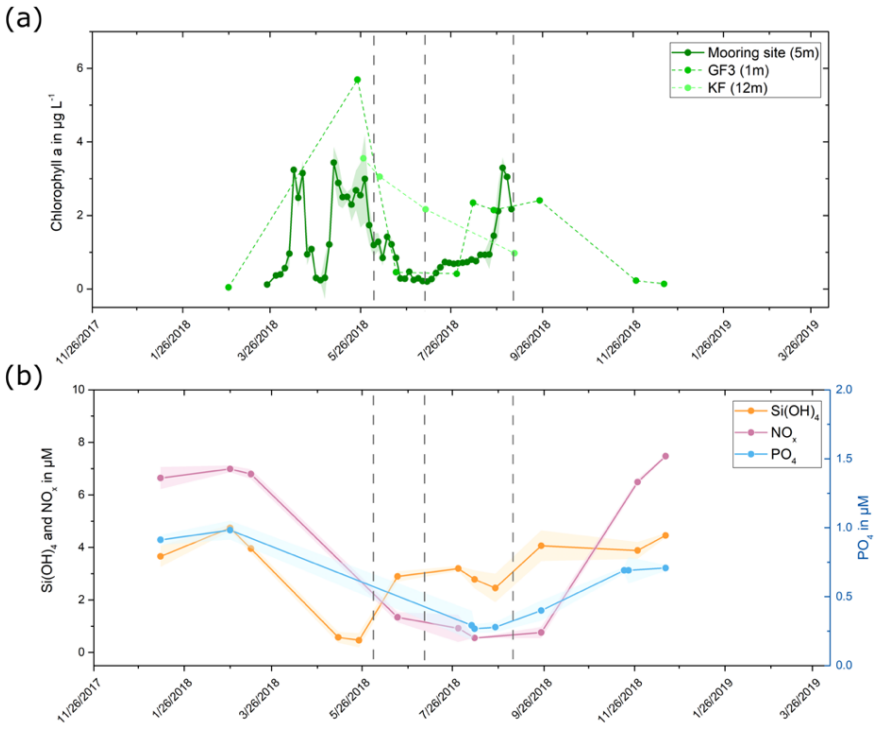

Figure 2: (a) Chlorophyll a concentration in 2018. Data was collected at 3 measurement sites and data points for each site are connected by lines for visualization purposes. The green shaded area for the mooring site data shows the standard deviation for the 3-day average. (b) Silicate, nitrate and nitrite, and phosphate concentrations measured at location GF3 (Fig. 1) in 2018. Data points are connected by lines for visualization purposes and the shaded areas indicate the standard deviations for measurements at 1, 5, 10, and 15 meter depth. The sampling dates are highlighted by vertical dashed lines in both graphs.

3.2 Seasonal variability and upconcentration of INPs in the SML

While freezing was initiated above -7 °C in all investigated SBW samples (Fig. S1), the concentration of INPs active at -10 °C (INP_{-10}) covered a wide range from $1.3 \cdot 10^4$ INPs per ~~liter~~ L to $6.1 \cdot 10^6$ INPs per L~~liter~~ (Fig. 3a). Typically, biological INPs are responsible for ice nucleation at temperatures higher than -15 °C (Murray et al., 2012), implying that the elevated onset freezing temperatures observed in our samples are attributable to INPs originating from biological sources. ~~-~~In addition, our study revealed higher T_{50} temperatures (temperature where 50% of the droplets were frozen)~~enhanced INP_{-10} concentrations~~ in the SML compared to the corresponding SBW samples (Fig. 3b, Fig. S2) showing that the highly active INPs are primarily found in the SML, which may affect their emissions into the atmosphere through wave breaking and bubble bursting (Ickes et al., 2020; Wilson et al., 2015).~~(Fig. 3b).~~ This finding aligns with observations by Wilson et al. (2015) and Hartmann et al. (2021), whereas Irish et al. (2017) observed no significant ~~up~~concentration of INPs in the SML comapared to the SBW. This is unlikely to be related to the sampling technique as our study and the studies by Hartmann et al. (2021) and Wilson et al. (2015) observed

~~an up~~concentration of INPs in the SML despite utilizing different approaches for collecting the samples. Consequently, it is more plausible that these differences arise from spatial and temporal variations in the properties of the SML.

Given that the SML serves as the interface between water and air, specific characteristics of INPs, such as hydrophobic sites, may lead to their partitioning into the SML. Moreover, elevated concentrations of organic material in the SML (Wurl et al., 2009) could provide energy for microorganisms in the SML and therefore lead to an increase in biogenic INP production, thereby explaining the higher INP concentrations observed in the SML.

Further, the ice nucleation tests revealed a seasonal variability with INPs having the highest onset freezing temperatures and significantly higher INP_{-10} concentrations in June (Fig. S3~~1~~). Notably, the INP concentrations in our study are generally higher than those reported by Wilson et al. (2015), Hartmann et al. (2021), and~~-~~ Irish et al. (2017). While INP concentrations for July and September fall well within the range observed by Irish et al. (2019) and Creamean et al. (2019), SBW samples in June exceed the previously reported INP concentrations and show higher onset freezing temperatures. Previous studies (Wilson et al., 2015; Irish et al., 2017; Irish et al., 2019; Creamean et al., 2019) utilized 0.6-2.5 µl droplets for ice nucleation analysis, resulting in a 12-50 times higher detection limit (assuming the same number of investigated droplets) than our method. Consequently, low-volume setups require higher concentrations of INPs for detection, thus not detecting highly active INPs that typically are present at lower concentrations. While small deviations in the reported freezing temperatures might occur due to methodological differences, INP concentrations in the two fjords observed in June are up to 4 orders of magnitude higher than previously reported values implying that these differences are not due to technical reasons.

We found a moderate correlation (r = 0.60) between the concentration of INP_{-10} in the SBW and the in~~-~~situ chlorophyll a concentration measured on the sampling dates in Kobbefjord. The correlation was stronger (r = 0.79) when focusing solely on the concentration of INP_{-10} in Kobbefjord, where samples for quantifying chlorophyll a and INP were collected at the same location and time (Fig. S4~~2~~). Thus, INPs in June may originate from algal exudates released during the decay of phytoplankton in the late stage of the bloom or from the bloom-associated heterotrophic bacterial community. Factors such as nutrient limitation (Nagata, 2000), the transition between different growth stages (Wetz and Wheeler, 2007), cell death, cell lysis, and excretion can enhance the release of dissolved organic matter (DOM) and dissolved organic carbon (DOC) by phytoplankton potentially including INA material (Thornton, 2014; Norrman et al., 1995). Aside from containing INA material (Ickes et al., 2020; Wilson et al., 2015), the released organics may also serve as nutrients for heterotrophic producers of INA material and may affect marine INP concentrations by shaping the heterotrophic community composition and enhancing abundance and activity of INA microorganisms (Mühlenbruch et al., 2018). ~~Further~~Alternatively, ~~external inputs, such as nutrients from terrestrial runoff, can change the community composition (Ardyna and Arrigo, 2020).~~ t~~T~~he observed correlation between the chlorophyll a concentration and the INP_{-10} concentration may ~~-~~not imply causality but may be attributed to the fact that ~~to~~ terrestrial runoff s~~i~~ymultaneously~~, which transports~~introduced INPs and nutrients~~ into the fjords~~, thereby enhancing the primary production in the fjords (Arrigo et al., 2017; Juul-Pedersen et al., 2015; Terhaar et al., 2021)~~ and potentially introducing~~

~~INPs originating from terrestrial environments~~. In line with this, external inputs such as nutrients from terrestrial runoff can change the community composition (Ardyna and Arrigo, 2020) and stimulate primary production (Juranek, 2022)~~(Juranek, 2022)~~. -INPs produced by aquatic microalgae ~~are~~ were typically ~~often~~ reported to be active below -12 °C (Tesson and Šantl-Temkiv, 2018; Thornton et al., 2023), however, INPs from epiphytic bacteria and fungi can nucleate ice at higher temperatures (as high as -2 °C and -2.5 °C, respectively (Fröhlich-Nowoisky et al., 2015; Huffman et al., 2013; Pouleur et al., 1992; Maki et al., 1974; Vali et al., 1976). As INP concentrations and onset freezing temperatures observed in the two fjords during June were higher than previously reported values, this might indicate that the highly-active INPs are originating from other, potentially terrestrial sources. The possibility of terrestrial runoff serving as a source of biological INPs in seawater has also been previously explored (Irish et al., 2019).

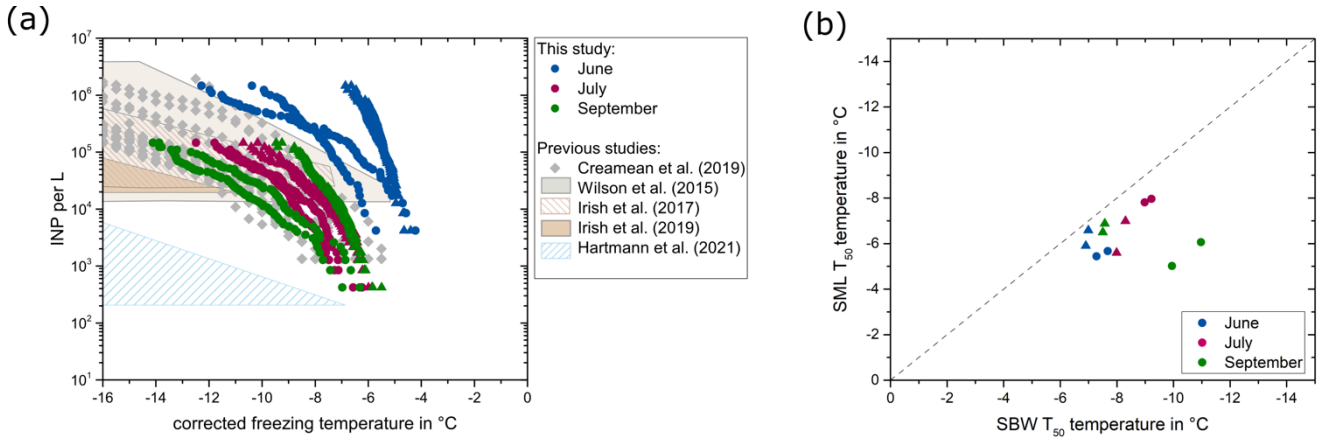

Figure 3: (a) Number of INPs per L seawater for the bulk water samples collected in the Kobbefjord (circles) and Godthåbsfjord (triangles). The INP data in June is derived from a 10-fold dilution due to the high activity. The boxes represent the data ranges reported by previous studies and the grey data points represent the data reported by Creamean et al. (2019). (b) ~~Number of INPs active at -10 °C in the~~Comparison of the T_{50} temperatures in the SBW in relation to the SML~~bulk water compared to the microlayer~~ for Kobbefjord (circles) and Godthåbsfjord (triangles). The dashed line represents the 1:1 fraction.

