Arctic phytoplankton spring bloom diversity across the marginal ice zone in Baffin Bay

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Abstract

Phytoplankton under-ice blooms have been recently recognized as an important Arctic phenomenon for global 2 primary production and biogeochemical cycling. Drastic sea-ice decline in both extension and thickness enables 3 the development of early blooms, sometimes hundreds of kilometers beneath the pack ice. Baffin Bay is a semi-enclosed sea where Arctic and North Atlantic water masses interact. It is totally covered by sea-ice by 5 March and ice-free by August/September. In the present work, we investigated the phytoplankton community 6 structure across the marginal ice zone between the ice-free, Atlantic-influenced, east and the ice-covered, Arctic-7 influenced, west Baffin Bay using 18S rRNA high-throughput amplicon sequencing, flow cytometry cell counting 8 and numerous environmental and biological data collected and compiled in the scope of the Green Edge project. 9 Sampling was performed during June-July 2016 in a total of 16 stations with around 6 depths each. Stations 10 were clustered into "Under Ice" (UI), "Marginal Ice Zone" (MIZ) and "Open Water" (OW) on the basis of its sea 11 ice cover upon sampling. Phytoplankton community structure was analyzed by 18S rRNA metabarcoding with 12 the microdiversity approach. The UI sector was characterized by a shallow nitracline, high pico-phytoplankton 13 abundance and a shared dominance between *Micromonas* and *Phaeocystis* in the 0.2-3 μ m size fraction, as well 14 as an increased contribution of Cryptophyceae and non-diatom Ochrophyta in the 3-20 μ m size fraction. Several 15 amplicon sequence variants (ASVs) were flagged as indicator for the UI+MIZ sector group, including known 16 ice-associated taxa such as the diatoms Melosira arctica and Pseudo-nitzschia seriata, but also specific ASVs 17 assigned to the green alga Micromonas polaris and the cryptophyte Falcomonas daucoides, the silicoflagellate 18 Dictyocha speculum, one member of the uncultivated MOCH-2 group, and a Pterosperma sp. (green algae) rarely 19 seen in other metabarcoding datasets, including from the Arctic. The OW sector harbored a community adapted 20 to a nutrient-depleted/high light environment, with a significant contribution of the haptophyte Phaeocystis 21 pouchetii and big centric diatoms, including several Thalassiosira species. 22

23 Introduction

The recognition of the occurrence of an annual under-ice bloom in the Arctic Ocean (Arrigo et al. 2012, 2014) 24 represented a paradigm shift that has impacted the estimates of primary production (Kinney et al. 2020), as well 25 as the understanding of the biogeochemical cycling in the region (Ardyna et al. 2020). The Arctic is undergoing 26 drastic changes directly linked to sea-ice decline in both extension and thickness (Meredith et al. 2019; Serreze 27 et al. 2007), enabling the early development of extensive under-ice blooms (Horvat et al. 2017). A recent model 28 indicates that the photosynthetically active radiation (PAR) transmission trough first and second-year sea ice 29 can now sustain net phytoplankton growth over most of the Arctic by July (Ardyna et al. 2020). The periods 30 when sea-ice is present have been shortened by earlier melting and delayed freezing seasons (Tedesco et al. 31 2019), impacting also the timing of the characteristic ice-edge phytoplankton spring blooms (Janout et al. 2016; 32 Perrette et al. 2011; Renaut et al. 2018), with cascading effects to higher trophic levels and nutrient fluxes (Leu 33 et al. 2011; Post et al. 2013). 34

Autotrophic communities from high latitude environments are subjected to a light regime mainly dictated by 35 the seasonally restricted input of solar energy, but also by the sea-ice extension/thickness and snowfall rates, 36 which have a light-attenuating effect (Leu et al. 2015). The sea-ice also provides a complex habitat for the 37 sympagic community (Niemi et al. 2011; Olsen et al. 2017), as well as seeding organisms to the water column 38 during melting (Hardge et al. 2017). The presence of sea-ice and its associated community has been linked to 39 higher abundance and better nutrition of pelagic organisms from higher trophic levels (Hop et al. 2011; Schmidt 40 et al. 2018). The Arctic sea-ice harbors complex communities with many metabolic strategies, where different 41 types of ice present different community structures (Comeau et al. 2013), and may act as a flagellate cyst 42 repository, for example for dinoflagellates such as *Polarella glacialis* (Kauko et al. 2018). Sympagic assemblages 43 have a great potential for the discovery of novel protist taxa (Hardge et al. 2017; Ribeiro et al. 2020). They 44 are now facing an imminent threat due to rapid decline on ice extension: a drastic decrease in sympagic protist 45 diversity has been reported in the Arctic due to the loss of multiyear sea ice, which harbors almost 40% more 46 species than first-year ice (Hop et al. 2020). It is expected that Arctic increasing temperatures, enhanced water 47 column stratification and ocean acidification will also favor specific pelagic populations, such as the pico-sized 48 green alga M. polaris (Benner et al. 2019; Hoppe et al. 2018; Li et al. 2009). 49

Diatoms tend to dominate Arctic sympagic communities and under-ice blooms, especially pennate diatoms from the genera *Nitzschia*, *Fragilariopsis*, *Navicula* and *Cylindrotheca* (Ardyna et al. 2020; Hop et al. 2020; Leu et al. 2015), with also the dominance of *Nitzschia frigida* during polar winter (Niemi et al. 2011). As the snow melts during spring/summer, the formation of melt ponds creates a new habitat which might be connected with the water column below. Melt pond communities are often dominated by flagellates (Mundy et al. 2011), and mixo/heterotrophic groups including Chrysophyceae, Filosa-Thecofilosea, and ciliates (Xu et al. 2020). Bottom-ice communities are rich, characterized by the presence of pennate diatoms and the strand-forming centric diatom *Melosira arctica* (Poulin et al. 2014). The seasonally retreating marginal ice zone is followed by massive phytoplankton blooms developing close to and below the ice edge (Perrette et al. 2011). The pelagic phytoplankton harbors a different diatom community from that of sea-ice (Oziel et al. 2019), with stronger presence of centric diatoms such as *Thalassiosira* and *Chaetoceros*, which are more adapted to lower nutrient concentrations and higher luminosity within the ice-free euphotic zone (Kvernvik et al. 2020; Morando and Capone 2018).

Apart from Bacillariophyta, other groups also play pivotal roles in the Arctic ecosystem. The Arctic pico-63 phytoplankton (0.2-2 μ m) is dominated by the Mamiellophyceae *M. polaris, Bathycoccus prasinos* and Man-64 toniella spp. (Joli et al. 2017; Lovejoy et al. 2007; Not et al. 2005). M. polaris is often the most abundant 65 (Balzano et al. 2012; Lovejoy and Potvin 2011) and is considered an Arctic sentinel species (Freyria et al. 2021) 66 due to the close relationship of its distribution patterns with temperature (Demory et al. 2019). *Phaeocystis* is a 67 globally distributed haptophyte genus, with a great impact on the carbon and sulfur exchange on the ocean/at-68 mosphere interface (Schoemann et al. 2005). The bloom-forming P. pouchetii has a pan-Arctic distribution 69 (Lasternas and Agusti 2010), with blooms detected even under thick snow-covered pack ice (Assmy et al. 2017), 70 and recently reported also in Antarctic waters (Trefault et al. 2021). 71

Among other perils to the Arctic ecosystem, the "atlantification" phenomena was first reported more than a decade ago (Hegseth and Sundfjord 2008), with hydrographic impacts on water column stratification and sea-ice decline due to increased heat fluxes from Atlantic Water (Polyakov et al. 2017), as well as biological impacts, via intrusion by advection of species of temperate origin (Neukermans et al. 2018; Oziel et al. 2020). Several studies also report a phytoplankton downsizing trend in warmer ocean waters (Hilligsøe et al. 2011; Morán et al. 2010). For example, warm anomalies in the Atlantic Water inflow to the Arctic Ocean seems to shift plankton dominance from diatoms cells to small coccolithophores (Lalande et al. 2013; Smyth et al. 2004).

