Nitrogen Fixation in Arctic Coastal Waters (Qeqertarsuaq, West Greenland): Influence of Glacial Melt on Diazotrophs, Nutrient Availability, and Seasonal Blooms

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Abstract. The Arctic Ocean is undergoing rapid transformation due to climate change, with decreasing sea ice contributing to a predicted increase in primary productivity. A critical factor determining future productivity in this region is the availability of nitrogen, a key nutrient that often limits biological growth in Arctic waters. The fixation of dinitrogen (N_2) gas, a biological process mediated by diazotrophs, provides a source of new nitrogen to marine ecosystems and has been increasingly recognized as a potential contributor to nitrogen supply in the Arctic Ocean. Historically it was believed to be limited to oligotrophic tropical and subtropical oceans, Arctic N_2 fixation has only garnered significant attention over the past decade, leaving a gap in our understanding of its magnitude, the diazotrophic community, and potential environmental drivers. In this study, we investigated N_2 fixation rates and the diazotrophic community in Arctic coastal waters, using a combination of isotope labeling, genetic analyses and biogeochemical profiling, in order to explore its response to glacial meltwater, nutrient availability and its impact on primary productivity. We observed N_2 fixation rates ranging from 0.16 to 2.71 nmol N L^{-1} d^{-1}, notably higher than many previously reported rates for Arctic waters. The diazotrophic community was predominantly composed of UCYN-A. The highest N_2 fixation rates co-occurred with peaks in chlorophyll *a* and primary production at a station in the Vaigat Strait, likely influenced by glacial meltwater input. On average, N_2 fixation contributed 1.6% of the estimated nitrogen requirement of primary production, indicating that while its role is modest, it may still represent a nitrogen source in certain conditions. These findings illustrate the potential importance of N_2 fixation in an environment previously not considered important for this process and provide insights into its response to the projected melting of the polar ice cover.

1 Introduction

Nitrogen is a key element for life and often acts as a growth-limiting factor for primary productivity (Gruber and Sarmiento, 1997; Gruber, 2004; Gruber and Galloway, 2008). Despite nitrogen gas (N_2) making up approximately 78% of the atmosphere, it remains inaccessible to most marine life forms. Diazotrophs, which are specialized bacteria and archaea, have the ability to convert N_2 into biologically available nitrogen, facilitated by the nitrogenase enzyme complex carrying out the process of biological nitrogen fixation (N_2 fixation) (Capone and Carpenter (1982)). Despite the fact that these organisms are highly spe-

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cialized and N_2 fixation is energetically demanding, the ability to carry out this process is widespread amongst prokaryotes. However, it is controlled by several factors such as temperature, light, nutrients and trace metals such as iron and molybdenum (Sohm et al., 2011; Tang et al., 2019). Oceanic N_2 fixation is the major source of nitrogen to the marine system (Karl et al., 2002; Gruber and Sarmiento, 1997), thus, diazotrophs determine the biological productivity of our planet (Falkowski et al. (2008), impact the global carbon cycle and the formation of organic matter (Galloway et al., 2004; Zehr and Capone, 2020). Traditionally it has been believed that the distribution of diazotrophs was limited to warm and oligotrophic waters (Buchanan et al., 2019; Sohm et al., 2011; Luo et al., 2012) until putative diazotrophs were identified in the central Arctic Ocean and Baffin Bay (Farnelid et al., 2011; Damm et al., 2010). First rate measurements have been reported for the Canadian Arctic by Blais et al. (2012) and recent studies have reported rate measurements in adjacent seas (Harding et al., 2018; Sipler et al., 2017; Shiozaki et al., 2017, 2018), drawing attention to cold and temperate waters as significant contributors to the global nitrogen budget through diverse organisms.

UCYN-A has been described as the dominant active N_2 fixing cyanobacterial diazotroph in arctic waters (Harding et al. (2018)), while other cyanobacteria have only occasionally been reported (Díez et al., 2012; Fernández-Méndez et al., 2016; Blais et al.,) However, other recent studies suggest, that the majority of the arctic marine diazotrophs are NCDs (non-cyanobacterial diazotroph) and those may contribute significantly to N_2 fixation in the Arctic Ocean (Shiozaki et al., 2018; Fernández-Méndez et al., 2016; Harding et al., 2018; Von Friesen and Rie- mann, 2020). Recent work by Robicheau et al. (2023) nearby Baffin Bay, geographically close to the sampling area, document low *nif*H gene abundance while still detecting diazotrophs in Arctic surface waters, highlighting the patchy distribution of diazotrophs across Arctic coastal environments. Studies on the Arctic diazotroph community remain scarce, leaving Arctic environments poorly understood regarding N_2 fixation. Shao et al. (2023) note the impossibility of estimating Arctic N_2 fixation rates due to the sparse spatial coverage, which currently represents only approximately 1 % of the Arctic Ocean. Increasing data coverage in future studies will aid in better constraining the contribution of N_2 fixation to the global oceanic nitrogen budget (Tang et al. (2019)).

The Arctic ecosystem is undergoing significant changes driven by rising temperatures and the accelerated melting of sea ice, a trend predicted to intensify in the future (Arrigo et al., 2008; Hanna et al., 2008; Haine et al., 2015). These climate-driven shifts have stimulated primary productivity in the Arctic by 57 % from 1998 to 2018, elevating nutrient demands in the Arctic Ocean (Ardyna and Arrigo, 2020; Arrigo and van Dijken, 2015; Lewis et al., 2020). This increase is attributed to prolonged phytoplankton growing seasons and expanding ice-free areas suitable for phytoplankton growth (Arrigo et al. (2008)). However, despite these dramatic changes, the role of N_2 fixation in sustaining Arctic primary production remains poorly understood. While recent studies suggest that diazotrophic activity may contribute to nitrogen inputs in polar regions (Sipler et al. (2017)), fundamental uncertainties remain regarding the extend, distribution and environmental drivers of N_2 Fixation in the Arctic Ocean. Specifically, it is unclear whether increased glacial meltwater input enhances or inhibits N_2 Fixation through changes in nutrient availability, stratification, and microbial community composition. Thus, the question of whether nitrogen limitation will emerge as a key factor constraining Arctic primary production under future climate scenarios remains unresolved. In this study, we investigate the diversity of diazotrophic communities alongside in situ N_2 fixation rate measurements in Disko Bay

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Deleted: The Greenland Ice Sheet is strongly affected by climate change and the waters of Baffin Bay have experienced a substantial sea surface temperature (SST) increase of 47.4 % along with a significant increase in chlorophyll *a* (Chl *a*) concentration of 26.4 % over the last two decades (1998-2018) (Lewis et al. (2020)). Coastal sites are particularly impacted by melting, receiving glacial runoff enriched with nutrients and trace elements triggering phytoplankton blooms and altering near-shore biogeochemical cycling (Ardyna and Arrigo, 2020; Arrigo et al., 2017; Hendry et al., 2019; Bhatia et al., 2013).

(Qeqertarsuaq), a coastal Arctic system strongly influenced by glacial meltwater input. By linking environmental parameters to N_2 fixation dynamics, we aim to clarify the role of diazotrophs in Arctic nutrient cycling and assess their potential contribution to sustaining primary production in a changing Arctic. Understanding these processes is essential for refining biogeochemical models and predicting ecosystem responses to future climate change.