3.3 Shift in INP size and properties over time

~~To~~ By further characterizing~~e~~ the INPs, we aimed at understanding how their properties fit with properties of ~~and to investigate~~ INA compounds produced by known INA organisms~~their sources~~. Thus,~~,~~ we examined ~~their~~ the size and heat sensitivity of the INPs based on changes in T_{50} temperatures ~~(temperature where 50% of the droplets were frozen)~~. In June, T_{50} temperatures remained constant until a molecular weight cut-off (MWCO) of 300 kDa, and decreased significantly after filtration with a 100 kDa MWCO (One-way ANOVA, $p < 0.05$, Supplementary Fig. S5~~3~~). Only the SBW sample collected in June in KF showed a reduction in the freezing temperatures after filtration with an MWCO of 1000 kDa (Fig. 4). The data suggests that

the ~~prevailing~~predominant size range of INPs in June falls between 100 kDa and 300 kDa. Contrary, in all samples collected in July, the T_{50} temperatures decreased to below -17 °C after filtration with an MWCO of 1000 kDa. Samples collected in September showed a size disparity between INPs from the SML and the SBW. SML samples showed higher freezing temperatures with INPs in the range of 300 kDa to 1000 kDa, while SBW samples followed the pattern observed in July, indicating INP sizes larger than 1000 kDa (Fig. 4). Overall, our data implies the presence of small biogenic ~~particles~~ INPs (molecular weight < 300 kDa) in June, coinciding with the late stage of the phytoplanktonic spring bloom. In contrast, for samples collected after the spring bloom in July and September, INPs are larger with a molecular weight greater than 1000 kDa and 300 kDa, respectively. Further, June samples showed no decrease in T_{50} temperatures after moderate heating (48 °C), while samples from July and September were negatively affected by moderate heating (Fig. 5). Thus, the INPs with the ability to trigger freezing at high temperatures, primarily present in June, are smaller (100-300 kDa) and less heat sensitive (not affected by 48 °C).

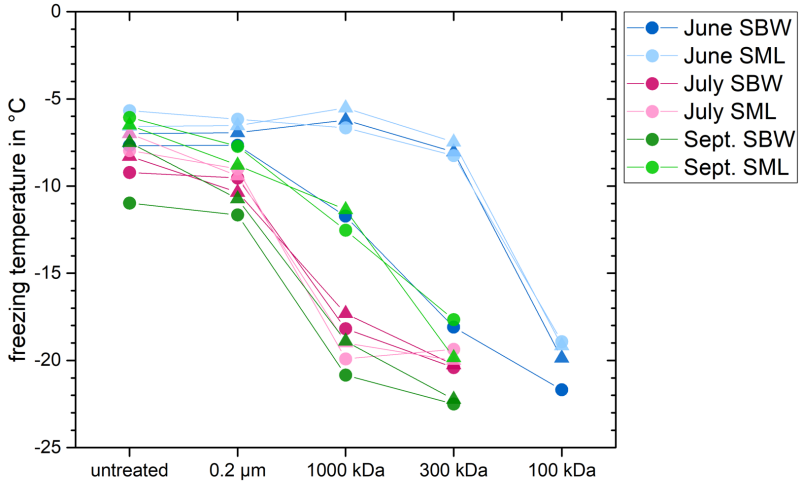

Figure 4: Freezing temperatures for a fraction frozen of 0.5 (T_{50} temperatures) after filtration with different pore size. Results from Kobbefjord are shown as circles and results from Godthåbsfjord are shown as triangles.

The characteristics observed by heat treatments and filtration provide insights into the nature of the INPs. While Hartmann et al. (2021) reported a removal of INPs with a 0.2 µm pore size filter in seawater collected from May to mid-July in the Arctic Ocean close to Svalbard, Irish et al. (2017) and Wilson et al. (2015) found that marine INPs were not affected by filtration through a 0.2 µm filter and could only be removed with a smaller pore size of 0.02 µm, approximately corresponding to a 300 kDa MWCO (Sartorius, 2022). Hartmann et al. (2021) suggest that their INPs were associated with larger particles, such as bacteria, algae, fungi, or biological material attached to minerals. Irish et al. (2017) and Wilson et al. (2015) hypothesized that the INPs they observed were small biological virus-size particles, probably phytoplankton or bacteria exudates, and that

they did not consist of whole cells or larger cell fragments. Similarly to Irish et al. (2017) and Wilson et al. (2015) we observed small virus-size particles in July and August. During June, however, we observed a different type of INPs, which are smaller than 300 kDa and have according to our knowledge not been previously reported in marine systems.~~-~~ Several studies have shown that while known bacterial ice-nucleating proteins are membrane-bound (Hartmann et al., 2022a; Roeters et al., 2021; Garnham et al., 2011) and thus primarily associated with cells, INPs ~~that~~ which were washed off pollen grains and fungal cells are within the size range between 100 and ~~-~~300 kDa (Pummer et al., 2012; Pouleur et al., 1992; Fröhlich-Nowoisky et al., 2015). Schwidetzky et al. (2023) showed that fungal INPs comprise cell-free proteinaceous aggregates, with 265 kDa aggregates initiating nucleation at -6.8 °C, while smaller aggregates nucleated at lower temperatures. ~~-~~Overall, t~~T~~he properties of the INPs observed in June correspond well with the properties reported for ~~these~~the INA exudates from fungi and pollen and ~~This~~ point ~~points~~ towards ~~potential~~ terrestrial environments as a potential source of INPs transported to the seawater.~~s of the INPs that we observed in June.~~

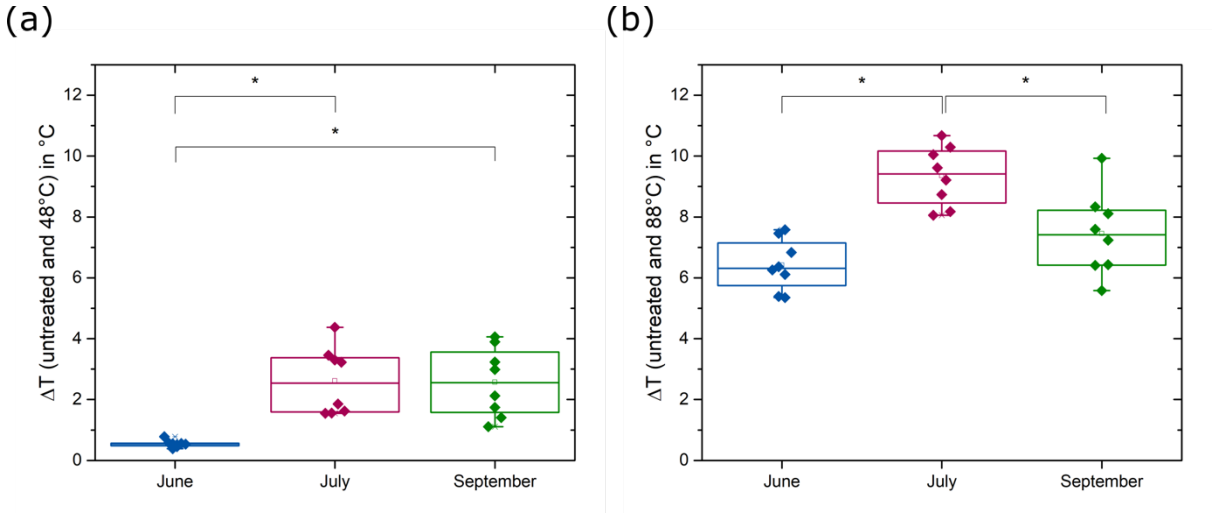

Figure 5: Difference between the T_{50} temperatures of untreated samples and samples heated to (a) 48 °C and (b) 88 °C. INPs in July and September are strongly influenced by moderate heating (48 °C), while INPs in June are less affected. All samples show significantly reduced T_{50} temperatures after heating to 88 °C.

Heat treatments are commonly performed to distinguish between biogenic INPs and inorganic INPs, assuming that the ice nucleation activity of biogenic INPs decreases when heated to sufficiently high temperatures, typically above 90 °C, due to protein denaturation (Daily et al., 2022). Although biological INPs can show distinct sensitivity to heating, heat treatments for environmental samples are often carried out at only one temperature (Daily et al., 2022, and the references therein). Few studies conducted ~~extended~~comprehensive heat treatments including more than a single denaturation temperature. Wilson et al. (2015) carried out heat treatments for SML samples for nine temperatures between 20 °C and 100 °C and observed decreasing activity with increasing heating temperatures. In combination with additional evidence, such as the results of filtrations, they attribute

the ice nucleation activity to phytoplankton exudates present in the SML. D'souza et al. (2013) found significantly reduced freezing temperatures for filamentous diatoms from ice-covered lakes after heating to 45 °C. Hara et al. (2016) showed that the majority of ice nuclei from snow samples that were active above −10 °C, are inactivated at 40 °C, similar to those associated with *Pseudomonas syringae* cells. While bacterial INPs are ~~often~~typically proteinaceous and denature at temperatures above 40 °C (Pouleur et al., 1992; Hara et al., 2016), INPs from pollen, fungal spores, and lichen (Kieft and Ruscetti, 1990) are more heat-resistant. INPs in pollen washing water were thermally stable up to 112°C (Pummer et al., 2012) and INPs from fungal spores of *Fusarium sp*. and *Mortierella alpina,* as well as INPs from lichen, were proteinaceous and heat stable up to 60 °C (Pouleur et al., 1992; Fröhlich-Nowoisky et al., 2015; Kieft and Ruscetti, 1990). While the INPs that we found in July and September behaved similarly to INPs studied by Wilson et al. (2015), the INPs that we observed in June behaved similarly to what has previously been found for terrestrial INPs stemming from fungi, lichens, and pollen (Pouleur et al., 1992; Fröhlich-Nowoisky et al., 2015; Kieft and Ruscetti, 1990).

The observation that INPs in June are smaller and exhibit distinct responses to heat treatments compared to those observed later in the summer supports the idea that they represent distinct types of INPs. We propose two alternative explanations for the ~~seasonal variations in INP properties that we observed in the sampling period~~origin of the specific type of INPs observed in June. ~~The~~ ~~Firstly, the difference in molecular weight could be due to different types of INPs present in June than later in summer. The observation that INPs in June are smaller and exhibit distinct responses to heat treatments compared to those observed later in the summer supports the idea that they represent distinct types of INPs.~~ These~~y~~ ~~INPs can~~could ~~be~~ either have been ~~produced by~~ produced by indigenous microbial processes in the seawater or be transported into ~~the~~ seawater from terrestrial environments by streams. Based on laboratory studies of known INA organisms, INPs in June may have been released by pollen, fungal spores, or lichen in terrestrial environments and introduced into the seawater by terrestrial runoff. Alternatively, ~~While bacterial INPro are often membrane bound proteins~~ (Hartmann et al., 2022a; Roeters et al., 2021; Garnham et al., 2011) ~~and thus often associated with cells, INPs of fungal spores, lichen and pollen can be released as exudates (Pummer et al., 2012; Pouleur et al., 1992; Fröhlich-Nowoisky et al., 2015) and thus present in a different environment as the microorganisms. Based on their properties, INPs in June may have been released by pollen, fungal spores, or lichen in terrestrial environments and transported into the seawater by streams. INPs present in July and September may have alternative sources, e.g. indigenous microbial processes in the fjord systems.~~ ~~Secondly, the~~ INPs ~~observed during the sampling period~~ could be yet unknown and uncharacterized molecules produced by ~~different~~ marine microorganisms ~~due to a changing microbial community following~~in the ~~post~~late-bloom season. INPs present in July and September have similar properties reported previously by several studies in marine systems indicating that indigenous microbial processes during post-bloom period were responsible for their production. ~~Secondly, t~~~~Further~~However, ~~the~~ INPs observed in July and September could also emerge due to aging processes modifying properties of INPs introduced in June. The increase in INP molecular weight could be due to aggregation ~~processes~~ in the seawater. Organic matter ~~may~~ is known to agglomerate over time or accumulate in transparent exopolymer particles (TEP), forming larger particles (Mari et al., 2017). TEPs are organic polymer gels primarily composed

of heteropolysaccharides that form a hydrogel matrix (Engel et al., 2017). TEPs are highly adhesive and can enhance the aggregation of particles in water. Assembly and disaggregation processes result in different size ranges of the gels, typically exceeding 0.4 µm (Meng and Liu, 2016). Small INPs, which would typically pass through the filters used, might adhere to TEP and would be consequently removed by filtration.