Baffin Bay is a seasonally ice-covered sea within the Canadian Arctic, with a complex interplay of the Atlantic 79 and Arctic, Pacific-originated water masses (see Material & Methods section). The longitudinal physico-chemical 80 gradient created by this system of water masses results in distinct stratification patterns (Randelhoff et al. 2019) 81 and differential sea-ice melting rates (Tang et al. 2004), greatly impacting food web structure and carbon export 82 (Saint-Béat et al. 2020), as well as the permeability of the sea-ice, influencing brine connectivity and nutrient 83 availability to sympagic algae (Tedesco et al. 2019). Baffin Bay is especially susceptible to drastic environmental 84 changes, with a reported increase of 20 days of the length of the melting season compared to four decades ago 85 (Stroeve et al. 2014), due to ongoing changes such as warming on its eastern subsurface boundaries caused by 86 Atlantic inflow, and freshening trends on its Arctic-influenced sectors (Zweng and Münchow 2006). 87

In the present work, we used high-throughput amplicon sequencing and a microdiversity approach to investigate how the plankton community structure changes across the marginal ice zone between the Atlantic-influenced east and Arctic-influenced west Baffin Bay. The present study provides important insights on the impact of sea-ice loss on ice-associated pelagic plankton.

92 Material and Methods

93 Study area

Baffin Bay is a seasonally ice-covered sea within the Canadian Arctic, delimited by Greenland in the west 94 and by Baffin Island in the east, where complex interactions between North Atlantic and Arctic water masses 95 take place. The temperate and salty West Greenland Current (WGC), product of the interaction of North 96 Atlantic waters with the Irminger current, flows northward on eastern Baffin Bay along the Greenland coast, 97 coming through the Davis Strait (Tang et al. 2004). Due to its higher density, the WGC cannot pass through 98 the Canadian Archipelago and recirculates counter-clockwise, interacting with the colder, less-saline, Pacific-99 originated Arctic waters, flowing southward as the Baffin Island Current (BIC) (Jones et al. 2003; Münchow 100 et al. 2015). Sea-ice formation starts in Baffin Bay during October and covers almost the totality of its area by 101 March, followed by the melting season onset in April, as sea-ice retreats westward until it reaches a minimum 102 extent by August/September (Tang et al. 2004). In the western Baffin Bay, the onset of snow cover melt 103 modulates the termination of the sea-ice algal bloom and the beginning of the under-ice phytoplankton spring 104 bloom, reaching similar magnitudes to its offshore counterparts (Oziel et al. 2019). 105

106 Sampling & DNA extraction

Samples were collected onboard the research icebreaker CCGS Amundsen on four longitudinal transects be-107 tween 68.4°N-70°N and 56.8°W-62.4°W, from 9 June to the 2nd July 2016, for a total of 16 sampling stations 108 (Figure 1). Sea water was sampled at six depths within the euphotic layer at each station, using 12-L Niskin 109 bottles attached to a rosette equipped with a Seabird SBE-911plus CTD unit (Sea-Bird Electronics, Bellevue, 110 WA, USA). The list of the sensors attached to the rosette carousel can be found in Bruyant et al. (2022). Three 111 liters of water from each sampling point were pre-filtered with a 100 μ m mesh and subsequently filtered with 112 a peristaltic pump through the following sets of polycarbonate filters: 20 μ m (47 mm), 3 μ m (47 mm), and 113 $0.22 \ \mu m$ (SterivexTM filters). Filters were placed in cryotubes (except for the SterivexTM), preserved with 1.8 114 mL of RNAlaterTM and stored at -80°C until processing. DNA was extracted using ZR Fungal/Bacterial DNA 115 MiniPrep (Zymo Research, Irvine, CA, USA) following instructions from the manufacturer, and its final con-116 centration was measured using PicoGreenTM (Thermo Fisher Scientific, Waltham, MA, USA) with a LabChip 117 GX (Perkin-Elmer, Waltham, MA, USA). 118

119 18S rRNA V4 PCR amplification and sequencing

The V4 region of the 18S rRNA (about 380 bp) was amplified using the V4 primers TAReuk454FWD1 (forward) and V4 18S Next.Rev (reverse), along with the Illumina Nextera (Illumina, San Diego, CA, USA) 5' end overhang sequence as described in Piredda et al. (2017). Reaction mixtures in a total of 20 μ L were performed using 10 μ L of Phusion High-Fidelity PCR Master Mix[®] 2×, 0.3 μ M final concentration of each primer, 3% DMSO,

2% BSA and H₂O. Thermal conditions were as follows: 98° C for 5 min, followed by 25 cycles of 98° C for 20 124 s, 52°C for 30 s, 72°C for 90 s, and a final cycle of 72°C for 5 min. Samples were amplified in triplicates 125 and pooled together subsequently in order to minimize the chance of amplification errors. PCR purification 126 was performed using AMPure XP Beads (Beckman Coulter, Brea, CA, USA) following instructions from the 127 manufacturer. DNA quantification and quality check was done using a LabChip GX Touch HT Nucleic Acid 128 Analyzer (PerkinElmer, Waltham, MA, USA). Libraries were prepared as detailed on the Illumina[®] support 129 website (http://support.illumina.com) with a final concentration of 1 nM and 1% of denaturated PhiX to prevent 130 sequencing errors due to low-diversity libraries. Sequencing was performed using a 2×250 bp MiSeq Reagent 131 Kit v2[®] at the GenoMer platform (Roscoff, France). 132

Sequence processing

Sequences were processed using the dada2 (Callahan et al. 2016) package within R (R Core Team 2021). 134 Reads were filtered and trimmed using the filterAndTrim function with the following parameters: truncLen 135 = c(250, 240), trimLeft equal to each primer length (for primer removal), maxN=0, maxEE=c(2, 2), and 136 truncQ=10. Merging of forward and reverse reads with the mergePairs function and chimeric sequences removal 137 with the removeBimeraDenovo function were both performed with default parameters. Resulting ASVs were 138 taxonomically assigned using assignTaxonomy function with PR2 database (Guillou et al. 2013) version 4.14 139 (https://pr2-database.org/). Samples with less than a total of 3,000 reads were excluded, and the number 140 of reads for each sample was normalized by the median sequencing depth. Autotrophic taxa were selected 141 by filtering-in divisions Chlorophyta, Cryptophyta, Haptophyta, Ochrophyta and Cercozoa. Classes known to 142 comprise only heterotrophic members (Chrysophyceae, Sarcomonadea and Filosa-Thecofilosea) were excluded. 143 Dinoflagellates were not considered because they contain both autotrophic and heterotrophic taxa, and the high 144 number of 18S rRNA gene copies per genome makes them dominate read numbers, obscuring patterns of other 145 autotrophs. Processing script can be found at https://github.com/vaulot/Paper-2021-Vaulot-metapr2/tree/ 146 main/R_processing. 147

148 Environmental data

Environmental variables obtained by other studies during the Green Edge cruise (Lafond et al. 2019; Randelhoff 149 et al. 2019; Saint-Béat et al. 2020) were used here in accordance with our different sectors UI, MIZ and OW. 150 All ancillary physico-chemical and biological data obtained from the Green Edge project used in the present 151 paper is available at http://www.obs-vlfr.fr/proof/php/GREENEDGE/x_datalist_1.php?xxop=greenedge& 152 xxcamp=amundsen as raw data, and at https://www.seanoe.org/data/00487/59892/ (Massicotte et al. 2020) 153 as formatted files, and described in detail by Bruyant et al. (2022) (see Data Availability section). The complete 154 list of variables sampled during the Amundsen Green Edge cruise, the principal investigator responsible for each 155 data set, and the protocols used to obtain and analyze physical, chemical and biological data can be found in 156 Bruyant et al. (2022). Further information on nutrient and pigment analysis can be found in Lafond et al. 157

¹⁵⁸ (2019). Data processing for light transmittance, sea-ice cover and water column stability can be found in ¹⁵⁹ Randelhoff et al. (2019).

¹⁶⁰ Flow cytometry analysis

Autotrophic and heterotrophic cell abundance was measured *in situ* using a BD AccuriTM C6 flow cytometer as previously described in (Marie et al. 2010). Pico- and nano-phytoplankton abundance was measured on unstained samples with fluorescent beads for parameter normalization (0.95 G Fluoresbrite[®] Polysciences, Warrington, PA), while heterotrophic cell enumeration was performed using SYBR Green[®] staining as described in (Marie et al. 1997).