2 Material and methods

2.1 Seawater sampling

The research expedition was conducted from August 16 to 26 in 2022 aboard the Danish military vessel P540 within the waters of Qeqertarsuaq, located in the western region of Greenland (Kalaallit Nunaat). Discrete water samples were obtained using a 10 L Niskin bottle, manually lowered with a hand winch to five distinct depths (surface, 5, 25, 50, and 100 m). A comprehensive sampling strategy was employed at 10 stations (Fig. 1), covering the surface to a depth of 100 m. The sampled parameters included water characteristics, such as nutrient concentrations, chl *a*, particulate organic carbon (POC) and nitrogen (PON), molecular samples for nucleic acid extractions (DNA), dissolved inorganic carbon (DIC) as well as CTD sensor data. At three selected stations (3,7,10) N_2 fixation and primary production rates were quantified through concurrent incubation experiments. Samples for nutrient analysis, nitrate (NO_3^-), nitrite (NO_2^-) and phosphate (PO_4^{3-}) were taken in triplicates, filtered through a 0.22 μm syringe filter (Avantor VWR® Radnor, Pa, USA) and stored at -20 ºC until further analysis. Concentrations were spectrophotometrically determined (Thermo Scientific, Genesys 1OS UV-VIS spectrophotometer) following the established protocols of Murphy and Riley (1962) for PO_4^{3-}; García-Robledo et al. (2014) for NO_3^- & NO_2^- (detection limits: 0.01 µmol L^{-1} (NO_3^-, NO_2^-, and PO_4^{3-}), 0.05 µmol L^{-1} (NH_4^+)). Chl *a* samples were filtered onto 47 mm ø GF/F filters (GE Healthcare Life Sciences, Whatman, USA), placed into darkened 15 mL LightSafe centrifuge tubes (Merck, Rahway, NJ, USA) and were subsequently stored at -20 ºC until further analysis. To determine the Chl *a* con- centration, the samples were immersed in 8 mL of 90 % acetone overnight at 5 ºC. Subsequently, 1 mL of the resulting solution was transferred to a 1.5 mL glass vial (Mikrolab Aarhus A/S, Aarhus, Denmark) the following day and subjected to analysis using the Triology® Fluorometer (Model #7200-00) equipped with a Chl *a* in vivo blue module (Model #7200-043, both Turner Designs, San Jose, CA, USA). Measurements of serial dilutions from a 4 mg L^{-1} stock standard and 90 % acetone (serving as blank) were performed to calibrate the instrument. In addition, measurements of a solid-state secondary standard were performed every 10 samples. Water (1 L) water from each depth was filtered for the determination of POC and PON concentrations, as well as natural isotope abundance (δ^{13}C POC / δ^{15}N PON) using 47 mm ø, 0.7μm nominal pore size precombusted GF/F filter (GE Healthcare Life Sciences, Whatman, USA), which were subsequently stored at -20 ºC until further analysis. Seawater samples for DNA were filtered through 47 mm ø, 0.22 μm MCE membrane filter (Merck, Millipore Ltd., Ireland) for a maximum of 20 minutes, employing a gentle vacuum (200 mbar). The filtered volumes varied depending

on the amount of material captured on the filter, ranging from 1.3 L to 2 L, with precise measurements recorded. The filters were promptly stored at -20 ºC on the ship and moved to -80 ºC upon arrival to the lab until further analysis.

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We explored the diazotroph diversity in combination with N_2 fixation rate measurements, to elucidate the importance of this process in the Arctic ecosystem. We hope that understanding the dynamics of N_2 fixation and its impact on the ecosystem pro- ductivity can inform predictions and help managing the consequences of ongoing environmental changes in the Arctic Ocean. Our study has been carried out in Disko Bay (Qeqertarsuaq), which can serve as a model for Arctic coastal systems influenced by large meltwater runoff and thus potentially an addition of high levels of iron and nutrients, both of which have the ability to affect N_2 fixation (Lewis et al., 2020; Bhatia et al., 2013).¶

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To achieve detailed vertical profiles, a conductivity-temperature-depth-profiler (CTD, Seabird X) equipped with supplementary sensors for dissolved oxygen (DO), photosynthetic active radiation (PAR), and fluorescence (Flourometer) was manually deployed.

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2.2 Nitrogen fixation and primary production

Water samples were collected at three distinct depths (0, 25 and 50 m) for the investigation of N_2 fixation rates and primary production rates, encompassing the euphotic zone, chlorophyll maximum, and a light-absent zone. Three incubation stations (Fig. 2: station 3, 7, 10) were chosen, in a way to cover the variability of the study area. This strategic sampling aimed to capture a gradient of the water column with varying environmental conditions, relevant to the aim of the study. N_2 fixation rates were assessed through triplicate incubations employing the modified ^{15}N-N_2 dissolution technique after Großkopf et al. (2012) and Mohr et al. (2010).

To ensure minimal contamination, 2.3 L glass bottles (Schott-Duran, Wertheim, Germany) underwent pre-cleaning and acid washing before being filled with seawater samples. Oxygen contamination during sample collection was mitigated by gently and bubble-free filling the bottles from the bottom, allowing the water to overflow. Each incubation bottle received a 100 mL amendment of ^{15}N-N_2 enriched seawater (98 %, Cambridge Isotope Laboratories, Inc.,USA) achieving an average dissolved N_2 isotope abundance (^{15}N atom %) of 3.90 ± 0.02 atom % (mean ± SD). Additionally, 1 mL of $H^{13}CO_3$ (1g/50 mL) (Sigma-Aldrich, Saint Louis Missouri US) was added to each incubation bottle, roughly corresponding to 10 atom % enrichment and thus measurements of primary production and N_2 fixation were conducted in the same bottle. Following the addition of both isotopic components, the bottles were closed airtight with septa-fitted caps and incubated for 24 hours on-deck incubators with a continuous surface seawater flow. These incubators, partially shaded (using daylight-filtering foil) to simulate in situ photosynthetically active radiation (PAR) conditions, aimed to replicate environmental parameters experienced at the sampled depths. Control incubations utilizing atmospheric air served as controls to monitor any natural changes in $\delta^{15}N$ not attributable to ^{15}N-N_2 addition. These control incubations were conducted using the dissolution method, like the ^{15}N-N_2 enrichment experiments, but with the substitution of atmospheric air instead of isotopic tracer.

After the incubation period, subsamples for nutrient analysis were taken from each incubation sample, and the remaining content was subjected to the filtration process and were gently filtered (200 mbar) onto precombusted GF/F filters (Advantec, 47 mm ø, 0.7 μm nominal pore size). This step ensured a comprehensive examination of both nutrient dynamics and the isotopic composition of the particulate pool in the incubated samples. Samples were stored at -20 ºC until further analysis.

Upon arrival in the lab, the filters were dried at 60 ºC and to eliminate particulate inorganic carbon, subsequently subject to acid fuming during which they were exposed to concentrated hydrochloric acid (HCL) vapors overnight in a desiccator. After undergoing acid treatment, the filters were carefully dried, then placed into tin capsules and pelletized for subsequent analysis. The determination of POC and PON, as well as isotopic composition ($\delta^{13}C$ POC / $\delta^{15}N$ PON), was carried out using an elemental analyzer (Flash EA, ThermoFisher, USA) connected to a mass spectrometer (Delta V Advantage Isotope Ratio MS, ThermoFisher, USA) with the ConFlo IV interface. This analytical setup was applied to all filters. These values, derived from

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2.3 Molecular methods

The filters were flash-frozen in liquid nitrogen, crushed and DNA was extracted using the Qiagen DNA/RNA AllPrep Kit (Qiagen, Hildesheim, DE), following the procedure outlined by the manufacturer. The concentration and quality of the extracted DNA was assessed spectrophotometrically using a MySpec spectrofluorometer (VWR, Darmstadt, Germany). The preparation of the metagenome library and sequencing were performed by BGI (China). Sequencing libraries were generated using MGIEasy Fast FS DNA Library Prep Set following the manufacturer's protocol. Sequencing was conducted with 2x150bp on a DNBSEQ-G400 platform (MGI). SOAPnuke1.5.5 (Chen et al. (2018)) was used to filter and trim low quality reads and adaptor contaminants from the raw sequence reads, as clean reads. In total, fifteen metagenomic datasets were produced with an average of 9.6G bp per sample.