3.4 Correlation of INP concentration to environmental variables, microbial abundance, and community composition

We performed qPCR and amplicon sequencing to link the abundance and diversity of bacteria and~~-~~ micro algae to the types and concentration of various INPs that we observed in the samples. While the 18S rRNA data aimed to decipher whether the INPs are linked to specific marine microalgae and thus likely produced indigenously in the seawater, the 16S rRNA data is used to both identify potential bacterial producers of INPs associated with phytoplankton blooms ~~andas well as~~and to provide~~s~~ insights into the source environment of INPs transported from terrestrial environments. Canonical Correspondence Analysis (CCA) was utilized to ~~explore~~ determine ~~the~~ correlations between environmental factors (salinity, chlorophyll a), ~~and~~ the microbial community compositions, and the INP concentrations in both SBW and SML samples.

Considering the correlation we observed between the chlorophyll a and the INP_{-10} concentration, we employed a community analysis of ~~the present~~ microalgae to search for potential indigenous producers of INPs. The ~~eukaryotic~~ microalgal community~~, (Fig. S4 and Fig. S5),~~ as derived from the 18S rRNA data, ~~was dominated by Dinophyceae such as *Nusuttodinium* (high abundance in June) and *Gyrodinium* (high abundance in July).~~is presented in Fig. S6 and Fig. S7. We ~~found~~identified several typical bloom-forming taxa ~~that are typically bloom-forming microalgae in the Arctic~~ such as centric diatom *Chaetoceros* (Biswas, 2022; Booth et al., 2002; Balzano et al., 2017), dinoflagellate *Gyrodinium* (Johnsen and Sakshaug, 1993; Hegseth and Sundfjord, 2008), and green algae *Micromonas* (Vader et al., 2015; Marquardt et al., 2016)~~ and *Strombidium* (Lavrentyev et al., 2019).~~ ~~The bacterial community (Fig. S86 and Fig. S97) was dominated by the classes Bacteroidia and Gammaproteobacteria. On the genus level, a high abundance of *Polaribacter* was observed throughout all months. The presence of *Polaribacter* was found to correlate with the post-bloom and declining stage of the phytoplanktonic bloom in an Arctic fjord (Feltracco et al., 2021). For the 18S rRNA data~~Further, ~~w~~We found a slight insignificant~~ly significantly increasing~~ ($p = 0.123$) increase in the 18S rRNA ~~ribosomal~~ gene copy numbers from June to September (Fig. S~~8~~8). While the observed alpha diversity was not significantly different ~~PerMANOVA analysis indicates a notable distinction among the months concerning the composition of the eukaryotic community~~ between the different months (Fig. S9~~1~~2), there was a significant distinction in the composition of the microalgal community (PerMANOVA, $p < 0.001$, Fig. S10~~9~~). ~~However, the observed alpha diversity was not significantly different (Fig. S120).~~ The CCA analysis ~~of the 18S rRNA data which represents the microalgal community~~ ~~suggests~~shows a correlation of the microalgal community composition with salinity and chlorophyll a (Fig. S11, Table S1), implying that a combination of bloom dynamics and terrestrial runoff may have affected the communities. There was no correlation between the community composition and the INP_{-10} concentrations (Table S1). We also investigated

the association between specific microalgal taxa and the concentration of INP$_{-10}$ using ~~Pearson~~Spearman's rank ~~-~~correlation analysis.~~In addition, only~~ that fewer organisms exhibit~~ed~~ ~~weak~~ correlations with INP$_{-10}$~~, and these correlations are weak (Fig. S11).Following up on the association between microalgal taxa and the concentration of INP$_{-10}$, we used the Pearson correlation analysis to show that~~ W~~w~~hile ~~While~~ 22 ~~microalgal~~ taxa significantly correlated with the INP$_{-10}$ concentration~~,~~ (see Dataset (Wieber, 2024)) ~~correlations were identified for 294 bacterial taxa ,~~.the majority of these taxa was~~as~~ present at low ~~average~~relative abundances (<0.01 of the total community), none of them was present across samples collected at different times, and they did not include putative bloom-associated taxa *Chaetoceros*, *Gyrodinium*, or *Micromonas*. Thus, bloom-associated ~~The Mantel test assessing the correlation between dissimilarities in eukaryotic communities and environmental parameters demonstrated a significant correlation with salinity and chlorophyll a, whereas all other variables exhibited no correlation (Table S1). This data underlines the hypothesis that the~~ marine microalgae ~~are likely not~~ do not ~~seem~~seem to be plausible~~the~~ producers of the observed INPs~~, but terrestrial sources might contribute to the input of freshwater and INPs to the marine environment~~.

Further, we used the bacterial community composition to identif~~d~~y potential marine bacterial producers of INPs and to obtain insights into the source environment of the observed INPs.

The 16S rRNA analysis showed increasing 16S rRNA gene copy numbers from June to September with a significantly higher alpha diversity of bacteria (observed and Shannon) in June (Fig. S12~~2~~). A comparably high microbial alpha diversity as we observed in June was previously reported for soils adjacent to Kobbefjord and may point to parts of the community introduced by terrestrial runoff (Šantl-Temkiv et al., 2018). Interestingly, although INPs were concentrated in the SML, bacterial cells did not show a similar pattern, as the differences in copy numbers and alpha diversity between the SML and SBW were not significant. The bacterial community (Fig. S13~~8~~ and Fig. S14~~9~~) was dominated by the classes Bacteroidia and Gammaproteobacteria. Throughout all months, we observed a high abundance of ASV affiliated with the genus *Polaribacter*, which was previously found to correlate with the post-bloom and declining stage of the phytoplanktonic bloom in an Arctic fjord (Feltracco et al., 2021). The p~~P~~rincipal component analysis (PCA) ~~followed by~~together with PerMANOVA demonstrated a significant difference between the bacterial community composition in June, July, and September ($p < 0.001$) (Fig. S15~~3~~). These findings underscore the seasonal differences in the bacterial community structure with a lower copy number but higher alpha diversity in June when INP$_{-10}$ concentrations ~~are~~ were highest. ~~Interestingly, although INPs were concentrated in the SML, bacterial cells did not show a similar pattern, as the differences in copy numbers and diversity between the SML and SBW were not significant.~~

The results of the CCA for the bacterial community ~~16S rRNA gene data~~ are presented in Fig. 6. The bacterial communities in July and September exhibit a higher degree of similarity ~~to~~ between each other than ~~to~~ the community observed in June.

Additionally, the analysis demonstrated similarities between the communities in the two fjords. The Mantel test was subsequently conducted to assess the correlation between bacterial community dissimilarities (measured using robust Aitchison distance) and environmental parameters. We found that the community composition was strongly correlated with the concentration of INP_{-10} ($r = 0.65$, $p = 0.003$). Chlorophyll a was weakly correlated with the bacterial community composition ($r = 0.31$, $p = 0.01$), implying that the bloom dynamics had some impact on the community (Table S2). ~~Notably,~~ ~~t~~The salinity exhibited a strong correlation~~s~~ ($r = 0.67$, $p = 0.003$), emphasizing its influential role in shaping the bacterial community composition (Table S2). Further, we found a strong negative correlation ($r = -0.81$, $p < 0.001$) between salinity and the concentration of INP_{-10} with significantly lower salinity but higher concentration of INPs observed in June (Fig. 7a). These correlations suggest a strong impact of salinity within the observed fjords, both impacting the bacterial community composition as well as the INP_{-10} concentrations. The observed freshening of the sea water can be attributed to ~~and pointing towards~~freshwater input, which may originate either from terrestrial runoff or the melting of sea ice~~c as input of freshwater and potentially INPs~~.

Terrestrial runoff could either contain INPs produced by terrestrial microorganisms that were introduced into the fjord system from the same source as the bacteria or it might provide nutrients to marine microorganisms, thereby enhancing microbial production of ice nucleation active material in the fjords (Irish et al., 2019; Irish et al., 2017; Meire et al., 2017; Arrigo et al., 2017). Alternatively, sea ice melt water could be a potential source of INPs, however, studies that demonstrate the presence of highly active INPs in sea ice are still lacking.

Using CCA ~~W~~we found a co-occurrence between three taxa, *Aquaspirillum arcticum*, *Colwellia sp.,* and *SUP05* (sulfur-oxidizing Proteobacteria cluster 05) and a high concentration of INP_{-10} in the samples (Fig. 6). ~~In addition, we identified correlations were identified for 294 bacterial taxa~~ As confirmed by ~~Pearson~~ Spearman correlation, the co-occurrence was strong~~est~~ between INP_{-10} and the abundance of *Aquaspirillum arcticum* ($r = 0.90$, $p < 0.001$) a psychrophilic bacterium found in ~~low-saline~~freshwater Arctic environments (Butler et al., 1989; Brinkmeyer et al., 2004) ~~(r = 0.90, p < 0.001) followed by~~and *Colwellia* sp. ($r = 0.83$, $p < 0.001$) ~~,~~ commonly found in sea ice and polar seas (Brinkmeyer et al., 2004). Further, we identified a strong correlation between the presence of ~300 ~~several~~ bacterial taxa ~~including *Pseudomonas*~~ and the concentration of INP_{-10} (see Dataset (Wieber, 2024)). The most abundant of these bacterial taxa were affiliated to known marine bacterial groups (e.g. SAR11 Clade Ia, Candidatus Aquiluna, Amylibacter…), but were negatively correlated with the INP_{-10}, exluding them as potential INP producers. Among the known INA genera, only Pseudomonas was found to correlate with the INP_{-10}. ~~Although~~ T~~h~~he properties of the highly active INPs reported in this study differ from what has been previously reported for ice-nucleating proteins ~~INpro~~ produced by several species of *Pseudomonas* (Hartmann et al., 2022b; Hara et al., 2016; Garnham et al., 2011), implying that members of this genus were not likely the producers of these INPs. ~~and we find no other common producers of INPs,~~ As we found several bacterial taxa correlating with INP_{-10}~~pr~~, it is possible that previously unknown INA bacteria, producing INA compounds different from known bacterial ice-nucleating proteins, could be responsible for the ice nucleation