166 Data analysis

Sampling stations (Figure 1) were clustered into "Open Water" (OW), "Marginal Ice Zone" (MIZ) and "Under Ice" (UI) on the basis of the temporal dynamics sea ice cover using the parameter "Open Water Days" (OWD). OWD corresponds to how many days a given station had been ice-free before sampling (positive values) or how many days it took for it to become ice-free after sampling (negative values) (see Randelhoff et al. 2019). Stations with OWD > 10 days of open water before sampling day were considered OW, stations with 10 to -10 days were considered within the MIZ, and stations with OWD < -10 days were considered UI (Table 1). The number of sampling points within each sector and size fractions can be found in Table 2.

Data analysis was performed within R, using the following packages: *phyloseq* (data filtering, heatmaps, alpha 174 diversity) (McMurdie and Holmes 2013), tidyr (Wickham et al. 2019), vegan (NMDS) (Dixon 2003), gqplot2 175 (plotting, Wickham 2016), ComplexUpset (upSet graphics, Krassowski 2020). Abundant ASVs for each size 176 fraction were selected by keeping only ASVs which were among the top 90% most abundant sequences in at 177 least one sample. Abundant taxa for the whole community (i.e. considering all size fractions) had to be among 178 the top 90% most abundant sequences in at least 10% of the samples, except for the intersection analysis (upSet 179 graphic), where taxa present in the top 70% of sequences in at least one sample were filtered. This was done with 180 the topf and genefilter sample functions of *phyloseq*. NMDS analysis was performed using Bray–Curtis distance 181 with the metaMDS function of the package *vegan*, and statistically significant environmental parameters (*p*-value 182 ≤ 0.001) and genera (p-value ≤ 0.05) were mapped against it using the function *envfit*. Indicator species analysis 183 (indicspecies package, De Cáceres et al. 2010) was performed with abundant taxa (selected as described above) 184 within each size fraction in order to find significant association between taxa and a given sector (or combination 185 of sectors), using the default IndVal index as statistic test and 9999 random permutations. Global distribution 186 of ASVs was performed using the meta PR^2 database (https://shiny.metapr2.org, Vaulot et al. 2022) which 187 contains metabarcodes from 41 public datasets representing more than 4,000 samples distributed over a wide 188 range of ecosystems. ASV sequences from the present study were entered in the "Query" panel, and matching 189 $metaPR^2$ ASVs (100% similarity) were displayed in the "Map" panel. 190

191 Results

We sampled the phytoplankton community across the marginal ice zone in Baffin Bay, Arctic, in June and July 2016, to assess changes related to sea-ice melt. The community was sequentially filtered for three size fractions (0.2-3 μ m, 3-20 μ m and > 20 μ m), and sampling stations were classified as Under Ice (UI), Marginal Ice Zone (MIZ) and Open Water (OW) sectors (Tables 1 and 2).

¹⁹⁶ Physical, chemical and biological variability

Temperature were lower in the Arctic-influenced UI sector and higher in terms of both absolute values and 197 median in the Atlantic-influenced OW sector. Temperature differences between the two sectors were statistically 198 significant (Figure 1 and 2A). Salinity was not significantly different between the two ice-influenced UI and 199 MIZ sectors, with a wider distribution towards less saline sampling points influenced by sea-ice melt. Salinity 200 values were less variable in the OW sector, narrowly ranging between 33.6 and 34 (Figure 2B, Supplementary 201 data S1). Chl fluorescence from the CTD was higher in MIZ and the well-lit OW sector, reaching its peak in the 202 former sector with 14.5 $mg.m^{-3}$ (Figure 2C). The mixed layer depth (MLD) was significantly different between 203 the UI and OW sectors, being deeper in the UI sector, varying from 27 to 46 m. UI and OW were also distinct 204 from MIZ, with the MLD ranging from 4 to 12 m (Figure 2D). PAR (mol photons⁻².d⁻¹) was not significantly 205 different between MIZ and OW, although variability was greater in the MIZ, in keeping with the variable ice 206 cover (Figure 2E). 207

Nitracline depth was significantly distinct between sectors, in general being deeper in the OW sector and 208 always larger than 30 m. In the UI sector it was never deeper than 8 m, while in the MIZ sector the nitracline 209 depth was variable, with values ranging from 0 and 20 m (Figure 2F). Nutrient concentrations were in general 210 higher in the UI sector, compared to MIZ and UI. MIZ was more similar to OW than UI for all nutrients and 211 ratios measured (Figure S1A-I). Nitrate, phosphate, silica, colored dissolved organic matter (CDOM), urea, 212 particulate organic nitrogen (PON) and carbon (POC) differed significantly between the UI and OW sectors 213 (Figure S1 and S2). Urea concentrations were higher in the UI sector, reaching $1.9 \ge 10^3 \mu M$, almost the double 214 the maximum concentration from the other sectors (Figure S1A). Although ammonium concentrations did not 215 differ significantly between the sectors, values higher than 0.8 μ M were only found in the UI sector, up to 7.7 216 μ M (Figure S1B). Ammonium assimilation and regeneration were significantly different between the different 217 sectors, with higher median values found in the MIZ sector (Figure S2G-H), while urea assimilation decreased in 218 the UI sector and nitrate assimilation was somewhat even among all sectors (Figure S2I-J). DON and primary 219 production were higher in the MIZ sector, although the highest values from the latter were obtained in the UI 220 sector, up to 88 μ gC.L⁻¹.day⁻¹ (Figure S2L). 221

222 Phytoplankton abundance

Phytoplankton abundance measured by flow cytometry revealed different distribution patterns between pico 223 $(0.2-3 \ \mu m)$ and nano $(3-20 \ \mu m)$ size fractions (Figure 2G-H). Pico-phytoplankton abundance was greatest in the 224 UI sector (up to 39 x 10^3 cells.mL⁻¹), and lowest values in the OW sector (0.95 x 10^3 cells.mL⁻¹ on average) 225 (Figure 2G). Differences between sectors were highly significant for the smallest size fraction, in contrast to nano-226 phytoplankton, where only the extremes UI and OW differed significantly. Nano-phytoplankton abundance was 227 the highest in the MIZ sector (up to 22×10^3 cells.mL⁻¹), although the median was the highest in OW 228 (Figure 2H). FCM cryptophyte abundance differed significantly among all sectors, with much higher values in 229 UI (up to 182 cells.mL⁻¹) than in MIZ and especially in OW, where they were virtually absent (Figure 2I). 230 Pico- and nano-phytoplankton abundance was in general higher in surface and decreased with depth in UI, while 231 in OW the pattern was the inverse (Figure 3). Within the MIZ pico-phytoplankton abundance was higher in 232 surface and subsurface, while nano-phytoplankton peaked in deeper samples. Cryptophyceae abundance in UI 233 sector was in general higher in surface/subsurface, but with some abundance peaks in deeper samples (Figure 3). 234

²³⁵ Phytoplankton diversity at the division and genus level

Diversity patterns at the division level had a marked difference between sectors, especially for the smaller 236 $(0.2-3 \text{ and } 3-20 \ \mu\text{m})$ size fractions. The 0.2-3 μm size fraction was mostly dominated by Chlorophyta in 237 the ice-associated (UI+MIZ) sectors throughout the water column, with an important share of Cryptophyta 238 239 and Ochrophyta, while in the OW sector Haptophyta reads were predominant, especially in deeper samples (Figure S3). Differences in diversity between sectors at the division level in the 3-20 μ m size fraction were less 240 marked, although there was in general an increase in Haptophyta towards the MIZ and OW sectors. This size 241 fraction separation was also marked with more Ochrophyta that dominated the OW sector in surface samples 242 (Figure S3). In the > 20 μ m size fraction, the Ochrophyta abundance dominated the three sectors with only a 243 small increase in Haptophyta relative abundance towards MIZ and OW sectors (Figure S3). 244

0.2-3 μ m. At the genus level, diversity in the 0.2-3 μ m size fraction did not differ greatly across sectors 245 from that observed at the division level, since the two most abundant divisions, Chlorophyta and Haptophyta, 246 were dominated by the genera *Micromonas* and *Phaeocystis*, respectively (Figure 4). Within Mamiellophyceae, 247 Bathycoccus and Mantoniella were mainly detected in ice-associated sectors, the former with higher relative 248 abundances in the deeper samples and the latter in surface samples. Cryptophyta was mainly dominated by 249 Falcomonas in UI and MIZ, and by Teleaulax in the OW sector. Although not very abundant, Bacillario-250 phyceae were extremely diverse in ice-associated sectors (Figure 4). It is important to note that the decrease in 251 Micromonas towards the OW sector is corroborated by the large drop in pico-phytoplankton cells abundance 252 within this sector (Figure 2G). 253

 $3-20 \ \mu m$. Mamiellophyceae were nearly absent in the 3-20 μm size fraction, except for a small contribution to surface samples in UI and MIZ. A higher contribution of *Chrysochromulina* within Haptophyta was observed ²⁵⁶ in ice-associated sectors, especially in deeper samples in the UI sector (Figure 4). A higher abundance of ²⁵⁷ *Teleaulax* relative to *Falcomonas* was observed when comparing the 3-20 μ m to the 0.2-3 μ m size fraction, ²⁵⁸ always more present in surface than deeper samples, including in the OW sector. As observed in the smallest ²⁵⁹ size fraction, Ochrophyta were fairly diverse in ice-associated sectors, with representatives of Bacillariophyceae, ²⁶⁰ Bolidophyceae, Dictyochophyceae, and Marine Ochrophyta (MOCH-2). *Chaetoceros* was dominant in the OW ²⁶¹ sector, especially in surface samples, with a small contribution of *Thalassiosira*.