2.3.1 Metagenomic De Novo assembly, gene prediction, and annotation

Megahit v1.2.9 (Li et al. (2015)) was used to assemble clean reads for each dataset with its minimum contig length as 500. Prodigal v2.6.3 (Hyatt et al. (2010)) with the setting of "-p meta" was then used to predict the open reading frames (ORFs) of the assembled contigs. ORFs from all the available datasets were filtered (>100bp), dereplicated and merged into a catalog of non-redundant genes using cd-hit-est (>95 % sequence identity) (Fu et al. (2012)). Salmon v1.10.0 (Patro et al. (2017)) with the "– meta" option was employed to map clean reads of each dataset to the catalog of non-redundant genes and generate the GPM (genes per million reads) abundance. Eggnog mapper v2.1.12 (Cantalapiedra et al. (2021)) was then performed to assign KEGG Orthology (KO) and identify specific functional annotation for the catalog of non-redundant genes. The marker genes, *nif*DK (K02586, K02591 nitrogenase molybdenum-iron protein alpha/beta chain) and *nif*H (K02588, nitrogenase iron protein), were used for the evaluation of microbial potential of N_2 fixation. *Rbc*L (K01601, ribulose-bisphosphate carboxylase large chain) and *psb*A (K02703, photosystem II P680 reaction center D1 protein) were selected to evaluate the microbial potential of carbon fixation and photosynthesis, respectively. The molecular datasets have been deposited with the accession number: Bioproject PRJNA1133027.

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3 Results and discussion

3.1 Hydrographic conditions in Qeqertarsuaq (Disco Bay) and Sullorsuaq (Vaigat) Strait

Disko Bay (Qeqertarsuaq) is located along the west coast of Greenland (Kalaallit Nunaat) at approximately 69 °N (Figure 1), and is strongly influenced by the West Greenland Current (WGC) which is associated with the broader Baffin Bay Polar Waters (BBPW) (Mortensen et al., 2022; Hansen et al., 2012). The WGC does not only significantly shape the hydrographic conditions within the bay but also plays an important role in the larger context of Greenland Ice Sheet melting (Mortensen et al. (2022)). Central to the hydrographic system of the Qeqertarsuaq area is the Jakobshavn Isbræ, which is the most productive glacier in the northern hemisphere and believed to drain about 7 % of the Greenland Ice Sheet and thus contributes substantially to the water influx into the Qeqertarsuaq (Holland et al. (2008)). A predicted increased inflow of warm subsurface water, originating from North Atlantic waters, has been suggested to further affect the melting of the Jakobshavn Isbræ and thus adds another layer of complexity to this dynamic system (Holland et al., 2008; Hansen et al., 2012).

The hydrographic conditions in Qeqertarsuaq have a significant influence on biological processes, nutrient availability, and the

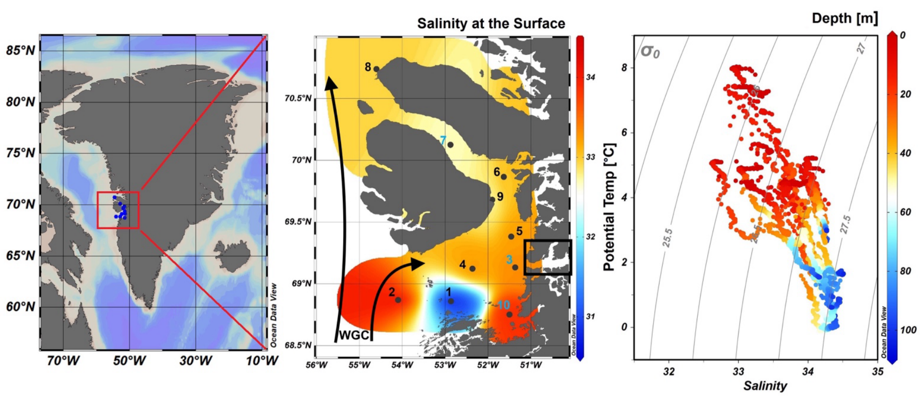

Figure 1. Map of Greenland (Kalaallit Nunaat) with indication of study area (red box), on the left. Interpolated distribution of Sea Surface Salinity (SSS) values with corresponding isosurface lines and indication of 10 sampled stations (normal stations in black, incubation stations in blue), black arrows indicate the West Greenland Current (WGC) and the black box indicate the location of the Jakobshavn Isbræ, in the middle. Scatterplot of the potential temperature and salinity for all station data. The plot is used for the identification of the main water masses within the study area. Isopycnals (kg m^{-3}) are depicted in grey lines, on the right. Figures were created in Ocean Data View (ODV) (Schlitzer (2022)).

broader marine ecosystem (Munk et al., 2015; Hendry et al., 2019; Schiøtt, 2023).

During our survey, we found very heterogenous hydrographic conditions at the different stations across Qeqertarsuaq (Fig. 1 & Fig. 2). The three selected stations for N_2 fixation analysis (stations 3, 7, and 10) were strategically chosen to capture the spatial variability of the area. Surface salinity and temperature measurements at these stations indicate the influence of freshwater input. The surface temperature exhibit a range of 4.5 to 8 ºC, while surface salinity varies between 31 and 34, as illustrated in Fig. 1. The profiles sampled during our survey extend to a maximum depth of 100 m. Comparison of temperature/salinity (T/S) plots with recent studies suggests the presence of previously described water masses, including Warm Fjord Water (WFjW)

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and Cold Fjord Water (CFjW) with an overlaying surface glacial meltwater runoff. Those water masses are defined with a density range of 27.20 ≤ σ_θ ≤ 27.31 but different temperature profiles. Thus water masses can be differentiated by their temperature within the same density range (Gladish et al. (2015)). Other water masses like upper subpolar mode water (uSPMW), deep subpolar mode water (dSPMW) and Baffin Bay polar Water (BBPW) which has been identified in the Disko Bay (Qeqertarsuaq) before, cannot be identified from this data and may be present in deeper layers (Mortensen et al., 2022; Sherwood et al., 2021; Myers and Ribergaard, 2013; Rysgaard et al., 2020). The temperature and salinity profiles across the 10

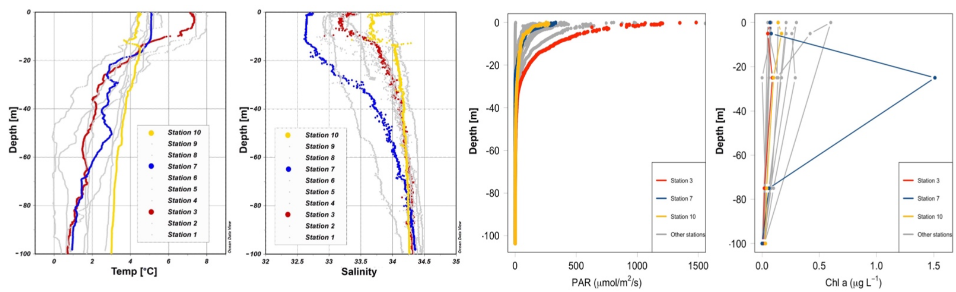

Figure 2. Profiles of temperature (ºC), salinity, photosynthetically active radiation (PAR) (µmol/m²/s) and Chl *a* (mg m^{-3}) across stations 1 to 10 with depth (m). Stations 3, 7, and 10 are highlighted in red, blue, and yellow, respectively, to emphasize incubation stations. Figures were created in Ocean Data View and R-Studio (Schlitzer (2022)).

stations in the study area show distinct stratification and variability, which is represented through the three incubation stations (highlighted stations 3, 7, and 10 in Fig. 2). They display varying degrees of stratification and mixing, with notable differences in the salinity and termperature profiles. Station 3 and station 7 exhibit clear stratification in both temperature and salinity marked by the presence of thermoclines and haloclines. These features suggest significant freshwater input influenced by local weather conditions and climate dynamics, like surface heat absorption. In contrast, Station 10 exhibits a narrower range of temperature and salinity values throughout the water column compared to Stations 3 and 7, indicating more well-mixed conditions. This uniformity is likely influenced by the regional circulation pattern and partial upwelling (Hansen et al., 2012; Krawczyk et al., 2022). The distinct characteristics observed at station 10, as illustrated in the surface plot (Fig. 1), show an elevated salinity and colder temperatures compared

to the other stations. This feature suggests upwelling of deeper waters along the shallower shelf, likely facilitated by the local seafloor topography. Specifically, the seafloor shallowing off the coast of Station 10 may act as a barrier, disrupting typical circulation and forcing deeper, saltier, and colder waters to the surface. This pattern aligns with previous studies that describe similar mechanisms in the region (Krawczyk et al. (2022)). Their description of the bathymetry in Qeqertarsuaq, featuring depths ranging from ca. 50 to 900 m, suggests its impact on turbulent circulation patterns, leading to the mixing of different

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Deleted: likely influenced by the seafloor shallowing off the coast of station 10, which acts as a barrier and disrupts typical circulation. The presence of water masses forced to the surface due to this topographical feature may explain the observed properties at station 10. Furthermore, the variability in temperature and salinity conditions between stations, particularly in relation to topography, aligns with the findings of water masses. Evident variability in oceanographic conditions that can be observed throughout the study area occurs particularly along characteristic topographical features like steep slopes, canyons, and shallower areas. The summer melting of sea ice and glaciers introduces freshwater influxes that create distinct vertical and horizontal gradients in salinity and temperature in the Qeqertarsuaq area Hansen et al. (2012). Additionally, the accelerated melting of the Jakobshavn Isbræ, influenced by the warmer inflow from the West Greenland Intermediate Current (WGIC), further alters the hydrographic conditions. Recent observations indicate significant warming and shoaling of the WGIC, potentially enabling it to overcome the sill separating the Illulissat Fjord from the Qeqertarsuaq area (Hansen et al., 2012; Holland et al., 2008; Myers and Ribergaard, 2013). This shift intensifies glacier melting, driving substantial changes in the local ecological dynamics (Ardyna et al., 2014; Arrigo et al., 2008; Bhatia et al., 2013).