activity observed. ~~this requires further confirmation through cultivation and testing in the Arctic environment.~~ In the environment, it is likely that the INPs released as exudates (Pummer et al., 2012; Pouleur et al., 1992; Fröhlich-Nowoisky et al., 2015), such as the ones we found predominant during June, may be disassociated from their producer both in the original environments and during their transport to other environments, which may affect the ability to detect both the INP and its producers simultaneously. Therefore, conclusions based on correlations should in cases, where INP exudates are involved, be taken with care and would require further confirmation of putative novel INA microorganisms through cultivation and testing~~.~~. Alternatively, INPs and bacterial taxa which correlated with the presence of INPs might not be their producers but could have been co-transported~~Another way to intepret these correlations is that the INPs and the bacterial taxa which correlated with the presence of INPs were co-transported~~ to the fjords from ~~their~~ terrestrial source environments. ~~Since INPs are rare, even a small fraction of bacteria could contribute to the marine INP pool. To clarify whether these bacteria are INA they would need to be isolated from the samples and tested for their ice nucleation activity. However,~~This is supported by the ~~fact that~~*Aquaspirillum arcticum* ~~is a psychrophilic bacterium with a low salt tolerance that was isolated (Butler et al., 1989) from snow and ice-covered Arctic sediment. Later, it is also found in low saline Arctic environments, particularly in snow (Harding et al., 2011) and in melt pools (Brinkmeyer et al., 2004). Its strong correlation with INP$_{-10}$ concentrations in the fjords that we observe in our study implies that INPs are either produced by *Aquaspirillum arcticum* or that both INPs and *Aquaspirillum arcticum* cells were introduced to the fjords through terrestrial runoff from the same sources. *Colwellia sp.* is commonly found in sea ice and polar seas (Brinkmeyer et al., 2004).~~ ~~In previous studies it was demonstrated that *Colwellia sp.* strains isolated from sea ice have ice-binding properties due to the presence of antifreeze proteins (Hanada et al., 2014; Raymond et al., 2007). Structural similarity between antifreeze proteins and ice nucleating proteins was shown, although they have opposite functions (Davies, 2014). While the strong correlation between the relative abundance of *Colwellia* sp. and INP$_{-10}$ indicates that *Colwellia sp.* may produce ice nucleating compounds, this has not been validated yet. While both melting sea ice and terrestrial runoff could account for the input of freshwater and thus low salinities in June,~~ ~~several~~ significantly positive~~y~~ correlation between INP$_{-10}$ and the presence of bacteria typically associated with soil and terrestrial environments such as *Rhodoferax* (Lee et al., 2022), *Glaciimonas* (Zhang et al., 2011), and ~~*(Baek et al., 2022)*~~*Janthibacterium* (Chernogor et al., 2022) (see Dataset (Wieber, 2024)) ~~and by~~ as well as the correlation between bacterial diversity and INP$_{-10}$ concentrations (Table S2). Overall, ~~the results of~~ the bacterial community analysis aligns~~fit~~ with the conclusion that~~a stronger correlation with the terrestrial *Aquaspirillum arcticum*~~which points at the~~ terrestrial runoff ~~as~~ may be the key source of the freshwater input and thus low salinities in June. The timely co-occurrence of high INP concentrations with the post-phytoplanktonic bloom is likely a spurious correlation as terrestrial runoff may ~~which delivered the INPs~~ also contain nutrients that could stimulate the phytoplanktonic bloom (Juranek, 2022)~~(Juranek 2022)~~. While the previosly presented results indicate that terrestrial runoff is reposible for the reduced salinity observed in June,

~~The terrestrial run-off could either contain INPs produced by terrestrial microorganisms or it might provide nutrients to marine microorganisms, thereby enhancing microbial production of ice nucleation active material in the fjords (Irish et al., 2019; Irish et al., 2017; Meire et al., 2017; Arrigo et al., 2017). To further decipher whether terrestrial runoff or sea ice melt water was~~

~~driving the freshening of the seawater in the fjord,~~ which correlated to high INP concentrations, we included the analysis of ~~the~~ stable oxygen isotopes $\delta^{18}O$ to exclude the possibility of melting sea ice driving the freshening of the seawater.

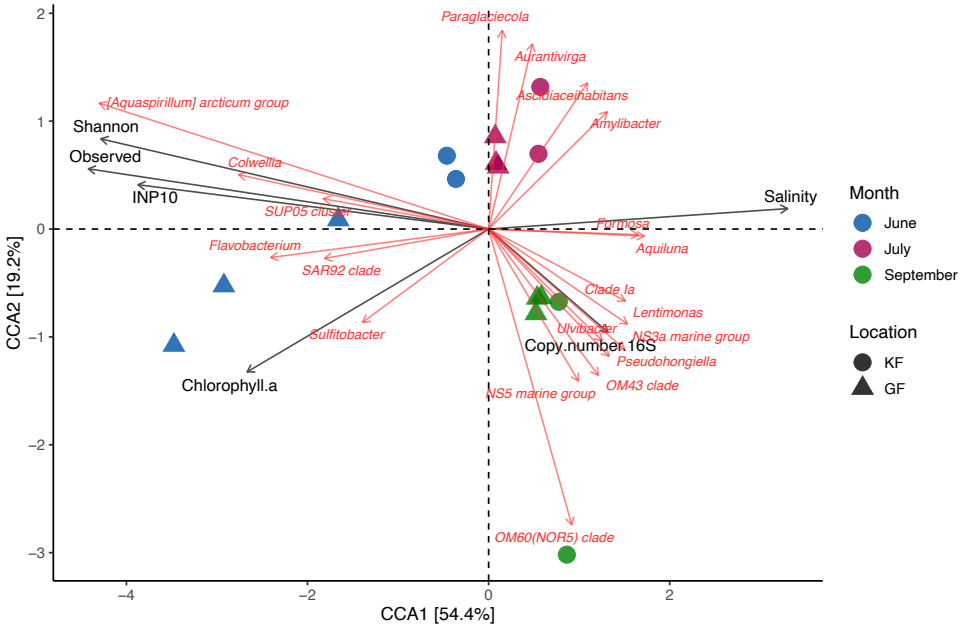

Figure 6: Canonical correspondence analysis for the 16S rRNA data (20 taxa). Small angles between the arrows indicate a good correlation between the taxa and the external parameter while the length of the arrow is indicated of the importance of this parameter. As we observed a negative correlation between the salinity and the ice nucleation activity, these arrows point into opposite directions.

3.5 Freshwater fractions from sea ice melt water and meteoric water

The freshwater fractions of sea ice melt water and meteoric water were calculated and correlated to the number of INPs active at -10 °C. A stronger correlation was found between the number of INP_{-10} and the fraction of meteoric water (r = 0.84,

$p < 0.001$) as shown in Fig. 7b, while correlations with sea ice meltwater were weaker ($r = 0.64$, $p < 0.001$, Fig. S164), implying a predominant influence of fresh-water from melting glaciers and/or from precipitation.

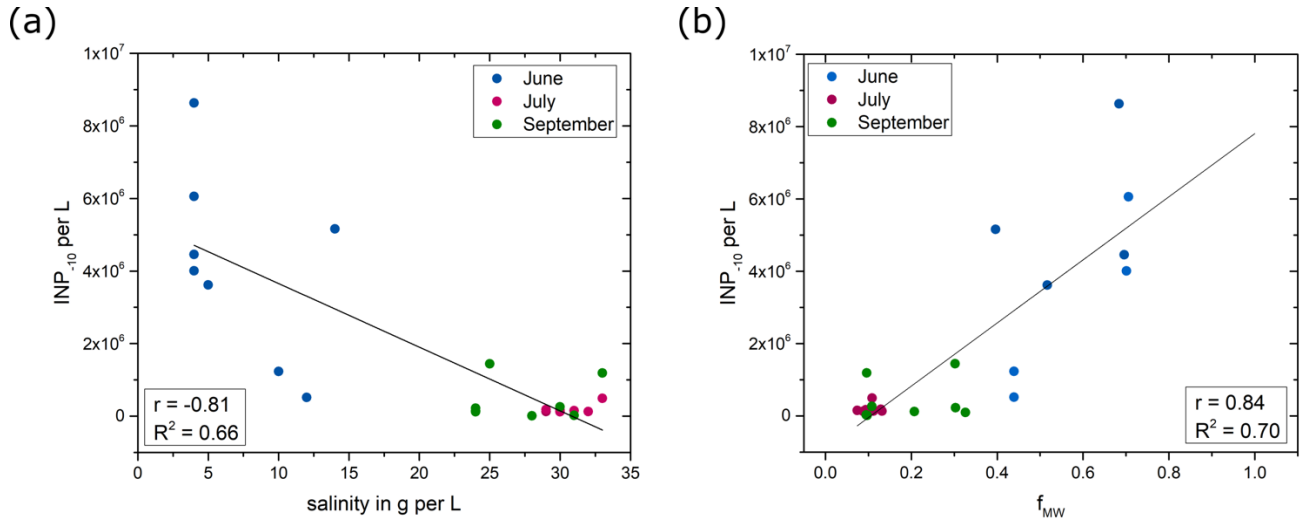

Figure 7: The INP_{-10} concentration as a function of (a) salinity and (b) freshwater fractions from meteoric water. The lines represent linear regressions of all data points shown in the graphs. Both correlations are significant ($p < 0.001$).

The study region is surrounded by six glaciers, including three marine-terminating glaciers, supplying melt water and runoff into the fjords (Van As et al., 2014). The~~A modeling~~modelling study by Van As et al. (2014) ~~Van As et al. (2014)~~ showed that melt and runoff in the Nuuk region doubled during the past two decades ~~(Van As et al., 2014)~~. The summer melt season in 2018 recorded exceptionally high surface melting across the Greenland Ice Sheet, surpassing ~~previous~~preceding records in early June, late July, and early August (Osborne, 2018). Previous studies have shown that meteoric water, including glacial outwash sediment (Tobo et al., 2019; Xi et al., 2022), rivers (Knackstedt et al., 2018), thawing permafrost and thermokarst lakes (Creamean et al., 2020; Barry et al., 2023) contains high concentrations of INPs active at high sub-zero temperatures. Glacial outwash from the Arctic region was found to contain highly active organic INPs (Tobo et al., 2019). Xi et al. (2022) also demonstrated the presence of INPs active above -15°C in glacial outwash sediments, albeit in smaller concentrations. Analysis of river samples revealed significant ice nucleation activity attributed to submicron-sized biogenic INPs, exhibiting comparable ice nucleus spectra to those produced by the soil fungus *Mortierella alpina*~~. These findings~~ implying a terrestrial source for these INPs (Knackstedt et al., 2018). The fact that the study region is impacted by terrestrial runoff and glacial melt water as well as the strong correlation between the fraction of meteoric water and the INP_{-10}~~is~~ concentration, supports the conclusion that terrestrial runoff is a major source of marine INPs in the investigated region. An extrapolation of the trendline in Fig. 7b leads to an estimated concentration of $7.8 \cdot 10^6$ INPs per L active at -10 °C in pure meteoric water ($f_{MW}=1$) which is

in good agreement with the average concentration of $1.0 \cdot 10^7$ INPs per L active at -10 °C reported for freshwater samples from streams in eastern Greenland by Jensen et al. (2024). With ongoing warming in the Arctic, microbial activity, and production of INP in terrestrial environments might increase, and thawing permafrost, glaciers, and ice sheets may become of increasing importance as contributors of INPs to coastal marine areas. Especially in fjord systems where the mixing with the open water is less pronounced terrestrial input might lead to increased INP concentrations in seawater and especially the SML. When these INPs get aerosolized from marine areas, they can trigger ice formation in clouds and in turn, impact the properties of clouds and thus their radiative forcing (Serreze and Barry, 2011; Tan and Storelvmo, 2019).