 262 > 20 μ m. There was a decrease in non-diatom Ochrophyta representatives in the > 20 μ m size fraction, although *Dictyocha* and *Triparma* were still present in ice-associated sectors, the former mostly in surface and the latter in deeper samples (Figure 4). With respect to diatoms, there was an increase in *Porosira*, *Actinocyclus*, and especially *Thalassiosira* in all the sectors in comparison with other size fractions, and in *Melosira* relative abundance in ice-associated sectors.

NMDS analysis revealed that samples clustered according to size fractions along the first axis and sectors 267 along the second axis. UI and MIZ were associated with higher nutrient concentration and Cryptophyceae cell 268 abundance, whereas OW sector presented higher temperatures and use of alternative source of nitrogen, such as 269 urea and ammonium, indicating the importance of regenerated production (Figure 5A). Statistically significant 270 genera had a distribution linked to both sectors and size fractions. For example, larger size fractions from ice-271 associated samples were correlated with pennate diatoms such as *Pseudo-nitzschia* and *Cylindrotheca*, whereas 272 smaller size fractions for the same samples were correlated with Falcomonas, Bathycoccus and Micromonas. 273 Larger size fractions from the OW sector were associated with centric diatoms such as Thalassiosira, Chaetoceros 274 and Eucampia, and smaller size fractions with Phaeocystis. 275

276 Phytoplankton microdiversity

Taxa grouped by genera mask variability at the species and ASV level. Looking at all the genera with more than two ASVs in the whole dataset, the ASV-level distribution of taxa yields potential information on nichepreference. In general, most genera had more ice-associated ASVs compared to OW (Table 3). Interestingly, several low-abundance taxa harbored high numbers of ice-associated ASVs, for example, the Dictyochophyceae genus *Pseudochattonella* and the environmental clade 2 of Bolidophyceae. Two groups presented a surprisingly large number of ASVs: the B clade of Dolichomastigaceae (Mamiellophyceae) with a total of 29 ASVs, and the centric diatom genus *Chaetoceros* with 35 ASVs (Table 3).

Alpha diversity indices indicate that, in general, diversity was higher in the smallest size fraction in the UI and MIZ sectors, and decreased towards bigger size fractions. However, the Simpson index was lowest in the 3-20 μ m size fraction and the highest in the > 20 μ m size fraction (Figure S4). When taking into consideration only the most abundant ASVs (ranking among the top 70% most abundant sequences in at least one sample), 41 ASVs were shared between all sectors, 16 were exclusive to the UI and MIZ sectors, and 2 were exclusive from the UI sector, while none was exclusive to the OW sector or to the MIZ and OW taken together (Figure S5). From the ten ASVs exclusive from ice-associated sectors, four were diatoms, three pennate and one centric diatom, which was also the most abundant, *M. arctica* (ASV_0025). Three of these ASVs were Haptophyta, two assigned as *Chrysochromulina* and one to *Phaeocystis cordata*, a species described from the Mediterranean Sea (Zingone et al. 1999). The other three ASVs were the only representatives of their classes: the uncultivated MOCH-2 (ASV_0061), the Cryptophyceae *F. daucoides* (ASV_0055), and the Mamiellophyceae *Mantoniella* squamata (ASV_0104) (Figure S5).

296 Indicator ASVs

In order to find patterns of taxa distribution that could be used as ecological indicators of niche preferences, we analyzed ASVs distribution on each sector and group of sectors using statistical indices described by De Cáceres et al., (2010).

0.2-3 μ m. The indicator species analysis identified 39 ASVs that were representatives of one sector or a 300 group of sectors within the 0.2-3 μ m size fraction, 30 of them related to UI (10), MIZ (2), or the UI+MIZ 301 sector group (18) (Table 4). Among the highly significant taxa within the UI sector (p-value < 0.001) there 302 were four Ochrophyta, three diatoms (M. arctica, Fragilariopsis cylindrus and Bacillaria paxillifer), and one 303 Pelagophyceae (assigned to the genus Ankylochrysis). Thirteen AVSs were highly correlated to the MIZ+UI 304 sector grouping, including two Mamiellophyceae (B. prasinos and Micromonas commoda A2), two cryptophytes, 305 both assigned to F. daucoides, seven non-diatom Ochrophyta (from the classes MOCH-2, Bolidophyceae, Dicty-306 ochophyceae, and Pelagophyceae), and two diatoms (Pseudo-nitzschia seriata and Chaetoceros neogracilis). A 307 M. polaris ASV (ASV 0154) was also considered indicator of the MIZ+UI site group, with a p-value of 0.002. 308 Taxa indicators of the OW sector (4) included three undescribed Dictyochophyceae (all assigned to *Pedinellales* 309 sp.), and one undescribed Dolichomastigaceae from clade B, while the three taxa indicators of the MIZ+OW 310 sector group comprised two centric diatoms (Porosira glacialis and Chaetoceros decipiens) and one undescribed 311 Prymnesiophyceae. 312

3-20 μ m. There was no significant association between taxa and the UI sector in the 3-20 μ m size frac-313 tion, and the six ASVs that were considered indicators of this sector presented lower p-values, with Bacillaria 314 paxillifer (p-value = 0.003) and Pterosperma sp. (p-value = 0.0095) presenting the highest association score 315 (Table 4). Considering only highly significant associations (p-value < 0.001), Navicula sp. (ASV_0049) was the 316 only ASV representative of the MIZ, while several Ochrophyta and one Cryptophyta member were identified 317 as indicators from the MIZ+UI sector group, all of them highly significant related to ice-associated sectors 318 also in the 0.2-3 µm size fraction: F. daucoides (ASV_0041), Fragilariopsis cylindrus (ASV_0015), Pseudo-319 nitzschia seriata (ASV_0046), C. neogracilis (ASV_0048), MOCH-2 sp. (ASV_0061), Triparma laevis clade 320 (ASV_0073) and Dictyocha speculum (ASV_0075). Two centric diatoms were significantly associated with the 321 OW sector, Thalassiosira sp. (ASV 0057) and Chaetoceros rostratus (ASV 0177), and another centric diatom 322 to the MIZ+OW sector group, *Eucampia* sp. (ASV 0079). 323

 $> 20 \ \mu m$. From the 30 highly significant indicator ASVs found in the $> 20 \ \mu m$ size fraction, only one was 324 related to the UI (Pseudo-nitzschia seriata, ASV_0046), one to the MIZ (Entomoneis ornata, ASV_0259), and 325 two to the OW sector (Chaetoceros contortus ASV_0334 and Chaetoceros diadema 1 ASV_0407) (Table 4). 326 Fifteen ASVs were highly related to the MIZ+UI sector group, including two M. arctica ASVs (0009 and 327 0025) and some also related to ice-associated sectors in the other size fractions: Navicula sp. (ASV 0049), 328 Triparma laevis clade (ASV 0073), Dictyocha speculum (ASV 0075), and Bacillaria paxillifer (ASV 0219). 329 From the eleven indicator ASVs strongly associated with the MIZ+OW sector group, ten were centric diatoms, 330 including four Chaetoceros, four Thalassiosira, one Eucampia sp. and one Detonula confervacea (ASV 0137). 331 Interestingly, the most abundant ASV from the whole dataset, P. pouchetii (ASV 0001), was also highly related 332 to the MIZ+OW sector group in the > 20 μ m size fraction (Table 4). 333