3.2 N_2 Fixation Rate Variability and Associated Environmental Conditions

We quantified N_2 fixation rates within the waters of Qeqertarsuaq, spanning from the surface to a depth of 50 m (Table 1). The rates ranged from 0.16 to 2.71 nmol N L^{-1} d^{-1} with all rates surpassing the minimum quantifiably rate (Appendix Table 1). Our findings represent rates at the upper range of those observed in the Arctic Ocean. Previous measurements in the region have been limited, with only one study in Baffin Bay by Blais et al. (2012), reporting rates of 0.02 nmol N L^{-1} d^{-1}, which are 1-2 orders of magnitude lower than our observations. Moreover, Sipler et al. (2017), reported rated in the coastal Chukchi Sea, with average values of 7.7 nmol N L^{-1} d^{-1} . These values currently represent some of the highest rates measured in Arctic shelf environments. Compared to these, our highest measured rate (2.71 nmol N L^{-1} d^{-1}) is lower, but still important, particularly considering the more Atlantic-influenced location of our study site. Sipler et al. (2017) also noted that a significant fraction of diazotrophs were <3 µm in size, suggesting that small unicellular diazotrophs play a dominant role in Arctic nitrogen fixation. Altogether, our data contribute to the growing evidence that N_2 fixation is a widespread and potentially significant nitrogen source across various Arctic regions. Simultaneous primary production rate measurements ranged from 0.07 to 3.79 µmol N L^{-1} d^{-1}, with the highest rates observed at station 7 and generally higher values in the surface layers. Employing Redfield stoichiometry, the measured N_2 fixation rates accounted for 0.47 to 2.6 % (averaging 1.57 %) of primary production at our stations. The modest contribution to primary production suggests that N_2 fixation does not exert a substantial influence on the productivity of these waters during the time of the sampling. Rather, our N_2 fixation rates suggest primary production to depend mostly on additional nitrogen sources including regenerated, meltwater or land based sources.

The N:P ratio, calculated as DIN to DIP, indicates a deficit in N for primary production based on Redfield stoichiometry (Fig. 3). This aligns with findings presented by Jensen et al. (1999) and Tremblay and Gagnon (2009), who observed a similar nitrogen limitation in this region. Such biogeochemical conditions would be expected to generate a niche for N_2 fixing organisms (Sohm et al. (2011)). While N_2 fixation did not chiefly sustain primary production during our sampling campaign, we hypothesize that N_2 fixation has the potential to play a role in bloom dynamics under certain conditions. As nitrogen availability decreases

during a bloom, it may provide a niche for N_2 fixation, potentially helping to extend the productive period of the bloom period

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0.12 nmol N L^{-1} d^{-1}, (SD ± 0.09 to 0.09) (Blais et al. (2012)). However, we observed some of the highest rates reported so far,
particularly at the surface.

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(Reeder et al. (2021)). Satellite data indicates that a fall bloom began in early August, following the annual spring bloom, as described by Ardyna et al. (2014). This double bloom situation may be driven by increased melting and the subsequent input of bioavailable nutrients and iron (Fe) from meltwater runoff (Arrigo et al., 2017; Hopwood et al., 2016; Bhatia et al., 2013). The meltwater from the Greenland Ice Sheet is a significant source of Fe (Bhatia et al., 2013; Hawkings et al., 2015, 2014), which is a limiting factor especially for diazotrophs (Sohm et al. (2011)). Consequently, it is plausible that Fe and nutrients from the Isbræ glacier create favorable conditions for both bloom development and diazotroph activity in Qeqertarsuaq. However, we emphasize that confirming a causal link between N_2 fixation and secondary bloom development requires further evidence, such as time-series data on nutrient concentrations, diazotroph abundance, and bloom dynamics.

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Table 1. N_2 fixation (nmol N L^{-1} d^{-1}), standard deviation (SD), primary productivity (PP; μmol C L^{-1} d^{-1}), SD, percentage of estimated new primary productivity (% New PP) sustained by N_2 fixation, dissolved inorganic nitrogen compounds (NO_x), phosphorus (PO_4), and the molar nitrogen-to-phosphorus ratio (N:P) at stations 3, 7, and 10.

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Station (no.)	Depth (m)	N_2 fixation (nmol N L^{-1} d^{-1})	SD (±)	Primary Productivity (μmol C L^{-1} d^{-1})	SD (±)	% New PP (%)	NO_x (μmol L^{-1} d^{-1})	PO_4 (μmol L^{-1} d^{-1})
3	0	1.20	0.21	0.466	0.08	1.71	0	0
3	25	1.88	0.11	0.588	0.04	2.11	0	0.70
3	50	0.29	0.01	0.209	0.00	0.91	0.33	1.48
7	0	2.49	0.44	0.63	0.20	2.60	0	0
7	25	2.71	0.22	3.79	2.45	0.47	0	0.45
7	50	0.53	0.24	0.33	0.36	1.08	0	0.97
10	0	1.48	0.12	0.74	0.15	1.33	0	0
10	25	0.31	0.01	0.29	0.07	0.73	0	0
10	50	0.16	0	0.07	0.07	1.40	0	0

A near-Redfield stoichiometry in POC:PON indicates that the particulate organic matter (POM) is freshly derived from an ongoing phytoplankton bloom, as phytoplankton generally assimilate carbon and nitrogen in relatively consistent proportions during active growth. In contrast, deviations from the Redfield ratio (e.g., elevated C:N or C:P) typically indicate microbial degradation and preferential remineralization of nitrogen and phosphorus (Redfield 1934; Geider and La Roche 2002; Sterner and Elser 2017). The absence of NOx and the observed low N:P ratios suggest that nitrogen from earlier bloom phases has been largely depleted, potentially creating a niche for N_2 fixation as a supplementary nitrogen source. The onset and development of the bloom would be expected to lead to high nitrogen demands and intense competition for nitrogen sources. Notably, despite the apparent balance in the POM pool, the N:P ratio indicates strong nitrogen depletion and nutrient exhaustion within the ecosystem. This deficiency can be partly alleviated by N_2 fixation, providing possibly increasing amounts of nitrogen