4 Conclusion

In this study, we investigated the ice nucleating particles in sea bulk water and in the sea surface microlayer samples in relation to phytoplanktonic blooms and terrestrial runoff in two fjords in southwest Greenland. We observed a high concentration of INPs in June which decreased in July and September. Filtration and heat treatments revealed a novel type of marine INPs in June, characterized by smaller sizes and lower heat sensitivity compared to INPs observed later in the summer and those previously identified in Arctic marine systems. Abundant INPs in June co-occurred with a low abundance of bacterial cells characterized by a high taxonomic diversity characteristic of terrestrial ecosystems. We noted a robust inverse relationship between salinity and the abundance of INPs, indicating that freshwater inputs likely contribute to increased INP concentrations. Stable oxygen isotopes in the freshwater fractions point towards meteoric water as the major source of the freshwater, that could wash ~~INPs and nutrients of~~ terrestrial originating INPs into the fjords. This was supported by the fact that INPs also strongly correlated with the presence of ~~a~~ terrestrial and freshwater ~~bacterium~~bacteria, e.g. *Aquaspirillum arcticum*, *Rhodoferax*, and *Glaciimonas*. The timely co-occurrence with the phytoplanktonic bloom is rather a correlation and not a causation of the elevated INP concentrations~~s~~ as the freshwater also contains nutrients that could stimulate the phytoplanktonic bloom. Vertical mixing of the water column may have diluted INP concentrations in the upper marine layer, resulting in decreased INP concentrations in the subsequent months. However, the types of INP observed in July and September were distinct from those in June, indicating that these came from another, potentially indigenous source. Based on several lines of evidence including the INP properties, the negative correlation with salinity, the stable oxygen isotope analysis, the correlation with microbial diversity, and the co-occurrence of INP with terrestrial bacterial species, we conclude that the highly active and abundant INPs that we observed in seawater in June originate from a terrestrial source, such as glacial and soil runoff. The quantitative significance of terrestrial INPs in marine environments outside fjord systems and coastal areas, as well as the extent to which sea spray contributes to their total atmospheric fluxes, needs to be determined through further investigation.

Appendix A1

Table A1: Overview of SBW and SML samples investigated in this study. All samples are collected and examined in duplicates.

location	date	type	T_{50} (°C)	INP_{10} (L^{-1})	heat sensitive at 48°C	salinity (g kg^{-1})
KF	04/06/2018	SBW1	-7.68	$5.16 \cdot 10^5$	no	12
KF	04/06/2018	SBW2	-7.28	$1.23 \cdot 10^6$	no	10
KF	04/06/2018	SML1	-5.67	$5.16 \cdot 10^6$	no	14
KF	04/06/2018	SML2	-5.44	$3.62 \cdot 10^6$	no	5
KF	09/07/2018	SBW1	-9.22	$1.31 \cdot 10^5$	yes	29
KF	09/07/2018	SBW2	-8.98	$1.84 \cdot 10^5$	yes	29
KF	09/07/2018	SML1	-7.96	$1.31 \cdot 10^5$	yes	30
KF	09/07/2018	SML2	-7.81	$1.71 \cdot 10^5$	yes	30
KF	07/09/2018	SBW1	-10.97	$1.25 \cdot 10^4$	yes	28
KF	07/09/2018	SBW2	-9.95	$2.57 \cdot 10^4$	yes	31
KF	07/09/2018	SML1	-6.06	$2.60 \cdot 10^5$	yes	30
KF	07/09/2018	SML2	-5.02	$1.19 \cdot 10^6$	yes	33
GF	05/06/2018	SBW1	-6.99	$4.01 \cdot 10^6$	no	4
GF	05/06/2018	SBW2	-6.90	$6.06 \cdot 10^6$	no	4
GF	05/06/2018	SML1	-6.58	$4.46 \cdot 10^6$	no	4
GF	05/06/2018	SML2	-5.90	$8.63 \cdot 10^6$	no	4
GF	13/07/2018	SBW1	-8.30	$1.25 \cdot 10^5$	yes	30
GF	13/07/2018	SBW2	-7.99	$1.50 \cdot 10^5$	yes	31
GF	13/07/2018	SML1	-6.99	$1.31 \cdot 10^5$	yes	32
GF	13/07/2018	SML2	-5.60	$4.93 \cdot 10^5$	yes	33
GF	07/09/2018	SBW1	-7.50	$9.59 \cdot 10^4$	yes	24
GF	07/09/2018	SBW2	-7.57	$1.19 \cdot 10^5$	yes	24
GF	07/09/2018	SML1	-6.50	$1.44 \cdot 10^6$	yes	25
GF	07/09/2018	SML2	-6.88	$2.23 \cdot 10^5$	yes	24

Data availability. The data presented in this study are deposited in the European Nucleotide Archive under the accession number PRJNA1108919. The Dataset for the taxa correlating with the INP_{-10} concentration is accessible at https://doi.org/10.5281/zenodo.14044414 (Wieber, 2024).

Author contributions. TST and KF designed and supervised the research project. LV collected the SML and SBW samples in Greenland. LM and TJP provided data for the chlorophyll concentrations. LZJ performed the microbial and bioinformatic

analysis. CW conducted the ice nucleation measurements and analysis and wrote the manuscript with contributions from the co-authors.

Competing interests. The authors declare that they have no conflict of interest.

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References

Adams, M. P., Atanasova, N. S., Sofieva, S., Ravantti, J., Heikkinen, A., Brasseur, Z., Duplissy, J., Bamford, D. H., and Murray, B. J.: Ice nucleation by viruses and their potential for cloud glaciation, Biogeosciences, 18, 4431-4444, 10.5194/bg-18-4431-2021, 2021.

Alkire, M. B., Morison, J., and Andersen, R.: Variability in the meteoric water, sea-ice melt, and Pacific water contributions to the central Arctic Ocean, 2000–2014, Journal of Geophysical Research: Oceans, 120, 1573-1598, https://doi.org/10.1002/2014JC010023, 2015.

Ardyna, M. and Arrigo, K. R.: Phytoplankton dynamics in a changing Arctic Ocean, Nature Climate Change, 10, 892-903, 10.1038/s41558-020-0905-y, 2020.

Arrigo, K. R.: Marine microorganisms and global nutrient cycles, Nature, 437, 349-355, 10.1038/nature04159, 2005.

Arrigo, K. R., van Dijken, G., and Pabi, S.: Impact of a shrinking Arctic ice cover on marine primary production, Geophysical Research Letters, 35, https://doi.org/10.1029/2008GL035028, 2008.

Arrigo, K. R., van Dijken, G. L., Castelao, R. M., Luo, H., Rennermalm, Å. K., Tedesco, M., Mote, T. L., Oliver, H., and Yager, P. L.: Melting glaciers stimulate large summer phytoplankton blooms in southwest Greenland waters, Geophysical Research Letters, 44, 6278-6285, https://doi.org/10.1002/2017GL073583, 2017.

Balzano, S., Percopo, I., Siano, R., Gourvil, P., Chanoine, M., Marie, D., Vaulot, D., and Sarno, D.: Morphological and genetic diversity of Beaufort Sea diatoms with high contributions from the Chaetoceros neogracilis species complex, J Phycol, 53, 161-187, 10.1111/jpy.12489, 2017.

Barry, K. R., Hill, T. C. J., Nieto-Caballero, M., Douglas, T. A., Kreidenweis, S. M., DeMott, P. J., and Creamean, J. M.: Active thermokarst regions contain rich sources of ice-nucleating particles, Atmospheric Chemistry and Physics, 23, 15783-15793, 10.5194/acp-23-15783-2023, 2023.

Bidle, K. D. and Azam, F.: Accelerated dissolution of diatom silica by marine bacterial assemblages, Nature, 397, 508-512, 10.1038/17351, 1999.

Biswas, H.: A story of resilience: Arctic diatom Chaetoceros gelidus exhibited high physiological plasticity to changing CO2 and light levels, Frontiers in Plant Science, 13, 10.3389/fpls.2022.1028544, 2022.

Booth, B. C., Larouche, P., Bélanger, S., Klein, B., Amiel, D., and Mei, Z. P.: Dynamics of Chaetoceros socialis blooms in the North Water, Deep Sea Research Part II: Topical Studies in Oceanography, 49, 5003-5025, https://doi.org/10.1016/S0967-0645(02)00175-3, 2002.

Box, J. E., Colgan, W. T., Christensen, T. R., Schmidt, N. M., Lund, M., Parmentier, F.-J. W., Brown, R., Bhatt, U. S., Euskirchen, E. S., Romanovsky, V. E., Walsh, J. E., Overland, J. E., Wang, M., Corell, R. W., Meier, W. N., Wouters, B., Mernild, S., Mård, J., Pawlak, J., and Olsen, M. S.: Key indicators of Arctic climate change: 1971–2017, Environmental Research Letters, 14, 045010, 10.1088/1748-9326/aafc1b, 2019.

Brinkmeyer, R., Glöckner, F.-O., Helmke, E., and Amann, R.: Predominance of β-proteobacteria in summer melt pools on Arctic pack ice, Limnology and Oceanography, 49, 1013-1021, https://doi.org/10.4319/lo.2004.49.4.1013, 2004.

Burgers, T. M., Miller, L. A., Thomas, H., Else, B. G. T., Gosselin, M., and Papakyriakou, T.: Surface Water pCO2 Variations and Sea-Air CO2 Fluxes During Summer in the Eastern Canadian Arctic, Journal of Geophysical Research: Oceans, 122, 9663-9678, https://doi.org/10.1002/2017JC013250, 2017.

Burkart, J., Gratzl, J., Seifried, T. M., Bieber, P., and Grothe, H.: Isolation of subpollen particles (SPPs) of birch: SPPs are potential carriers of ice nucleating macromolecules, Biogeosciences, 18, 5751-5765, 10.5194/bg-18-5751-2021, 2021.

Butler, B. J., McCallum, K. L., and Inniss, W. E.: Characterization of Aquaspirillum arcticum sp. nov., a New Psychrophilic Bacterium, Systematic and Applied Microbiology, 12, 263-266, https://doi.org/10.1016/S0723-2020(89)80072-4, 1989.

Callahan, B. J., McMurdie, P. J., and Holmes, S. P.: Exact sequence variants should replace operational taxonomic units in marker-gene data analysis, ISME J, 11, 2639-2643, 10.1038/ismej.2017.119, 2017.

Callahan, B. J., McMurdie, P. J., Rosen, M. J., Han, A. W., Johnson, A. J., and Holmes, S. P.: DADA2: High-resolution sample inference from Illumina amplicon data, Nat Methods, 13, 581-583, 10.1038/nmeth.3869, 2016.

Chadburn, S. E., Burke, E. J., Cox, P. M., Friedlingstein, P., Hugelius, G., and Westermann, S.: An observation-based constraint on permafrost loss as a function of global warming, Nature Climate Change, 7, 340-344, 10.1038/nclimate3262, 2017.

Chernogor, L., Bakhvalova, K., Belikova, A., and Belikov, S.: Isolation and Properties of the Bacterial Strain Janthinobacterium sp. SLB01, Microorganisms, 10, 10.3390/microorganisms10051071, 2022.