334 Distribution of abundant ASVs

The distribution of the ten most abundant ASVs within each division demonstrated that although the dominant 335 community might be comprised of few genera, ASV-level distribution follows distinct patterns within these gen-336 era and even within the same species (Figure 6). It is also notable that some ASVs were particularly adapted 337 to distinct environments, regardless of differences between sectors, since they were present (and abundant) 338 throughout the dataset, such as M. polaris (ASV 0003), Teleaulax glacialis (ASV 0038) and P. pouchetii 339 (ASV 0001) (Figure 6). Chlorophyta top 10 ASVs belonged to five genera: Bathycoccus, Mantoniella, Mi-340 cromonas, Pterosperma and Pyramimonas, from which five ASVs were significantly correlated to ice-associated 341 sectors. M. polaris ASV 0154 had a single base pair difference with M. polaris ASV 0003 (Figure S6) and 342 was less abundant than the latter in our dataset (Figure 6), as well as in other Arctic datasets (Figure S7). M. 343 squamata (ASV 0104) and Pterosperma sp. (ASV 0244) were present in UI samples, mainly within 0.2-3, but 344 also in the 3-20 μ m size fraction. 345

Within the top 10 most abundant Cryptophyta ASVs, three were assigned as *F. daucoides*. While ASV_0041 *F. daucoides* was strongly associated with MIZ+UI samples for both 0.2-3 and 3-20 μ m size fractions but also found in the OW sector, ASV_0055 was exclusively found in ice-associated sectors in the smaller size fraction (Figure 6). *T. gracilis* ASV_0038 was highly abundant at all sectors, but was flagged as indicator ASV for the MIZ+UI sector group in the > 20 μ m size fraction.

Five *Chrysochromulina* and three *Phaeocystis* ASVs comprised the ten most abundant Haptophyta, three of them only found in ice-associated sectors. Interestingly, *P. cordata* ASV_0105 and *Phaeocystis* sp. ASV_0125 were strongly associated with both UI or MIZ+UI sector group, while *P. pouchetii* ASV_0001 was associated with the larger size fraction of MIZ+OW, although highly abundant at all stations (Figure 6).

The most abundant non-diatom Ochrophyta were MOCH-2 ASV_0061, *D. speculum* ASV_0075 and *T. laevis* ASV_0073, all of them flagged as ice-associated indicator ASVs in all size fractions, except for MOCH-2, which was not an indicator for the > 20 μ m size fraction (Figure 6).

Many diatoms were flagged as indicator species for ice-associated sectors, including pennate diatoms such as P. 358 seriata, Navicula sp., and Fragilaria sp., and centric diatoms such as M. arctica and C. neogracilis. Interestingly, 359 from the five Thalassiosira ASVs ranking as most abundant Ochrophyta, four were considered indicator species 360 of OW or MIZ+OW sectors, while Thalassiosira antarctica was mainly associated with the smaller size fractions 361 of the MIZ sector, although present at all sectors. Other centric diatoms were also indicators of the MIZ+OW 362 sectors, such as Eucampia sp. ASV 0079 and P. glacialis ASV 0016 ASV 0073 (Figure 6). The distribution 363 of three abundant *Thalassiosira* flagged as OW or MIZ+OW indicators ASVs have been previously described as 364 having a broad distribution in both lower and higher latitudes in relation to the sampled area from the present 365

³⁶⁶ study (Figure S8).

367 Discussion

368 General bloom progression

Under-ice blooms are reported from throughout the Arctic, but the onset conditions, biogeochemical dynamics 369 and taxa succession are subjected to regional features (Ardyna et al. 2020). Although the Green Edge cruise 370 transects were east-west spatial snapshots, the sampling strategy recovered nutrients, cell abundance, plankton 37 diversity and metabolism variability as the bloom progressed from UI to OW (Lafond et al. 2019; Randelhoff 372 et al. 2019; Saint-Béat et al. 2020; Vilgrain et al. 2021). During pre-bloom conditions, photosynthetic activity 373 is limited by light availability, and under-ice populations are shade-acclimated (Ardyna et al. 2020). During the 374 Green Edge campaign, however, light availability and vertical mixing should have permitted a bloom initiation 375 under nearly 100% sea-ice cover (UI sector), but the bloom peaked in terms of chlorophyll-a approximately 10 376 days after ice retreat (Randelhoff et al. 2019), around the limit between the MIZ and the OW sector. 377

In general, FCM abundance data indicated higher pico- and nano-phytoplankton abundances within the MIZ 378 and the OW sectors, respectively. Although the micro-phytoplankton size fraction was not counted by FCM, the 379 amplicon data suggests a community structure shift from smaller to larger size fractions as the bloom progresses. 380 FCM data shows that while UI pico-phytoplankton reached its maximum and was relatively well distributed 38: down the euphotic zone of the water column, nano-phytoplankton community was particularly abundant right 382 beneath the sea-ice, indicating a close association between the top of the water column and the bottom of the 383 sea-ice (Figure 3). Interestingly, contrary to cell abundance, the relative abundance of the main genera did 384 not seem to change with depth within the UI sector, except for a higher contribution of *Phaeocystis* spp. and 385 Teleaulax sp. reads in surface. Diversity decreased eastward from the UI to the OW sector, which represents the 386 different stages of the phytoplankton spring bloom but is also influenced by the different water masses within 387 Baffin Bay. Ice-associated stations, most still covered with sea-ice and categorized as low-productivity stations 388 by Lafond et al. (2019), harbored the most diverse community, from the genus to the ASV level, and within 389 every size fraction (Figure 4, Table 3). Under-ice communities are adapted to low-light environments, capable of 390 maximizing light absorption by increasing intracellular concentrations of accessory and photosynthetic pigments 39: (Lewis et al. 2019). Smaller phytoplankton cells from the Beaufort Sea were reported to be more efficient at 392 harvesting light due partially to an increase in chlorophyll b content, which is associated with the low light 393 conditions in autumn and winter (Matsuoka et al. 2009). Such recruitment due to polar dark conditions might 394 explain the dominance of *Micromonas*, an early-bloom taxa (Lovejoy et al. 2007) with known persistence during 395 winter (Joli et al. 2017; Vader et al. 2015), within the UI and MIZ sectors, which represented almost the 396 total bulk of pico-sized plankton. Several abundant non-diatom ASVs were flagged as indicator ASVs from ice-397 associated sectors, especially in the smaller size fraction (Figure 6). Many of these indicator ASVs were found in 308 datasets from the high Arctic (see ASV diversity subsection below), suggesting that UI and MIZ phytoplankton 399 communities are highly diverse, probably low-light adapted populations of smaller organisms, which seem to be 400

connected to higher-latitude communities (Kalenitchenko et al. 2019) probably via water mass intrusions from
the Nares Strait and the Smith, Jones and Lancaster Sounds (Bluhm et al. 2015; Tang et al. 2004).

We observed a general increase in pico- and nano-phytoplankton cells within MIZ, with a sharp decline towards 403 the OW sector. The MIZ sector showed evidence of increased biological activity: pico- and nano-phytoplankton 404 abundance, dissolved and particulate organic carbon concentration, particulate organic nitrogen concentration, 405 dissolved organic nitrogen release and primary production in general were higher in the MIZ than in the UI 406 or OW sectors. Vilgrain et al. (2021) reported that near the ice-edge, copepods were heavily pigmented due 407 partially to full gut content. In the present study, the relatively steady community composition between UI and 408 MIZ, which comprised the peak of the bloom, may be explained by the seeding of taxa through ice melt water 409 (Mundy et al. 2011) combined with the "priming" effect suggested by Lewis et al. (2019). The "priming" effect 410 arises from the acclimation of pre-bloom, under-ice communities to low and highly variable light input due to 411 patchy snow cover and melt-pond/open water leads formation, resulting in a competitive advantage to rapidly 412 exploit increasing irradiation (Lewis et al. 2019). 413