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over the course of the bloom. Moreover, DIP is generally limited in the environment (Table 1); however, some organisms may still access it through luxury phosphorus uptake, storing excess phosphate when it is sporadically available. A recent study by Laso Perez et al. (2024) documented changes in microbial community composition during an Arctic bloom, focusing on nitrogen cycling. They observed a shift from chemolithotrophic to heterotrophic organisms throughout the summer bloom and noted increased activity to compete for various nitrogen sources. However, no *nif* H gene copies, indicative of nitrogen-fixing organisms, were found in their dataset based on metagenome-assembled genomes (MAGs). This is not unexpected due to the classically low abundance of diazotrophs in marine microbial communities which has often been described (Turk-Kubo et al., 2015; Farnelid et al., 2019). Given the high productivity and metabolic activity observed in Qeqertarsuaq during a similar bloom period, the detected diazotrophs (Section 3.3) may play a more significant role than previously thought. Across the 10 stations there is considerable variability in POC and PON concentrations (Fig. 3). PON concentrations range from 0.0 µmol N L^{-1} to 3.48 µmol N L^{-1} (n=124), while POC concentrations range from 2.7 µmol C L^{-1} to 27.2 µmol C L^{-1} (n=144). The highest concentrations for both PON and POC were observed at station 7 at a depth of 25 m and coincide with the highest reported N_2 fixation rate (Figure Appendix A2 & A3). Generally, POC and PON concentrations decrease with depth, peaking at the deep chl *a* maximum (DCM), identified between 15 to 30 m across all stations. The DCM was identified based on measured chl *a* concentrations and previous descriptions in the region (Fox and Walker, 2022; Jensen et al., 1999). The variability in chl *a* concentrations indicates differences in phytoplankton abundance among the stations, with concentrations ranging between 0 to 0.42 mg m^{-3}. Excluding station 7, which exhibited the highest chl *a* concentration at the DCM (1.51 mg m^{-3}). While Tang et al. (2019) found that N_2 fixation measurements strongly correlated to satellite estimates of chl *a* concentrations, our results did not show a statistically significant correlation between nitrogen fixation rates and chl a concentrations overall (Figures A2 & A3). However, as noted, Station 7 at 25 m represents a unique case. The elevated concentration of chl a at this station likely resulted from a local phytoplankton bloom induced by meltwater outflow from the Isbræ glacier and sea ice melting, which may help explain the observed nitrogen fixation rates (Arrigo et al., 2017; Wang et al., 2014). This study's findings are in agreement with prior reports of analogous blooms occurring in the region (Fox and Walker, 2022; Jensen et al., 1999).

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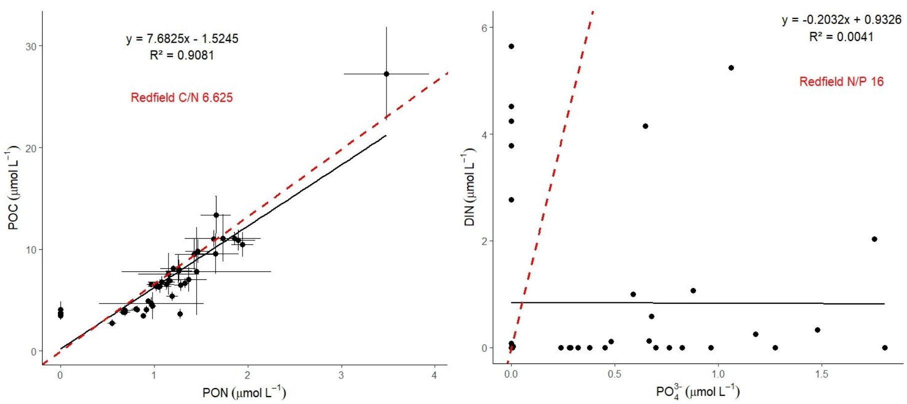

Figure 3. The POC/PON and DIN/DIP ratios at all 10 stations. The red line represents the Redfield ratios of POC/PON (106:16) and DIN/DIP (16:1).

3.3 Potential Contribution of UCYN-A to Nitrogen Fixation During a Diatom Bloom: Insights and Uncertainties

In our metagenomic analysis, we filtered the *nif*H, *nif*D, *nif*K genes, which code for the nitrogenase enzyme responsible for catalyzing N_2 fixation. We could identify sequences related to UCYN-A, which dominated the sequence pool of diazotrophs, particularly in the upper water masses (0 to 5 m) (Fig. 4). UCYN-A, a unicellular cyanobacterial symbiont, has a cosmopolitan distribution and is thought to substantially contribute to global N_2 fixation, as documented by (Martínez-Pérez et al., 2016; Tang et al., 2019). This conclusion is based on our metagenomic analysis, in which we set a sequence identity threshold of 95% for both *nif* and photosystem genes. Notably, we only recovered sequences related to UCYN-A within our *nif* sequence pool, suggesting its predominance among detected diazotrophs. However, metagenomic approaches may underestimate overall diazotroph diversity, and we cannot fully exclude the presence of other, less abundant diazotrophs thatmay have been missed using this method. While UCYN-A was primarily detected in surface waters, we also observed relatively high *nifK* values at S3_100m, an unusual finding given that UCYN-A is typically constrained to the euphotic zone. Previous studies have predominantly reported UCYN-A in surface waters; for instance Harding et al. (2018) and Shiozaki et al. (2017) detected UCYN-A exclusively in the upper layers of the Arctic Ocean. Additionally, Shiozaki et al. (2020) found UCYN-A2 at depths extending to the 0.1% light level but not below 66 m in the Chukchi Sea. The detection of UCYN-A at 100 m in our study suggests that alternative mechanisms, such as particle association, vertical transport, or local environmental conditions, may

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facilitate its presence at depth. Interestingly, despite very low *nif*H copy numbers being reported in nearby Baffin Bay by Robicheau et al. (2023), UCYN-A dominated the metagenomic *nif*H community in our study, further underscoring this organisms's presence in Arctic surface coastal areas under certain environmental conditions. This warrants further investigation into the environmental drivers and potential processes enabling its occurrence in Arctic waters.

Due to the lack of genes such as those encoding Photosystem II and Rubisco, UCYN-A plays a significant role within the host cell and participates in fundamental cellular processes. Consequently it has evolved to become a closely integrated component of the host cell. Very recent findings demonstrate that UCYN-A imports proteins encoded by the host genome and has been described as an early form of N_2 fixing organelle termed a "Nitroplast" (Coale et al. (2024)).

Previous investigations document that they are critical for primary production, supplying up to 85% of the fixed nitrogen to their haptophyte host (Martínez-Pérez et al. (2016)). In addition to its high contribution to primary production, studies have shown that UCYN-A in high latitude waters fix similar amounts of N_2 per cell as in the tropical Atlantic Ocean, even in nitrogen-replete waters (Harding et al., 2018; Shiozaki et al., 2020; Martínez-Pérez et al., 2016; Krupke et al., 2015; Mills et al., 2020). However, estimating their contribution to N_2 fixation in our study is challenging, particularly since we detected cyanobacteria only at the surface but observe significant N_2 fixation rates below 5 m. The diazotrophic community is often underrepresented in metagenomic datasets due to the low abundance of nitrogenase gene copies, implying our data does not present a complete picture. We suspect a more diverse diazotrophic community exists, with UCYN-A being a significant contributor to N_2 fixation in Arctic waters. However, the exact proportion of its contribution requires further investigation.

The contribution of N_2 fixation to carbon fixation (as percent of PP) is relatively low, at the time of our study. We identified genes such as *rbc*L, which encodes Rubisco, a key enzyme in the carbon fixation pathway and *psb*A, a gene encoding Photosystem II, involved in light-driven electron transfer in photosynthesis, in our metagenomic dataset. The gene *rbc*L (for the carbon fixation pathway) and the gene *psb*A (for primary producers) were used to track the community of photosynthetic primary producers in our metagenomic dataset. At station 7, elevated carbon fixation rates are correlated with high diatom (*Bacillariophyta*) abundance and increased chl *a* concentration (Fig. 4), suggesting the onset of a bloom, which is also observable via satellite images (Appendix A1). We hypothesize that meltwater, carrying elevated nutrient and trace metal concentrations, was rapidly transported away from the glacier through the Vaigat Strait by strong winds, leading to increased productivity, as previously described by Fox and Walker (2022) & Jensen et al. (1999). The elevated diatom abundance and primary production rates at station 7 coincide with the highest N_2 fixation rates, which could possibly point toward a possible diatom-diazotroph symbiosis (Foster et al., 2022, 2011; Schvarcz et al., 2022). However, we did not detect a clear diazotrophic signal directly associated with the diatoms in our metagenomic dataset, which might be due to generally underrepresentation of diazotrophs in metagenomes due to low abundance or low sequencing coverage. To investigate this further, we examined the taxonomic composition of *Bacillariophyta* at higher resolution. Among the various abundant diatom genera, *Rhizosolenia* and *Chaetoceros* have been identified as symbiosis with diazotrophs (Grosse, *et al.*, 2010; Foster, et al., 2010), representing less than 6% or 15% of *Bacillariophyta*, based on *rbc*L or *psb*A, respectively (Figure Appendix A4). Although we underestimate diazotrophs to an extent, the presence of certain diatom-diazotroph symbiosis could help

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explain the high nitrogen fixation rates in the diatom bloom to a certain degree. Compilation of *nif* sequences identified from this study as well as homologous from their NCBI top hit were added in Table S1. However, we cannot tell if the diazotrophs belong to UCYN-A1 or UCYN-A2, or UCYN-A3. Based on the Pierella Karlusich et al. (2021), they generated clonal *nif*H sequences from Tara Oceans, which the length of *nif*H sequences is much shorter than the two *nif*H sequences we generated in our study. Also, the available UCYN-A2 or UCYN-A3 *nif*H sequences from NCBI were shorter than the two *nif*H sequences we generated. Therefore, it would be not accurate to assign the *nif*H sequences to either group under UCYN-A. Furthermore, not much information is available regarding the different groups of UCYN-A using marker genes of *nif*D and *nif*K.