Creamean, J. M., Hill, T. C. J., DeMott, P. J., Uetake, J., Kreidenweis, S., and Douglas, T. A.: Thawing permafrost: an overlooked source of seeds for Arctic cloud formation, Environmental Research Letters, 15, 084022, 10.1088/1748-9326/ab87d3, 2020.

Creamean, J. M., Cross, J. N., Pickart, R., McRaven, L., Lin, P., Pacini, A., Hanlon, R., Schmale, D. G., Ceniceros, J., Aydell, T., Colombi, N., Bolger, E., and DeMott, P. J.: Ice Nucleating Particles Carried From Below a Phytoplankton Bloom to the Arctic Atmosphere, Geophysical Research Letters, 46, 8572-8581, https://doi.org/10.1029/2019GL083039, 2019.

Creamean, J. M., Barry, K., Hill, T. C. J., Hume, C., DeMott, P. J., Shupe, M. D., Dahlke, S., Willmes, S., Schmale, J., Beck, I., Hoppe, C. J. M., Fong, A., Chamberlain, E., Bowman, J., Scharien, R., and Persson, O.: Annual cycle observations of aerosols capable of ice formation in central Arctic clouds, Nat Commun, 13, 3537, 10.1038/s41467-022-31182-x, 2022.

D'Souza, N. A., Kawarasaki, Y., Gantz, J. D., Lee, R. E., Jr., Beall, B. F., Shtarkman, Y. M., Kocer, Z. A., Rogers, S. O., Wildschutte, H., Bullerjahn, G. S., and McKay, R. M.: Diatom assemblages promote ice formation in large lakes, ISME J, 7, 1632-1640, 10.1038/ismej.2013.49, 2013.

Daily, M. I., Tarn, M. D., Whale, T. F., and Murray, B. J.: An evaluation of the heat test for the ice-nucleating ability of minerals and biological material, Atmos. Meas. Tech., 15, 2635-2665, 10.5194/amt-15-2635-2022, 2022.

Davis, N. M., Proctor, D. M., Holmes, S. P., Relman, D. A., and Callahan, B. J.: Simple statistical identification and removal of contaminant sequences in marker-gene and metagenomics data, Microbiome, 6, 226, 10.1186/s40168-018-0605-2, 2018.

Dixon, P.: VEGAN, a package of R functions for community ecology, Journal of Vegetation Science, 14, 927-930, 10.1111/j.1654-1103.2003.tb02228.x, 2003.

Engel, A., Piontek, J., Metfies, K., Endres, S., Sprong, P., Peeken, I., Gäbler-Schwarz, S., and Nöthig, E.-M.: Inter-annual variability of transparent exopolymer particles in the Arctic Ocean reveals high sensitivity to ecosystem changes, Scientific Reports, 7, 4129, 10.1038/s41598-017-04106-9, 2017.

Eufemio, R. J., de Almeida Ribeiro, I., Sformo, T. L., Laursen, G. A., Molinero, V., Fröhlich-Nowoisky, J., Bonn, M., and Meister, K.: Lichen species across Alaska produce highly active and stable ice nucleators, Biogeosciences, 20, 2805-2812, 10.5194/bg-20-2805-2023, 2023.

Feltracco, M., Barbaro, E., Hoppe, C. J. M., Wolf, K. K. E., Spolaor, A., Layton, R., Keuschnig, C., Barbante, C., Gambaro, A., and Larose, C.: Airborne bacteria and particulate chemistry capture Phytoplankton bloom dynamics in an Arctic fjord, Atmospheric Environment, 256, 118458, https://doi.org/10.1016/j.atmosenv.2021.118458, 2021.

Fransson, A., Chierici, M., Granskog, M. A., Dodd, P. A., and Stedmon, C. A.: Impacts of glacial and sea-ice meltwater, primary production, and ocean CO2 uptake on ocean acidification state of waters by the 79 North Glacier and northeast Greenland shelf, Frontiers in Marine Science, 10, 10.3389/fmars.2023.1155126, 2023.

Fröhlich-Nowoisky, J., Hill, T. C. J., Pummer, B. G., Yordanova, P., Franc, G. D., and Pöschl, U.: Ice nucleation activity in the widespread soil fungus Mortierella alpina, Biogeosciences, 12, 1057-1071, 10.5194/bg-12-1057-2015, 2015.

Garnham, C. P., Campbell, R. L., Walker, V. K., and Davies, P. L.: Novel dimeric β-helical model of an ice nucleation protein with bridged active sites, BMC Structural Biology, 11, 36, 10.1186/1472-6807-11-36, 2011.

Govindarajan, A. G. and Lindow, S. E.: Size of bacterial ice-nucleation sites measured in situ by radiation inactivation analysis, Proceedings of the National Academy of Sciences, 85, 1334-1338, 10.1073/pnas.85.5.1334, 1988.

Greenland Ecosystem Monitoring: MarineBasis Nuuk - Water column - Silicate Concentration (µmol/L), Greenland Ecosystem Monitoring [dataset], 10.17897/VVQP-F862, 2020a.

Greenland Ecosystem Monitoring: MarineBasis Nuuk - Water column - Phosphate Concentration (µmol/L), Greenland Ecosystem Monitoring [dataset], 10.17897/PZNK-SP15, 2020b.

Greenland Ecosystem Monitoring: MarineBasis Nuuk - Water column - Nitrate+Nitrite Concentration (µmol/L), Greenland Ecosystem Monitoring [dataset], 10.17897/3NQX-FA50, 2020c.

Griesche, H. J., Ohneiser, K., Seifert, P., Radenz, M., Engelmann, R., and Ansmann, A.: Contrasting ice formation in Arctic clouds: surface-coupled vs. surface-decoupled clouds, Atmos. Chem. Phys., 21, 10357-10374, 10.5194/acp-21-10357-2021, 2021.

Guillou, L., Bachar, D., Audic, S., Bass, D., Berney, C., Bittner, L., Boutte, C., Burgaud, G., de Vargas, C., Decelle, J., Del Campo, J., Dolan, J. R., Dunthorn, M., Edvardsen, B., Holzmann, M., Kooistra, W. H., Lara, E., Le Bescot, N., Logares, R., Mahé, F., Massana, R., Montresor, M., Morard, R., Not, F., Pawlowski, J., Probert, I., Sauvadet, A. L., Siano, R., Stoeck, T., Vaulot, D., Zimmermann, P., and Christen, R.: The Protist Ribosomal Reference database (PR2): a catalog of unicellular eukaryote small sub-unit rRNA sequences with curated taxonomy, Nucleic Acids Res, 41, D597-604, 10.1093/nar/gks1160, 2013.

Gute, E. and Abbatt, J. P. D.: Ice nucleating behavior of different tree pollen in the immersion mode, Atmospheric Environment, 231, 117488, https://doi.org/10.1016/j.atmosenv.2020.117488, 2020.

Hara, K., Maki, T., Kakikawa, M., Kobayashi, F., and Matsuki, A.: Effects of different temperature treatments on biological ice nuclei in snow samples, Atmospheric Environment, 140, 415-419, https://doi.org/10.1016/j.atmosenv.2016.06.011, 2016.

Harrison, W. G. and Li, W. K.: Phytoplankton growth and regulation in the Labrador Sea: light and nutrient limitation, Journal of Northwest Atlantic Fishery Science, 39, doi:10.2960/J.v39.m592, 2007.

Hartmann, M., Gong, X., Kecorius, S., van Pinxteren, M., Vogl, T., Welti, A., Wex, H., Zeppenfeld, S., Herrmann, H., Wiedensohler, A., and Stratmann, F.: Terrestrial or marine – indications towards the origin of ice-nucleating particles during melt season in the European Arctic up to 83.7° N, Atmos. Chem. Phys., 21, 11613-11636, 10.5194/acp-21-11613-2021, 2021.

Hartmann, S., Ling, M., Dreyer, L. S. A., Zipori, A., Finster, K., Grawe, S., Jensen, L. Z., Borck, S., Reicher, N., Drace, T., Niedermeier, D., Jones, N. C., Hoffmann, S. V., Wex, H., Rudich, Y., Boesen, T., and Santl-Temkiv, T.: Structure and Protein-Protein Interactions of Ice Nucleation Proteins Drive Their Activity, Front Microbiol, 13, 10.3389/fmicb.2022.872306, 2022a.

Hartmann, S., Ling, M., Dreyer, L. S. A., Zipori, A., Finster, K., Grawe, S., Jensen, L. Z., Borck, S., Reicher, N., Drace, T., Niedermeier, D., Jones, N. C., Hoffmann, S. V., Wex, H., Rudich, Y., Boesen, T., and Santl-Temkiv, T.: Structure and Protein-Protein Interactions of Ice Nucleation Proteins Drive Their Activity, Front Microbiol, 13, 872306, 10.3389/fmicb.2022.872306, 2022b.

Harvey, G. W. and Burzell, L. A.: A simple microlayer method for small samples, Limnology and Oceanography, 17, 156-157, https://doi.org/10.4319/lo.1972.17.1.0156, 1972.

Hegseth, E. N. and Sundfjord, A.: Intrusion and blooming of Atlantic phytoplankton species in the high Arctic, Journal of Marine Systems, 74, 108-119, https://doi.org/10.1016/j.jmarsys.2007.11.011, 2008.

Huffman, J. A., Prenni, A. J., DeMott, P. J., Pöhlker, C., Mason, R. H., Robinson, N. H., Fröhlich-Nowoisky, J., Tobo, Y., Després, V. R., Garcia, E., Gochis, D. J., Harris, E., Müller-Germann, I., Ruzene, C., Schmer, B., Sinha, B., Day, D. A., Andreae, M. O., Jimenez, J. L., Gallagher, M., Kreidenweis, S. M., Bertram, A. K., and Pöschl, U.: High concentrations of biological aerosol particles and ice nuclei during and after rain, Atmospheric Chemistry and Physics, 13, 6151-6164, 10.5194/acp-13-6151-2013, 2013.

Huot, Y., Babin, M., Bruyant, F., Grob, C., Twardowski, M. S., and Claustre, H.: Relationship between photosynthetic parameters and different proxies of phytoplankton biomass in the subtropical ocean, Biogeosciences, 4, 853-868, 10.5194/bg-4-853-2007, 2007.

Ickes, L., Porter, G. C. E., Wagner, R., Adams, M. P., Bierbauer, S., Bertram, A. K., Bilde, M., Christiansen, S., Ekman, A. M. L., Gorokhova, E., Höhler, K., Kiselev, A. A., Leck, C., Möhler, O., Murray, B. J., Schiebel, T., Ullrich, R., and Salter, M. E.: The ice-nucleating activity of Arctic sea surface microlayer samples and marine algal cultures, Atmos. Chem. Phys., 20, 11089-11117, 10.5194/acp-20-11089-2020, 2020.

IPCC: Ocean, Cryosphere and Sea Level Change, in: Climate Change 2021 – The Physical Science Basis: Working Group I Contribution to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change, edited by: Intergovernmental Panel on Climate Change (IPCC), Cambridge University Press, Cambridge, 1211-1362, DOI: 10.1017/9781009157896.011, 2021a.