As the phytoplankton spring bloom progresses, the phytoplankton community must transition from light-414 limited conditions, characteristic of a pre-bloom state, to a high-light, nutrient-limited environment (Lewis et 415 al. 2019). The nitracline deepened from 0 in UI to more than 30 meters in OW, along with the development of 416 a subsurface chlorophyll a maximum (Randelhoff et al. 2019), as a result of the rapid consumption of inorganic 417 nutrients in surface, following an expected trend in Arctic plankton phenology (Ardyna et al. 2020; Martin 418 et al. 2010). In the post-bloom conditions such as found within the OW sector, new production is confined to 419 deeper layers, and the euphotic layer is then dominated by regenerative production (Sakshaug 2004). Within 420 ice-free Arctic waters, species might also be subjected to detrimental effects of high UV exposure resulting in low 421 cell viability and photosynthetic performance decline, a scenario where, in general, diatoms out-compete other 422 microalgae (Alou-Font et al. 2016). The increase in *Chaetoceros* spp. observed here in the OW sector, especially 423 in the upper layers within the 3-20 μm size fraction, may reflect an ecological advantage within a post-bloom 424 scenario, since this genus has a high growth irrespective of nitrogen source in polar (Schiffrine et al. 2020) and 425 subtropical (Morando and Capone 2018) environments. The only abundant diatoms flagged as indicator ASVs 426 for OW or MIZ+OW sectors belonged to Thalassiosira and Eucampia, two genera that were also reported to 427 be effective scavengers for different nitrogen sources, out-competing other plankton community members within 428 nutrient poor waters (Morando and Capone 2018). NMDS analysis highlighted the gradient from the UI sector 429 with higher concentration of major nutrients such as nitrate and phosphate, to the MIZ/OW sector with higher 430 ammonium and urea assimilation, together with an increase of large (> 20 μ m) diatoms. Besides the bottom-431 up pressure favoring such specialized taxa, the community structure responsible for the secondary production 432 within the OW sector might also play a role in the differential top-down control of smaller taxa, since, in the 433 westernmost stations, the copepod populations were dominated by smaller organisms, in particular nauplii and 434 young copepod stages (Vilgrain et al. 2021). 435

436 Autotroph microdiversity

⁴³⁷ Different ASVs within the same species can represent distinct ecotypes, leading to resilience and adaptation ⁴³⁸ of microbial populations under changing environmental conditions (García-García et al. 2019; Needham and ⁴³⁹ Fuhrman 2016), and the persistence of particular lineages over time. We have identified several species com-⁴⁴⁰ prising more than one ASV. Sjöqvist & Kremp (2016) reported that genetic diversity within diatom species ⁴⁴¹ ensured an optimized ecological performance, including carbon uptake and overall resistance to environmental ⁴⁴² changes.

Diatoms. Sea-ice has been long recognized as an important substrate for marine diatoms (Horner et al. 1992; 443 Poulin et al. 2011), where brine channels and pockets serve as habitat for a specific interstitial and sub-ice 444 community. The centric diatom *M. arctica* is an ice-associated taxon, forming long strands in the water column 445 attached to the sea-ice (Poulin et al. 2014; Wassmann et al. 2006). This diatom is readily released as ice melts, 446 rapidly sinking and forming vast sea-floor deposits down to more than 4,000 m depth, with a high impact on 447 carbon export and benthic fauna (Boetius et al. 2013). Our data indicated two highly abundant M. arctica 448 ASVs not only in UI but also in the MIZ sector, the latter with several ice-free stations. Sampling roughly 449 the same stations and using microscopy and pigment-based analysis, Lafond et al. (2019) showed that M. 450 arctica in the MIZ was mostly in the form of actively silicifying resting spores, reaching up to 82% of biogenic 451 silica production. The high degree of significance associating *M. arctica* with ice-sectors in the present study 452 corroborate its assignation as a sea-ice specialist taxa, but the high number of reads in the intermittently 453 ice-covered Baffin Bay challenges previous work hypothesizing its preference for multi-year sea-ice (Hop et al. 454 2020). 455

Lafond et al. (2019) observed that diatoms during the melting season in Baffin Bay formed two distinct 456 community clusters: one less productive, associated with Pacific-originating waters, and another associated 457 with the core of the diatom bloom, within Atlantic-influenced stations, mainly in open waters or at an advanced 458 state of sea-ice melting. Our data are consistent with the current view of the succession pattern of the Arctic 459 diatom bloom, where ice-associated early bloom stages are characterized by a higher diversity of pennate diatoms 460 while its full development consists of larger centric diatoms, such as Thalassiosira and Chaetoceros (Oziel et 461 al. 2019). Such dynamics are partly explained by differences in nutrient acquisition strategies (Morando and 462 Capone 2018) and by increased photochemical damage experienced by sympagic pennate diatoms under ice-463 free, high-luminosity environments (Kvernvik et al. 2020). In the present study, abundant pennate diatoms, 464 P. seriata ASV 0046, Navicula sp. ASV 0049, and Fragilaria sp ASV 0064, were all flagged as indicator 465 species for ice-associated sectors. Interestingly, one of the most abundant Chaetoceros ASVs (C. neogracilis 466 ASV_0048) was considered a highly significant ice-associated indicator ASV, but only for the smaller size 467 fraction. C. neogracilis is a species complex with at least four known clades which share identical 18S rRNA 468 sequences (Balzano et al. 2017), so it is possible that the C. neogracilis distribution observed in the present 469

470 study is masking a finer clade-specific distribution.

One of the hypothesis from the present work was that taxa significantly associated with Atlantic-influenced 471 east Baffin Bay could be due to Atlantification processes that include input of warm-adapted taxa from the 472 eastern side of Davis Strait, which could thrive after ice melt. However, OW+MIZ indicator taxa that made 473 up the abundant community, such as Thalassiosira anguste-lineata ASV 0071, Thalassiosira sp. ASV 0057, 474 and T. rotula ASV_0013 , although sometimes displaying a wider distribution towards lower latitudes, are 475 considered part of the Arctic phytoplankton community, as shown by their distribution over many polar studies 476 in meta PR^2 (Figure S8). Those ASVs were also found within UI sector, indicating that their attribution as 477 MIZ+OW indicator taxa was mainly due to a better adaptation to low nutrient post-bloom conditions. 478

Non-diatom Ochrophyta. Although Lafond et al. (2019) identified the core of the diatom bloom within Atlanticinfluenced Baffin Bay, our FCM and metabarcoding data indicate the importance of smaller size fractions within ice-associated sectors in terms of cell abundance and overall plankton diversity. For example, nanophytoplankton Ochrophyta diversity within OW was dominated by a single diatom genus, *Chaetoceros*, while in the UI and MIZ both diatom and non-diatom Ochrophyta were much more diverse, with high abundances of MOCH-2, *Dictyocha speculum*, *Triparma laevis* clade, flagged as indicator ASVs for ice-associated sectors along with an unidentified Florenciellales.

The presence of the silicoflagellate *D. speculum* (synonym of *Octactis speculum*, Chang et al. 2017) in Arctic waters was first reported in the region more than a century ago (Lovejoy et al. 2002) and since regularly cited in the literature (Crawford et al. 2018). Its assignation as an indicator ASV for ice-associated sectors within all size classes in the present study might be a consequence of the presence of several life stages, including amoeboid, multinucleate and skeleton-bearing stages with different cell sizes (Chang et al. 2017; Moestrup and Thomsen 1990). Studying a 35-year sampling series, Hop et al. (2020) reported that this species has a higher frequency of occurrence in multiyear ice (24 %) in comparison to first-year ice samples (6 %).