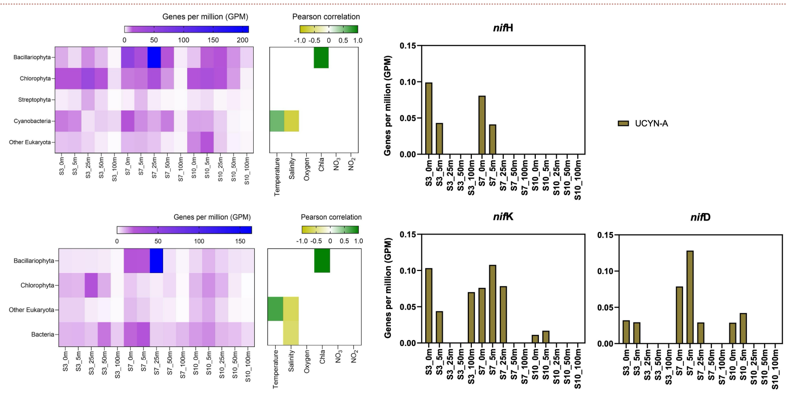

Figure 4. Upper left image: *psb*A with correlation plot. Lower left image: *rbc*L with correlation plot. Right image: *nif*H, *nif*D, *nif*K genes per million reads in the metagenomic datasets. All figures display molecular data from metagenomic dataset for all sampled depth of station 3,7,10

There is evidence that UCYN-A have a higher Fe demand, with input through meltwater or river runoff potentially being advantageous to those organisms (Shiozaki et al., 2017, 2018; Cheung et al., 2022). Consequently, UCYN-A might play a more critical role in the future with increased Fe-rich meltwater runoff. UCYN-A can potentially fuel primary productivity by supplying nitrogen, especially with increased melting, nutrient inputs, and more light availability due to rising temperatures associated with climate change. This predicted enhancement of primary productivity may contribute to the biological drawdown of CO_2, acting as a negative feedback mechanism. These projections are based on studies forecasting increased temperatures, melting, and resulting biogeochemical changes leading to higher primary productivity. However large uncertainties make predictions very difficult and should be handled with care. Thus we can only hypothesize that UCYN-A might be coupled to these

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dynamics by providing essential nitrogen.

3.4 δ^{15}N Signatures in particulate organic nitrogen show no clear evidence of nitrogen fixation

Stable isotopic composition, expressed using the δ^{15}N notation, serve as indicators for understanding nitrogen dynamics because different biogeochemical processes fractionate nitrogen isotopes in distinct ways (Montoya (2008)). However, it is important to keep in mind that the final isotopic signal is a combination of all processes and an accurate distinction between processes cannot be made. N_2 fixation tends to enrich nitrogenous compounds with lighter isotopes, producing OM with isotopic values ranging approximately from -2 to +2 ‰(Dähnke and Thamdrup (2013)). Upon complete remineralization and oxidation, organic matter contributes to a reduction in the average δ-values in the open ocean (e.g.Montoya et al. (2002); Emeis et al. (2010)). Whereas processes like denitrification and anammox preferentially remove lighter isotopes, leading to enrichment in heavier isotopes and delta values up to -25 ‰.

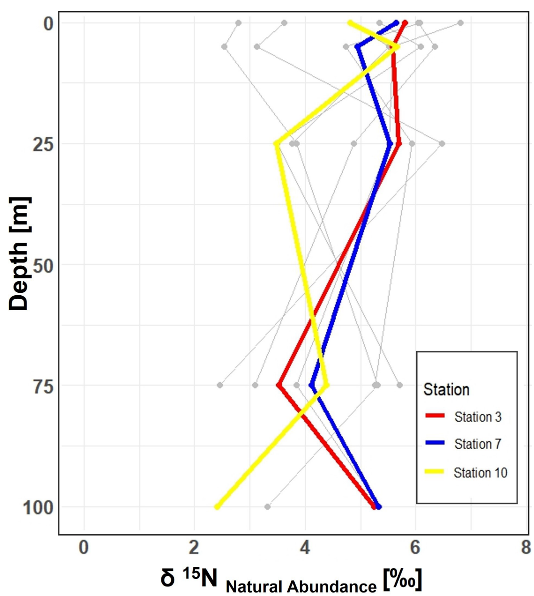

Figure 5. Vertical profiles of δ^{15}N natural abundance signatures in PON across 10 stations in the study area. Incubation stations 3, 7, and 10 are highlighted in red, blue, and yellow, respectively. The figure shows variations in δ^{15}N signatures with depth at each station, providing

insight into nitrogen cycling in the study area.

Thus, $\delta^{15}N$ values help to identify different processes of the nitrogen cycle generally present in a system (Dähnke and Thamdrup (2013)). In our study, the $\delta^{15}N$ values of PON from all 10 stations, range between 2.45 ‰ and 8.30 ‰ within the 0 to 100 m depth range, thus do not exhibit a clear signal indicative of N_2 fixation. This suggests that N_2 fixation may contributes only a certain fraction to export production or that it might have begun to play a role in isotopic fractionation during later stages of the bloom. However, due to the limited temporal resolution and lack of direct measurements of N sources over time, we cannot confirm this dynamic. Additional data – including time-series isotopic profiles and turnover measurements of subsurface nitrate and diazotroph activity – would be needed to establish a causal link between N_2 fixation and the observed isotopic patterns in the bloom context. The composition of OM in the surface ocean is influenced by the nitrogen substrate and the fractionation factor during photosynthesis. When nitrate is depleted in the surface ocean, the isotopic signature of OM produced during photosynthesis will mirror that of the nitrogen substrate. This substrate can originate from either nitrate in the subsurface or N_2 fixation. Notably, nitrate, the primary form of dissolved nitrogen in the open ocean, typically exhibits an average stable isotope value of around 5 ‰. No fractionation occurs during photosynthesis because the nitrogen source is entirely taken up in the surface waters (Sigman et al. (2009)). In Qeqertarsuaq, where similar conditions prevail, this suggests that factors other than N_2 fixation are influencing the observed δ-values and POM is sustained by nitrogen sources from deeper subsurface waters, as observed in earlier studies (Fox and Walker (2022)).

In the eastern Baffin Bay waters, Atlantic water masses serve as an important source of nitrate for sustaining primary productivity, which is also reflected in the nitrogen isotopic signature in this study (Sherwood et al. (2021)). The influx of Atlantic waters, characterized by NO_3^- values of approximately 5 ‰, closely matches the $\delta^{15}N$ values of observed PON concentrations in our study. This suggests that Atlantic-derived NO_3^- serves as a primary source of new nitrogen to the initial stages of bloom development (Fox and Walker, 2022; Knies, 2022). The mechanisms through which subsurface nitrate reaches the euphotic layer are not well understood. However, potential pathways include vertical migration of phytoplankton and physical mixing. Subsequently, nitrogen undergoes rapid recycling and remineralization processes to meet the system's nitrogen demands (Jensen et al. (1999)).