IPCC: Global Carbon and Other Biogeochemical Cycles and Feedbacks, in: Climate Change 2021 – The Physical Science Basis: Working Group I Contribution to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change, edited by: Intergovernmental Panel on Climate Change (IPCC), Cambridge University Press, Cambridge, 673-816, DOI: 10.1017/9781009157896.007, 2021b.

Irish, V. E., Hanna, S. J., Xi, Y., Boyer, M., Polishchuk, E., Ahmed, M., Chen, J., Abbatt, J. P. D., Gosselin, M., Chang, R., Miller, L. A., and Bertram, A. K.: Revisiting properties and concentrations of ice-nucleating particles in the sea surface microlayer and bulk seawater in the Canadian Arctic during summer, Atmos. Chem. Phys., 19, 7775-7787, 10.5194/acp-19-7775-2019, 2019.

Irish, V. E., Elizondo, P., Chen, J., Chou, C., Charette, J., Lizotte, M., Ladino, L. A., Wilson, T. W., Gosselin, M., Murray, B. J., Polishchuk, E., Abbatt, J. P. D., Miller, L. A., and Bertram, A. K.: Ice-nucleating particles in Canadian Arctic sea-surface microlayer and bulk seawater, Atmos. Chem. Phys., 17, 10583-10595, 10.5194/acp-17-10583-2017, 2017.

Jensen, L. Z., Glasius, M., Gryning, S.-E., Massling, A., Finster, K., and Šantl-Temkiv, T.: Seasonal Variation of the Atmospheric Bacterial Community in the Greenlandic High Arctic Is Influenced by Weather Events and Local and Distant Sources, Front Microbiol, 13, 10.3389/fmicb.2022.909980, 2022.

Jensen, L. Z., Simonsen, J. K., Pastor, A., Pearce, C., Nørnberg, P., Lund-Hansen, L. C., Finster, K., and Šantl-Temkiv, T.: Linking Biogenic High-Temperature Ice Nucleating Particles in Arctic soils and Streams to Their Microbial Producers, Aerosol Research Discuss., 2024, 1-29, 10.5194/ar-2024-18, 2024.

Johnsen, G. and Sakshaug, E.: Bio-optical characteristics and photoadaptive responses in the toxic and bloom-forming dinoflagellates Gyrodinium aureolum, Gymnodinium galatheanum, and two strains of Prorocentrum minimum, Journal of Phycology, 29, 627-642, https://doi.org/10.1111/j.0022-3646.1993.00627.x, 1993.

Joly, M., Attard, E., Sancelme, M., Deguillaume, L., Guilbaud, C., Morris, C. E., Amato, P., and Delort, A.-M.: Ice nucleation activity of bacteria isolated from cloud water, Atmospheric Environment, 70, 392-400, https://doi.org/10.1016/j.atmosenv.2013.01.027, 2013.

Juranek, L. W.: Changing biogeochemistry of the Arctic Ocean: Surface nutrient and CO2 cycling in a warming, melting north, Oceanography, 35, 144–155, https://doi.org/10.5670/oceanog.2022.120, 2022.

Juul-Pedersen, T., Arendt, K. E., Mortensen, J., Blicher, M. E., Søgaard, D. H., and Rysgaard, S.: Seasonal and interannual phytoplankton production in a sub-Arctic tidewater outlet glacier fjord, SW Greenland, Marine Ecology Progress Series, 524, 27-38, 2015.

Kanji, Z. A., Ladino, L. A., Wex, H., Boose, Y., Burkert-Kohn, M., Cziczo, D. J., and Krämer, M.: Overview of Ice Nucleating Particles, Meteorological Monographs, 58, 1.1-1.33, 10.1175/amsmonographs-d-16-0006.1, 2017.

Kelley, D., Richards, C., and Layton, C.: oce: an R package for Oceanographic Analysis, Journal of Open Source Software, 7, 3594, 10.21105/joss.03594, 2022.

Kieft, T. L. and Ruscetti, T.: Characterization of biological ice nuclei from a lichen, J Bacteriol, 172, 3519-3523, 10.1128/jb.172.6.3519-3523.1990, 1990.

Knackstedt, K. A., Moffett, B. F., Hartmann, S., Wex, H., Hill, T. C. J., Glasgo, E. D., Reitz, L. A., Augustin-Bauditz, S., Beall, B. F. N., Bullerjahn, G. S., Fröhlich-Nowoisky, J., Grawe, S., Lubitz, J., Stratmann, F., and McKay, R. M. L.: Terrestrial Origin for Abundant Riverine Nanoscale Ice-Nucleating Particles, Environmental Science & Technology, 52, 12358-12367, 10.1021/acs.est.8b03881, 2018.

Krawczyk, D. W., Kryk, A., Juggins, S., Burmeister, A., Pearce, C., Seidenkrantz, M. S., Moros, M., Høyer, J. L., Kuijpers, A., and Witkowski, A.: Spatio-temporal changes in ocean conditions and primary production in Baffin Bay and the Labrador Sea, Palaeogeography, Palaeoclimatology, Palaeoecology, 563, 110175, https://doi.org/10.1016/j.palaeo.2020.110175, 2021.

Kröger, N. and Poulsen, N.: Diatoms—From Cell Wall Biogenesis to Nanotechnology, Annual Review of Genetics, 42, 83-107, https://doi.org/10.1146/annurev.genet.41.110306.130109, 2008.

Kunert, A. T., Pöhlker, M. L., Tang, K., Krevert, C. S., Wieder, C., Speth, K. R., Hanson, L. E., Morris, C. E., Schmale Iii, D. G., Pöschl, U., and Fröhlich-Nowoisky, J.: Macromolecular fungal ice nuclei in Fusarium: effects of physical and chemical processing, Biogeosciences, 16, 4647-4659, 10.5194/bg-16-4647-2019, 2019.

Lee, Y. M., Park, Y., Kim, H., and Shin, S. C.: Complete genome sequence of Rhodoferax sp. PAMC 29310 from a marine sediment of the East Siberian Sea, Marine Genomics, 62, 100891, https://doi.org/10.1016/j.margen.2021.100891, 2022.

Letterly, A., Key, J., and Liu, Y.: Arctic climate: changes in sea ice extent outweigh changes in snow cover, The Cryosphere, 12, 3373-3382, 10.5194/tc-12-3373-2018, 2018.

Lever, M. A., Torti, A., Eickenbusch, P., Michaud, A. B., Šantl-Temkiv, T., and Jørgensen, B. B.: A modular method for the extraction of DNA and RNA, and the separation of DNA pools from diverse environmental sample types, Front Microbiol, 6, 10.3389/fmicb.2015.00476, 2015.

Liu, C., Cui, Y., Li, X., and Yao, M.: microeco: an R package for data mining in microbial community ecology, FEMS Microbiol Ecol, 97, 10.1093/femsec/fiaa255, 2021.

Maki, L. R., Galyan, E. L., Chang-Chien, M. M., and Caldwell, D. R.: Ice nucleation induced by pseudomonas syringae, Appl Microbiol, 28, 456-459, 1974.

Mari, X., Passow, U., Migon, C., Burd, A. B., and Legendre, L.: Transparent exopolymer particles: Effects on carbon cycling in the ocean, Progress in Oceanography, 151, 13-37, https://doi.org/10.1016/j.pocean.2016.11.002, 2017.

Marquardt, M., Vader, A., Stübner, E. I., Reigstad, M., and Gabrielsen, T. M.: Strong Seasonality of Marine Microbial Eukaryotes in a High-Arctic Fjord (Isfjorden, in West Spitsbergen, Norway), Appl Environ Microbiol, 82, 1868-1880, doi:10.1128/AEM.03208-15, 2016.

Martin, M.: Cutadapt removes adapter sequences from high-throughput sequencing reads, 2011, 17, 3, 10.14806/ej.17.1.200, 2011.

Mayzel, B., Aram, L., Varsano, N., Wolf, S. G., and Gal, A.: Structural evidence for extracellular silica formation by diatoms, Nature Communications, 12, 4639, 10.1038/s41467-021-24944-6, 2021.

McMurdie, P. J. and Holmes, S.: phyloseq: An R Package for Reproducible Interactive Analysis and Graphics of Microbiome Census Data, PLoS One, 8, e61217, 10.1371/journal.pone.0061217, 2013.

Meire, L., Mortensen, J., Meire, P., Juul-Pedersen, T., Sejr, M. K., Rysgaard, S., Nygaard, R., Huybrechts, P., and Meysman, F. J. R.: Marine-terminating glaciers sustain high productivity in Greenland fjords, Global Change Biology, 23, 5344-5357, https://doi.org/10.1111/gcb.13801, 2017.

Meng, S. and Liu, Y.: New insights into transparent exopolymer particles (TEP) formation from precursor materials at various Na+/Ca2+ ratios, Scientific Reports, 6, 19747, 10.1038/srep19747, 2016.

Morgan, M., Anders, S., Lawrence, M., Aboyoun, P., Pagès, H., and Gentleman, R.: ShortRead: a bioconductor package for input, quality assessment and exploration of high-throughput sequence data, Bioinformatics, 25, 2607-2608, 10.1093/bioinformatics/btp450, 2009.

Mühlenbruch, M., Grossart, H.-P., Eigemann, F., and Voss, M.: Mini-review: Phytoplankton-derived polysaccharides in the marine environment and their interactions with heterotrophic bacteria, Environmental Microbiology, 20, 2671-2685, https://doi.org/10.1111/1462-2920.14302, 2018.

Murray, B. J., O'Sullivan, D., Atkinson, J. D., and Webb, M. E.: Ice nucleation by particles immersed in supercooled cloud droplets, Chemical Society Reviews, 41, 6519-6554, 10.1039/C2CS35200A, 2012.

Nagata, T., Kirchman, D. (Ed.): Production mechanisms of dissolved organic matter, Microbial Ecology of the Oceans, Wiley-Liss, New York, 121-152 pp.2000.

Norrman, B., Zwelfel, U. L., Hopkinson Jr., C. S., and Brian, F.: Production and utilization of dissolved organic carbon during an experimental diatom bloom, Limnology and Oceanography, 40, 898-907, https://doi.org/10.4319/lo.1995.40.5.0898, 1995.

Osborne, E., J. Richter-Menge, and M. Jeffiries: Arctic Report Card, 2018.

Park, J.-Y., Kug, J.-S., Bader, J., Rolph, R., and Kwon, M.: Amplified Arctic warming by phytoplankton under greenhouse warming, Proceedings of the National Academy of Sciences, 112, 5921-5926, doi:10.1073/pnas.1416884112, 2015.

Pereira Freitas, G., Adachi, K., Conen, F., Heslin-Rees, D., Krejci, R., Tobo, Y., Yttri, K. E., and Zieger, P.: Regionally sourced bioaerosols drive high-temperature ice nucleating particles in the Arctic, Nature Communications, 14, 5997, 10.1038/s41467-023-41696-7, 2023.

Pouleur, S., Richard, C., Martin, J. G., and Antoun, H.: Ice Nucleation Activity in Fusarium acuminatum and Fusarium avenaceum, Appl Environ Microbiol, 58, 2960-2964, 10.1128/aem.58.9.2960-2964.1992, 1992.

Previdi, M., Smith, K. L., and Polvani, L. M.: Arctic amplification of climate change: a review of underlying mechanisms, Environmental Research Letters, 16, 093003, 10.1088/1748-9326/ac1c29, 2021.