Chlorophyta. The most striking difference between ASV distribution patterns among a dominant species in the 493 present study was observed within *M. polaris* populations. The Chlorophyta genus *Micromonas* is diverse and 494 widely distributed from coastal to oceanic waters through all the global latitudinal ranges (Simon et al. 2017; 495 Tragin and Vaulot 2019). It exhibits a wide thermal niche and is considered a sentinel for polar (Freyria et al. 496 2021) and global plankton diversity (Demory et al. 2019) in relation to temperature changes in the oceans. The 497 use of metabarcoding datasets combined with microdiversity approaches has previously allowed the discovery 498 of new polar Micromonas ecotypes, such as the Micromonas B3 clade, which displays a wider distribution band 499 towards lower latitudes than *M. polaris* (Tragin and Vaulot 2019). 500

The *M. polaris* CCMP2099 strain, isolated from North Water Polynya (Lovejoy et al. 2007) and the RCC2306 strain from the Beaufort Sea (holotype of the species, Simon et al. 2017) are 100% similar in the V4 region of the 18S rRNA to the *M. polaris* ASV_0003 from the present study. *M. polaris* ASV_0003 has a widespread

distribution pattern with a high abundance in all sectors, in accordance with its dominant role within the Arctic 504 (Balzano et al. 2012; Lovejoy et al. 2002, 2007; Not et al. 2005). Although M. polaris ASV_0154 differs from 505 ASV 0003 by a single nucleotide (Fig. S6), its significantly different distribution (Fig. S7), and the assignation 506 of ASV_0003 as an indicator species, suggests it might represent a new ecotype. There is no 100% similarity 507 match in GenBank with *M. polaris* ASV 0154, either to strains or environmental sequences. The distribution 508 of *M. polaris* ASV 0154 is pan-Arctic, although it always contributes to a small fraction of *Micromonas* reads. 509 M. polaris ASV 0154 has also been found in the Nares Strait (metaPR² set #42, Kalenitchenko et al. 2019) 510 (Figure S7), also comprising a small fraction of *Micromonas* reads. The Nares Strait is connected to northern 511 Baffin Bay and is responsible for southward transport of waters and ice from the Arctic Ocean into the region 512 (Tang et al. 2004). Using a decade-long 18S rRNA data series, Freyria et al. (2021) have identified *M. polaris* as 513 a summer specialist favored by nutrient-poor waters, in contrast to the present study, which identifies the species 514 either as a generalist, present in all sectors (ASV_0003) or as an ice-associated indicator ASV (ASV_0154). 515 The difference in *M. polaris* distribution patterns between Freyria et al. (2021) and the present study might be 516 related to the distinct geographic location, time of sampling and data processing. Freyria et al. (2021) sampled 517 the northernmost sector of Baffin Bay, more precisely the North Water, a hydrographically distinct region, close 518 to 77°N, bordered by Ellesmere Island and Greenland. The authors sampled the transition from summer to 519 autumn, while the present study focus on the transition between spring and summer. M. polaris abundance 520 was previously reported decreasing in numbers and activity towards winter, partially due to vulnerability to 521 specific viral infection during this period, and then recovering rapidly even at low irradiances (Joli et al. 2017). 522

One Chlorophyta ASV was associated with under-ice samples: Pterosperma sp. ASV 0244, which was 523 found exclusively in the UI sector, and flagged as one of the few abundant indicator species from it, and 524 not from the MIZ+UI sector group. Although the genus Pterosperma has been reported from several regions 525 within the Arctic (Joli et al. 2017; Lovejoy et al. 2002), with a preference for multi-year ice over first-year ice 526 (Hop et al. 2020), there was no 100% match between ASV 0244 and any strain or environmental sequence 527 in GenBank. Pterosperma sp. ASV 0244 was only found in three other samples from the 41 global datasets 528 in the meta PR^2 database, in the east coast of Greenland (Kopf et al. 2015) and the Nansen Basin (Metfies 529 et al. 2016). Although previous studies have identified sea-ice associated communities harboring a high relative 530 abundance of Pyramimonas (Gradinger 1996; Mundy et al. 2011), our indicator analysis did not detect any 531 specific distribution linked to sea ice for this genus. 532

⁵³³ **Haptophyta.** *P. pouchetii* is ubiquitous throughout the Arctic (Lasternas and Agusti 2010; Schoemann et al. ⁵³⁴ 2005) and has been reported to be capable of early blooms, even under snow-covered ice pack (Assmy et al. ⁵³⁵ 2017). Although *P. pouchetii* ASV_0001 reads were present in all size fractions and sectors, the species was ⁵³⁶ flagged as an indicator ASV for the MIZ+OW sector in the > 20 μ m size fraction. This might indicate a ⁵³⁷ prevalence of large *P. pouchetii* colonies towards eastern side of Baffin Bay, as the bloom progresses. In general, ⁵³⁸ blooming species of the genus *Phaeocystis* increase their C:N ratios under high light/low nutrient conditions,

mainly through the production of the polysaccharide-based mucilaginous matrix embedding colonies reaching 539 up to 3 cm, which serve as energy storage and a defense against grazers (Schoemann et al. 2005) and references 540 therein). The dominance of *P. pouchetii* colonial form was reported during the Arctic 2007 ice-melt record 543 (Lasternas and Agusti 2010), while the single-cell form was reported during overwintering (Vader et al. 2015). 542 The fact that P. pouchetii is adapted to grow in nutrient-replete waters with 100% sea-ice cover such as found in 543 the UI sector to the nutrient-depleted/high light OW sector corroborates earlier studies identifying this taxa as 544 a potential winner for future Arctic scenarios, where its plasticity regarding life cycle stages, and flexibility for 545 light and nutrient uptake, as well as resistance to zooplankton grazing will likely impact polar phytoplankton 546 community structuring, trophic energy transfer and carbon export (Lasternas and Agusti 2010; Verity et al. 547 2007; Wassmann et al. 2006). 548

The higher relative contribution of *Chrysochromulina* in deeper samples agrees with previous reports linking 549 this genus with deep chlorophyll maximum communities (Balzano et al. 2012). Many Chrysochromulina spp. 550 ASVs were exclusively found or flagged as indicator taxa for ice-associated sectors. *Chrysochromulina* frequently 55 occurs in sympagic communities and is considered one of the few ice-associated haptophytes (Mundy et al. 2011), 552 but it is also present in ice-free waters from the Arctic (Balzano et al. 2012; Lovejoy et al. 2002) and the Antarctic 553 (Luo et al. 2016; Trefault et al. 2021). The fact that the genus *Chrysochromulina* is morphometrically highly 554 diverse (Egge et al. 2014) down to the subspecies level (Balzano et al. 2012; Needham and Fuhrman 2016) 555 implies that monitoring diversity should comprise high-resolution analysis of species/ecotypes distributions. 556 Although not really abundant in the present study, Chrysochromulina sp. ASV 0542 was found exclusively 557 in under-ice samples. It was found previously to reach up to 2% of total eukaryotic reads in the Nares Strait 558 (metaPR² set #42, Kalenitchenko et al. 2019), but not detected elsewhere.559

The distribution of Pterosperma sp. ASV_0244 and Chrysochromulina sp. ASV_0542 restricted to a limited 560 Arctic latitudinal band suggests a narrow ecological niche, and its significant association with ice-covered sites 561 from the present study indicate that those taxa might be good proxies for diversity changes within the region. 562 Some taxa flagged as indicator ASVs for ice-associated sectors do have a broader range of distribution towards 563 lower latitudes, such as *Phaeocystis* ASV_0125 and *M. commoda* A2 ASV_0235. Whether this distribution 564 results from the combination of different ecotypes masked by the resolution of the marker gene, or simply 565 represents taxa out-competed within an ice-free, high-light and low nutrient environment, is still an open 566 question. 567

568 Conclusions

Taking the spatial transects as a temporal snapshot of the phytoplankton spring bloom dynamics over Baffin Bay, we observed a shift from a highly diverse under-ice and ice-edge community comprised of smaller taxa, to a low-diversity, highly specialized community where larger centric diatoms and *P. pouchetii* were better adapted to the harsh high light/low nutrient post-bloom environment. The taxa abundant in the ice-free

Atlantic-influenced Baffin Bay were in general also present in Arctic-influenced sectors and other polar studies, 573 indicating that the advection of warm-adapted taxa by Atlantic inflow was not detectable or significant in this 574 region. This conclusion must be taken with caution, however, due to the limited space and time sampling range 575 of the present study. The presence of taxa with intra-species variability such as F. daucoides, M. arctica and M. 576 *polaris* reinforces the urgency of renewed culturing efforts to better comprehend its ecological impacts. Although 577 thinner sea-ice might increase the magnitude of the sub-ice blooms of taxa with a high carbon export rate such 578 as M. arctica (Poulin et al. 2014) earlier in the season, our data indicate that as Baffin Bay ice cover shrinks 579 sooner and faster with spring blooms onset (Stroeve et al. 2014), this might lead to widespread post-bloom 580 conditions dominated by a much less diverse community, which might have implications in the recruitment of 581 sympagic communities in subsequent years. 582

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Author contributions statement

⁵⁹¹ CGR, ALS, DM and DV processed the samples and produced data; CGR, DV, NT, CL and ALS analyzed and ⁵⁹² interpreted data; CGR and DV wrote the paper; All authors read and approved the final manuscript.