4 Conclusion

Our study highlights the occurrence of elevated rates of N_2 fixation in Arctic coastal waters, particularly prominent at station 7, where they coincide with high chl *a* values, indicative of heightened productivity. Satellite observations tracing the origin of a bloom near the Isbræ Glacier, subsequently moving through the Vaigat strait, suggest a recurring phenomenon likely triggered by increased nutrient-rich meltwater originating from the glacier. This aligns with previous reports by Jensen et al. (1999) & Fox and Walker (2022), underlining the significance of such events in driving primary productivity in the region. The contribution of N_2 fixation to primary production was low (average 1.57 %) across the stations. Since the demand was high relative to

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the new nitrogen provided by N_2 fixation, the observed primary production must be sustained by the already present or adequate amount of subsurface supply of NO_x nutrients in the seawater. This is also visible in the isotopic signature of the POM (Fox and Walker, 2022; Sherwood et al., 2021). However, the detected N_2 fixation rates are likely linked to the development of the fresh secondary summer bloom, which could be sustained by high nutrient and Fe availability from melting, potentially leading the system into a nutrient-limited state. The ongoing high demand for nitrogen compounds may suggest an onset to further sustain the bloom, but it remains speculative whether Fe availability definitively contributes to this process. The occurrence of such double blooms has increased by 10 % in the Qeqertarsuaq and even 33 % in the Baffin Bay, with further projected increases moving north from Greenland (Kalaallit Nunaat) waters (Ardyna et al. (2014)). Thus, nutrient demands are likely to increase, and the role of N_2 fixation can become more significant. The diazotrophic community in this study is dominated by UCYN-A in surface waters and may be linked to diatom abundance in deeper layers. This co-occurrence of diatoms and N_2 fixers in the same location is probably due to the co-limitation of similar nutrients, rather than a symbiotic relationship. Thus, this highlights the significant presence of diazotrophs despite their limited representation in datasets. It also highlights the potential for further discoveries, as existing datasets likely underestimate the full extent of the diazotrophic community (Laso Perez et al., 2024; Shao et al., 2023; Shiozaki et al., 2017, 2023). The reported N_2 fixation rates in the Vaigat strait within the Arctic Ocean are notably higher than those observed in many other oceanic regions, emphasizing that N_2 fixation is an active and significant process in these high-latitude waters. When compared to measured rates across various ocean systems using the ^{15}N approach, the significance of these findings becomes clear. For instance, N_2 fixation rates are sometimes below the detection limit and often relatively low ranging from 0.8 to 4.4 nmol N L^{-1} d^{-1} (Löscher et al., 2020, 2016; Turk et al., 2011). In contrast, higher rates reach up to 20 nmol N L^{-1} d^{-1} (Rees et al. (2009)) and sometime exceptional high rates range from 38 to 610 nmol N L^{-1} d^{-1} (Bonnet et al. (2009)). The Arctic Ocean rates are thus significant in the global context, underscoring the region's role in the global nitrogen cycle and the importance of N_2 fixation in supporting primary productivity in these waters.

These findings highlight the urgent need to understand the interplay between seasonal variations, sea-ice dynamics, and hydrographic conditions in Qeqertarsuaq. As climate change accelerates the melting of the Greenland Ice Sheet at Jakobshavn Isbræ, shifts in hydrodynamic patterns and hydrographic conditions in Qeqertarsuaq are anticipated. The resulting influx of warmer waters could significantly reshape the bay's hydrography, making it crucial to comprehend the coupling of climate-driven changes and oceanic processes in this vital Arctic region. Our study provides key insights into these dynamics and underscores the importance of continued investigation to predict Qeqertarsuaq's future hydrographic state. By detailing the environmental and hydrographic changes, we contribute valuable knowledge to the broader context of N_2 fixation in the Arctic Ocean. Given nitrogen's pivotal role in Arctic ecosystem productivity, it is essential to explore diazotrophs, quantify N_2 fixation, and assess their impact on ecosystem services as climate change progresses.

Appendix A

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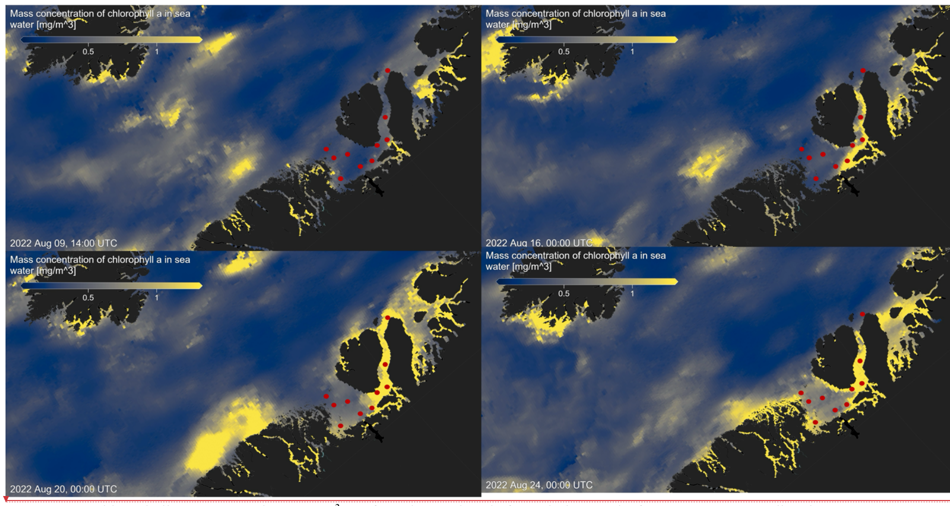
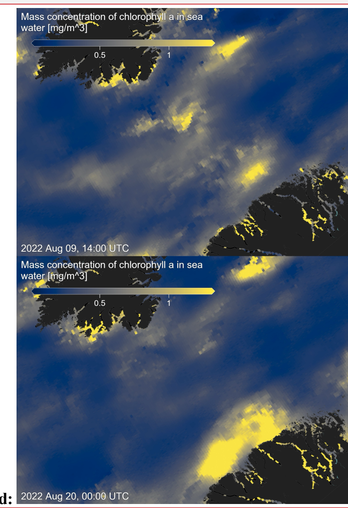


Figure A1. Chlorophyll *a* concentration mg m^{-3} at four time points before, during, and after sea water sampling in August 2022 (sampling stations indicated by red dots), obtained from MODIS-Aqua; https://giovanni.gsfc.nasa.gov (Aqua MODIS Global Mapped Chl *a* Data, version R2022.0, DOI:10.5067/AQUA/MODIS/L3M/CHL/2022), 4 km resolution, last access 03 June 2024

Deleted: 

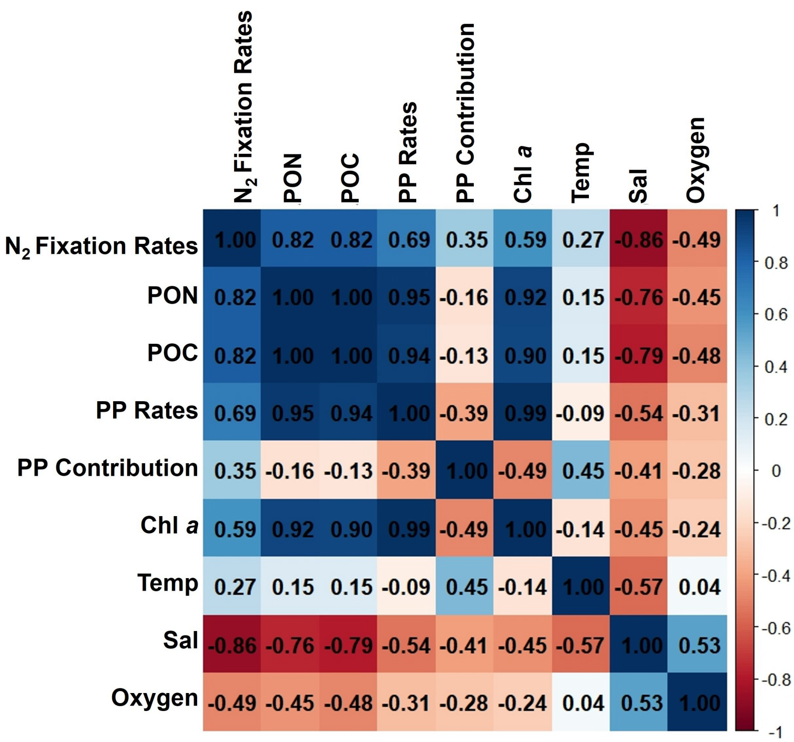


Figure A2. Correlation matrix of environmental and biological variables. The plot shows the correlation coefficients between the following parameters: N_2 fixation rates, PON, POC, PP rates, the contribution N_2 fixation to PP (PP contribution), Chl *a*, temperature (Temp), salinity (Sal), and Oxygen. The scale ranges from -1 to 1, where values close to 1 or -1 indicate strong positive or negative correlations, respectively, and values near 0 indicate weak or no correlation. The color intensity represents the strength and direction of the correlations, facilitating the identification of relationships among the variables