Pummer, B. G., Bauer, H., Bernardi, J., Bleicher, S., and Grothe, H.: Suspendable macromolecules are responsible for ice nucleation activity of birch and conifer pollen, Atmos. Chem. Phys., 12, 2541-2550, 10.5194/acp-12-2541-2012, 2012.

Quast, C., Pruesse, E., Yilmaz, P., Gerken, J., Schweer, T., Yarza, P., Peplies, J., and Glöckner, F. O.: The SILVA ribosomal RNA gene database project: improved data processing and web-based tools, Nucleic Acids Research, 41, D590-D596, 10.1093/nar/gks1219, 2012.

Rantanen, M., Karpechko, A. Y., Lipponen, A., Nordling, K., Hyvärinen, O., Ruosteenoja, K., Vihma, T., and Laaksonen, A.: The Arctic has warmed nearly four times faster than the globe since 1979, Communications Earth & Environment, 3, 168, 10.1038/s43247-022-00498-3, 2022.

Ravindran, S., Pant, V., Mitra, A. K., and Kumar, A.: Spatio-temporal variability of sea-ice and ocean parameters over the Arctic Ocean in response to a warming climate, Polar Science, 30, 100721, https://doi.org/10.1016/j.polar.2021.100721, 2021.

Reunamo, A., Szabo, H., Nikinmaa, M., and Leskinen, P.: Comparison of sea surface microlayer and subsurface water bacterial communities in the Baltic Sea, Aquatic Microbial Ecology, 65, 29, 10.3354/ame01532, 2011.

Roeters, S. J., Golbek, T. W., Bregnhoj, M., Drace, T., Alamdari, S., Roseboom, W., Kramer, G., Santl-Temkiv, T., Finster, K., Pfaendtner, J., Woutersen, S., Boesen, T., and Weidner, T.: Ice-nucleating proteins are activated by low temperatures to control the structure of interfacial water, Nat Commun, 12, 1183, 10.1038/s41467-021-21349-3, 2021.

Šantl-Temkiv, T., Gosewinkel, U., Starnawski, P., Lever, M., and Finster, K.: Aeolian dispersal of bacteria in southwest Greenland: their sources, abundance, diversity and physiological states, FEMS Microbiol Ecol, 94, 10.1093/femsec/fiy031, 2018.

Šantl-Temkiv, T., Lange, R., Beddows, D., Rauter, U., Pilgaard, S., Dall'Osto, M., Gunde-Cimerman, N., Massling, A., and Wex, H.: Biogenic Sources of Ice Nucleating Particles at the High Arctic Site Villum Research Station, Environ Sci Technol, 53, 10580-10590, 10.1021/acs.est.9b00991, 2019.

Šantl-Temkiv, T., Sahyoun, M., Finster, K., Hartmann, S., Augustin-Bauditz, S., Stratmann, F., Wex, H., Clauss, T., Nielsen, N. W., Sørensen, J. H., Korsholm, U. S., Wick, L. Y., and Karlson, U. G.: Characterization of airborne ice-nucleation-active bacteria and bacterial fragments, Atmospheric Environment, 109, 105-117, https://doi.org/10.1016/j.atmosenv.2015.02.060, 2015.

Laboratory Ultrafiltration Frequently asked questions: https://www.sartorius.com/download/410706/laboratory-ultrafiltration-faq-2020-1-13-20-pdf-data.pdf, last access: 24/01/2024.

Schwidetzky, R., de Almeida Ribeiro, I., Bothen, N., Backes, A. T., DeVries, A. L., Bonn, M., Fröhlich-Nowoisky, J., Molinero, V., and Meister, K.: Functional aggregation of cell-free proteins enables fungal ice nucleation, Proceedings of the National Academy of Sciences, 120, e2303243120, doi:10.1073/pnas.2303243120, 2023.

Schwidetzky, R., Lukas, M., YazdanYar, A., Kunert, A. T., Pöschl, U., Domke, K. F., Fröhlich-Nowoisky, J., Bonn, M., Koop, T., Nagata, Y., and Meister, K.: Specific Ion–Protein Interactions Influence Bacterial Ice Nucleation, Chemistry – A European Journal, 27, 7402-7407, https://doi.org/10.1002/chem.202004630, 2021.

Serreze, M. C. and Barry, R. G.: Processes and impacts of Arctic amplification: A research synthesis, Global and Planetary Change, 77, 85-96, 10.1016/j.gloplacha.2011.03.004, 2011.

Stoeck, T., Bass, D., Nebel, M., Christen, R., Jones, M. D., Breiner, H. W., and Richards, T. A.: Multiple marker parallel tag environmental DNA sequencing reveals a highly complex eukaryotic community in marine anoxic water, Mol Ecol, 19 Suppl 1, 21-31, 10.1111/j.1365-294X.2009.04480.x, 2010.

Tan, I. and Storelvmo, T.: Evidence of Strong Contributions From Mixed-Phase Clouds to Arctic Climate Change, Geophysical Research Letters, 46, 2894-2902, 10.1029/2018gl081871, 2019.

Terhaar, J., Lauerwald, R., Regnier, P., Gruber, N., and Bopp, L.: Around one third of current Arctic Ocean primary production sustained by rivers and coastal erosion, Nature Communications, 12, 169, 10.1038/s41467-020-20470-z, 2021.

Tesson, S. V. M. and Šantl-Temkiv, T.: Ice Nucleation Activity and Aeolian Dispersal Success in Airborne and Aquatic Microalgae, Front Microbiol, 9, 10.3389/fmicb.2018.02681, 2018.

Thornton, D. C. O.: Dissolved organic matter (DOM) release by phytoplankton in the contemporary and future ocean, European Journal of Phycology, 49, 20-46, 10.1080/09670262.2013.875596, 2014.

Thornton, D. C. O., Brooks, S. D., Wilbourn, E. K., Mirrielees, J., Alsante, A. N., Gold-Bouchot, G., Whitesell, A., and McFadden, K.: Production of ice-nucleating particles (INPs) by fast-growing phytoplankton, Atmospheric Chemistry and Physics, 23, 12707-12729, 10.5194/acp-23-12707-2023, 2023.

Tobo, Y., Adachi, K., DeMott, P. J., Hill, T. C. J., Hamilton, D. S., Mahowald, N. M., Nagatsuka, N., Ohata, S., Uetake, J., Kondo, Y., and Koike, M.: Glacially sourced dust as a potentially significant source of ice nucleating particles, Nature Geoscience, 12, 253-258, 10.1038/s41561-019-0314-x, 2019.

Vader, A., Marquardt, M., Meshram, A. R., and Gabrielsen, T. M.: Key Arctic phototrophs are widespread in the polar night, Polar Biology, 38, 13-21, 10.1007/s00300-014-1570-2, 2015.

Vali, G., Christensen, M., Fresh, R. W., Galyan, E. L., Maki, L. R., and Schnell, R. C.: Biogenic Ice Nuclei. Part II: Bacterial Sources, Journal of Atmospheric Sciences, 33, 1565-1570, 10.1175/1520-0469(1976)033<1565:Binpib>2.0.Co;2, 1976.

Van As, D., Andersen, M. L., Petersen, D., Fettweis, X., Van Angelen, J. H., Lenaerts, J. T. M., Van Den Broeke, M. R., Lea, J. M., Bøggild, C. E., Ahlstrøm, A. P., and Steffen, K.: Increasing meltwater discharge from the Nuuk region of the Greenland ice sheet and implications for mass balance (1960–2012), Journal of Glaciology, 60, 314-322, 10.3189/2014JoG13J065, 2014.

Wetz, M. and Wheeler, P.: Release of Dissolved Organic Matter by Coastal Diatoms, Limnology and Oceanography - LIMNOL OCEANOGR, 52, 798-807, 10.4319/lo.2007.52.2.0798, 2007.

Wieber, C., Rosenhøj Jeppesen, M., Finster, K., Melvad, C., and Šantl-Temkiv, T.: Micro-PINGUIN: microtiter-plate-based instrument for ice nucleation detection in gallium with an infrared camera, Atmos. Meas. Tech., 17, 2707-2719, 10.5194/amt-17-2707-2024, 2024.

Wieber, C., Jensen, L. Z., Vergeynst, L., Maire, L., Juul-Pedersen, T., Finster, K., & Šantl-Temkiv, T.: Dataset to: Terrestrial runoff is the dominant source of a new type of biological INPs observed in Arctic fjords [Data set], Zenodo, https://doi.org/10.5281/zenodo.14044414, 2024.

Wilson, T., Ladino, L., Alpert, P., Breckels, M., Brooks, I., Browse, J., Burrows, S., Carslaw, K., Huffman, J. A., Judd, C., Kilthau, W. P., Mason, R. H., McFiggans, G., Miller, L. A., Nájera, J. J., Polishchuk, E., Rae, S., Schiller, C. L., Si, M., Temprado, J. V., Whale, T. F., Wong, J. P. S., Wurl, O., Yakobi-Hancock, J. D., Abbatt, J. P. D., Aller, J. Y., Bertram, A. K., Knopf, D. A., and Murray, B. J.: A marine biogenic source of atmospheric ice-nucleating particles, Nature, 525, 234-238, 10.1038/nature14986, 2015.

Wurl, O., Miller, L., Röttgers, R., and Vagle, S.: The distribution and fate of surface-active substances in the sea-surface microlayer and water column, Marine Chemistry, 115, 1-9, https://doi.org/10.1016/j.marchem.2009.04.007, 2009.

Xi, Y., Xu, C., Downey, A., Stevens, R., Bachelder, J. O., King, J., Hayes, P. L., and Bertram, A. K.: Ice nucleating properties of airborne dust from an actively retreating glacier in Yukon, Canada, Environmental Science: Atmospheres, 2, 714-726, 10.1039/D1EA00101A, 2022.

Yamamoto-Kawai, M., Tanaka, N., and Pivovarov, S.: Freshwater and brine behaviors in the Arctic Ocean deduced from historical data of δ18O and alkalinity (1929–2002 A.D.), Journal of Geophysical Research: Oceans, 110, https://doi.org/10.1029/2004JC002793, 2005.

Zäncker, B., Cunliffe, M., and Engel, A.: Bacterial Community Composition in the Sea Surface Microlayer Off the Peruvian Coast, Front Microbiol, 9, 10.3389/fmicb.2018.02699, 2018.

Zeppenfeld, S., van Pinxteren, M., Hartmann, M., Bracher, A., Stratmann, F., and Herrmann, H.: Glucose as a Potential Chemical Marker for Ice Nucleating Activity in Arctic Seawater and Melt Pond Samples, Environmental Science & Technology, 53, 8747-8756, 10.1021/acs.est.9b01469, 2019.

Zhang, D.-C., Redzic, M., Schinner, F., and Margesin, R.: Glaciimonas immobilis gen. nov., sp. nov., a member of the family Oxalobacteraceae isolated from alpine glacier cryoconite, International Journal of Systematic and Evolutionary Microbiology, 61, 2186-2190, https://doi.org/10.1099/ijs.0.028001-0, 2011.

Zhu, F., Massana, R., Not, F., Marie, D., and Vaulot, D.: Mapping of picoeucaryotes in marine ecosystems with quantitative PCR of the 18S rRNA gene, FEMS Microbiol Ecol, 52, 79-92, 10.1016/j.femsec.2004.10.006, 2005.