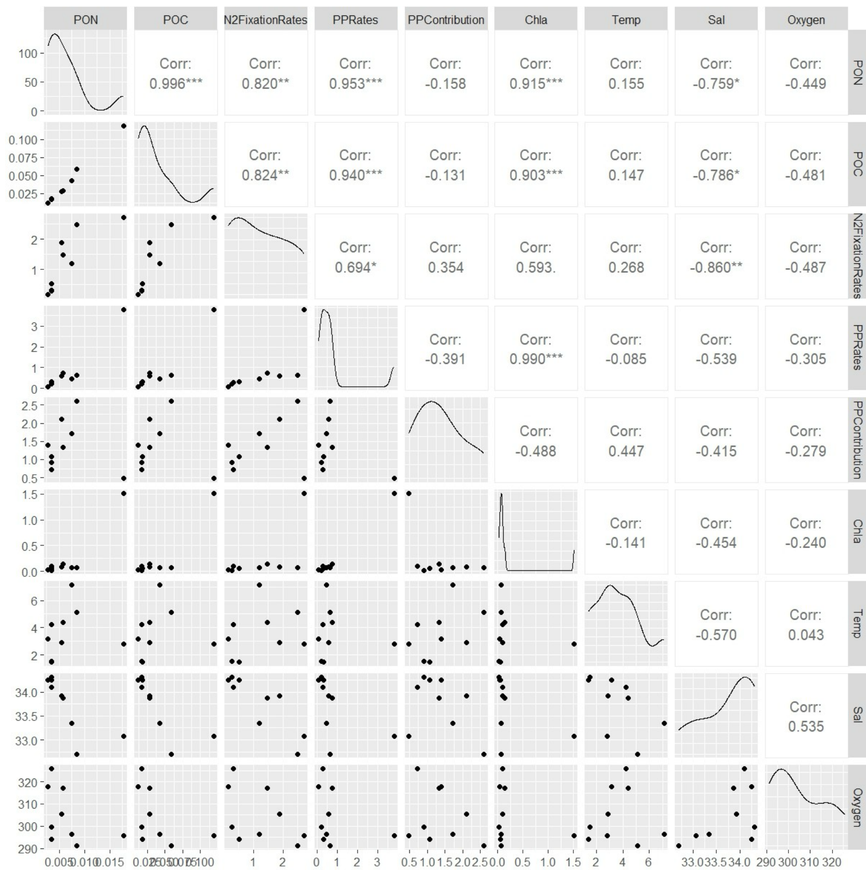


Figure A3. This figure displays a ggpairs plot, showing pairwise relationships and correlations between biological and environmental variables. Pearson correlation coefficients displayed in the upper triangular panel, indicating the strength and significance of linear relationships. Statistical significance levels are indicated by stars (*), where * indicates $p < 0.05$, ** indicates $p < 0.01$ and *** indicates $p < 0.001$

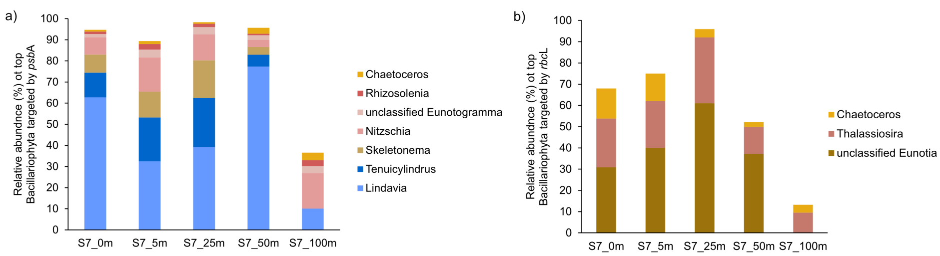


Figure A4 . Taxonomic composition of Bacillariophyta at Station 7 based on a) psbA and b) rbcL marker genes. The figure shows the relative abundance of Bacillariophyta genera detected in the metagenomic dataset, grouped by gene-specific classifications.

Station	**Parameter (X)**	**Value**	**SD**	**δNFR/ δX**	**Error contribution (SD x [δNFR/δX])2**	**% Total error**	**Summary (nmol N L^{-1} d^{-1})**
3	Δt	1.00	0.00	0.00	0.00	0.00	Mean = 1.13 LOD = 0.73 MQR = 0.12
	A_{N2}	3.92%	0.00	0.00	0.00	0.00	
	A_{PNO}	0.370%	4.24 x 10^{-6}	2.63 x 10^{6}	2.46 x 10^{2}	29.49	
	A_{PNf}	0.420%	3.7 x 10^{-5}	2.36 x 10^{5}	3.03 x 10^{2}	35.54	
	$[PN]_f$	1.69 x 10^{3}	1.24 x 10^{2}	5.12 x 10^{-2}	3.21 x 10^{2}	34.97	
7	Δt	1.00	0.00	0.00	0.00	0.00	Mean = 1.92 LOD = 1.91 MQR = 0.47
	A_{N2}	3.92%	0.00	0.00	0.00	0.00	
	A_{PNO}	0.369%	4.0 x	1.57 x 10^{7}	2.06 x 10^{3}	25.17	

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			10^{-6}				
	A_{PNf}	0.407%	5.47×10^{-5}	9.25×10^{5}	2.79×10^{3}	36.88	
	$[PN]_f$	4.62×10^{3}	8.2×10^{2}	6.77×10^{-2}	2.87×10^{3}	37.95	
10	Δt	1.00	0.00	0.00	0.00	0.00	Mean = 0.90 LOD = 0.96 MQR = 0.06
	A_{N2}	3.92%	0.00	0.00	0.00	0.00	
	A_{PNO}	0.371%	1.89×10^{-6}	-2.01×10^{2}	1.44×10^{-3}	31.24	
	A_{PNf}	0.371%	2.22×10^{-6}	2.01×10^{2}	2.05×10^{-3}	34.85	
	$[PN]_f$	5.91×10^{2}	1.89×10^{2}	-1.56×10^{-4}	3.69×10^{-3}	33.91	

Appendix Table 1: Sensitivity analysis for N_2 fixation rates. The contribution of each source of error to the total uncertainty was determined and calculated after Montoya et al., (1996). Average values and standard deviations (SD) are provided for all parameters at each station. The partial derivative (δNFR/ δX) of the N_2 fixation rate measurements is calculated for each parameter and evaluated using the provided average and standard deviation. The total and relative error are given for each parameter. Mean represents the average N_2 fixation rate measurement. MQR (minimal quantifiable rate) represents the total uncertainty linked to every measurement and is calculated using standard propagation of error. LOD (limit of detection) represents an alternative detection limit defined as ΔAPN = 0,00146.

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Data availability. The presented data collected during the cruise will be made accessible on PANGEA.The molecular datasets have been deposited with the accession number: Bioproject PRJNA1133027

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Author contributions. IS carried out fieldwork and laboratory work at the University of Southern Denmark, and wrote the majority of the manuscript. ELP, AM, and EL conducted fieldwork and laboratory work at the University of Southern Denmark. PX performed metagenomic analysis and created the corresponding graphs. CRL designed the study, provided supervision and guidance throughout the project, and contributed to the writing and revision of the manuscript. All authors contributed to the conception of the study and participated in the writing and revision of the manuscript.

Competing interests. The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper. One of the authors, CRL, serves as an Associate Editor for Biogeosciences.

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