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603 Additional information

- ⁶⁰⁴ To include, in this order:
- 605 Accession codes (where applicable);

606 Data availability

- ⁶⁰⁷ Physicochemical and biological data from the Green Edge project are available at http://www.obs-vlfr.fr/proof/
- ⁶⁰⁸ php/GREENEDGE/x_datalist_1.php?xxop=greenedge&xxcamp=amundsen and at https://www.seanoe.org/
- data/00487/59892/ as described in detail in Bruyant et al. (2022). Raw metabarcoding sequences are available
- ⁶¹⁰ under the Accession Code PRJNA810033 from GenBank SRA. Source code for sequence processing is available
- at https://github.com/vaulot/Paper-2021-Vaulot-metapr2/tree/main/R_processing.
- 612 **Competing interests** The authors declare no competing financial interests.

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948 List of Tables

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- Fig. 2 Environmental variables for the three sectors: UI (gray), MIZ (yellow) and OW (blue); (A) temperature (°C); (B) salinity; (C) fluorescence; (D) mixed layer depth (m); (E) Photosynthetically Active Radiation at 3 m (mol photons.m⁻².d⁻¹); (F) nitracline depth (m); (G) pico-phytoplankton abundance (cells.mL⁻¹); (H) nano-phytoplankton abundance (cells.mL⁻¹); (I) Cryptophyceae abundance (cells.mL⁻¹). Number of asterisks represent p-value obtained with the Wilcox test as follows: (*) $p \le 0.05$; (**) $p \le 0.01$; (***) $p \le 0.001$; (***) $p \le 0.001$; (***) $p \le 0.001$; (***) $p \le 0.0001$; "ns" = not significant.
- 978Fig. 3Abundance (cells.mL⁻¹) measured by FCM of pico-phytoplankton (top panels), nano-979phytoplankton (middle panels) and Cryptophyceae (lower panels) according to depth, di-980vided between the three sectors: UI (gray), MIZ (yellow) and OW (blue).
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- Non-metric multidimensional scaling (NMDS) analysis using Bray-Curtis dissimilarities of Fig. 5 985 the phytoplankton community composition; only statistically significant (A) environmen-986 tal parameters (p-value = 0.001) and (B) genera (p-value = 0.05) were plotted against 987 ordination. Parameters: ammonium assimilation (NH4 assimilation), bacteria abundance 988 (bact_ml), Cryptophyceae abundance (crypto_ml), fluorescence (fluo), nano-phytoplankton 989 abundance (nano ml), nitrates, silica, particulate organic carbon (poc), particulate organic 990 nitrogen (pon), phosphate, salinity, temperature, urea, and urea assimilation (urea assim-991 ilation). Stress: 0.11. 992

- Taxa distribution of the most abundant ASVs for each sector, divided by sampling stations; Fig. 6 993 the top 10 ASVs were selected within Chlorophyta (green), Cryptophyta (orange), Hapto-994 phyta (blue), and the top 20 most abundant within the highly diverse Ochrophyta division 995 (red); symbols indicate if a given ASV was reported as indicator ASV for UI (triangles), 996 MIZ (inverted triangles), OW (squares), MIZ+UI (diamonds) or MIZ+OW (circles) sector 997 groups within 0.2-3 μ m (white), 3-20 μ m (grey) or > 20 μ m (black) size fractions; asterisks 998 indicate the *p*-values associated with the indicator ASV: 0 (***), 0.001 (**), and 0.01 (*); 999 red and blue stars indicate if a given ASV was found exclusively in ice-associated sectors, 1000 being blue stars not abundant ASVs; SIC = sea-ice concentration on each sampling station. 1001 Fig. S1 Nutrients for the three sectors: UI (grey), MIZ (yellow) and OW (blue); (A) nitrates (μ M); 1002 (B) nitrites (μM) ; (C) phosphates (μM) ; (D) orthosilicic acid (μM) ; (E) colored dissolved 1003 organic matter (mg.m³); (F) dissolved organic carbon (μ M); (G) phosphate to nitrate ratio; 1004 (H) nitrate to orthosilicic acid ratio; (I) nitrate to phosphate ratio. Number of asterisks 1005 represent p-value obtained with the Wilcox test as follows: (*) $p \leq 0.05$; (**) $p \leq 0.01$; 1006 (***) $p \le 0.001$; (****) $p \le 0.0001$; "ns" = not significant. 1007
- Nutrients and metabolic rates for the three sectors: UI (grey), MIZ (yellow) and OW (blue); Fig. S2 1008 (A) urea (μ M); (B) ammonium (μ M); (C) dissolved organic nitrogen (μ M); (D) particulate 1009 organic nitrogen (μ M); (E) particulate organic carbon (mg.m³); (F) nitrification (μ M); (G) 1010 ammonium assimilation $(nM.L^{-1}.day^{-1})$; (H) ammonium regeneration $(nM.L^{-1}.day^{-1})$; 1011 (I) urea assimilation $(nM.L^{-1}.day^{-1})$; (J) nitrate assimilation; (K) dissolved organic nitro-1012 gen (μ M); (L) primary production (μ gC.L⁻¹.day⁻¹). Number of asterisks represent *p*-value 1013 obtained with the Wilcox test as follows: (*) $p \le 0.05$; (**) $p \le 0.01$; (***) $p \le 0.001$; 1014 (****) $p \le 0.0001$; "ns" = not significant. 1015
- Fig. S3 Relative abundance of reads at the division level between sectors and size fractions. UI: Under Ice; MIZ: Marginal Ice Zone; OW: Open Water; letters on the y-axis refer to the depth level where "a" corresponds to the surface and "f" to the deepest sampled depth, usually between 40 m and 60 m.
- Fig. S4 Chao1, Shannon and Simpson alpha diversity indices divided by size fraction; sectors are represented by the colors grey (UI), yellow (MIZ) and blue (OW).
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- Fig. S6 Sequence alignment of the 18S rRNA of *Micromonas* ASVs showing two *M. polaris* ASVs with a single nucleotide difference, and a *M. commoda* A2 ASV.

1029	Fig. S7	Partial snapshot of M . polaris ASV_0003 (top panel) and ASV_0154 (lower panel) distri-
1030		bution in the meta PR² database showing 100% similar reads from other studies. Colors
1031		indicate different sampling campaigns within $metaPR^2$. Size of bubbles represent the per-
1032		centage in relation to other eukaryotes within each station. Note that maximum percent-
1033		ages are distinct between panels to compensate for the lower abundance of ASV_0154.

Fig. S8 Partial snapshot of *Thalassiosira* ASV_0013 (top panel), ASV_0057 (middle panel), and ASV_0071 (lower panel) distribution in the metaPR² database showing 100% similar reads from other studies. Colors indicate different sampling campaigns within metaPR². Size of bubbles represent the percentage in relation to other eukaryotes within each station. Note that maximum percentages are distinct between panels. The approximate region of sampling from the present study is marked by a red square.

1040 Tables

Station	Longitude	Latitude	Day	Sector	Ice(%)	OWD	Size fractions
G100	-56.8	68.5	161	OW	0	12	0.2/20
G102	-57.5	68.5	162	OW	0	12	0.2/20
G107	-59.3	68.5	163	UI	100	-19	0.2/20
G110	-60.1	68.5	164	UI	100	-25	0.2/3/20
G115	-61.4	68.4	165	UI	93	-27	0.2/3/20
G201	-59.9	68.6	166	UI	99	-21	0.2/3/20
G204	-59.3	68.7	167	UI	93	-14	0.2/3/20
G207	-58.5	68.8	168	MIZ	41	2	0.2/3/20
G300	-56.8	69	169	OW	0	26	0.2/3/20
G309	-58.7	69	170	MIZ	0	2	0.2/3/20
G312	-59.6	69	171	MIZ	100	-10	0.2/3/20
G318	-61	69	172	UI	99	-15	0.2/3/20
G324	-62.3	69	173	UI	100	-23	0.2/3/20
G507	-59.1	70	182	MIZ	0	3	3/20
G512	-60.4	70	183	MIZ	0	2	3/20
G519	-62.4	70	184	MIZ	84	-3	3/20

Table 1: Stations with their geographical coordinates, julian day, the sectors where it belongs (under ice, marginal ice zone or open water), the percentage of ice cover and how many days it has been ice free upon sampling, and size fractions analyzed.

 Table 2: Number of samples within each sector for each size fraction.

Sector	0.2-3 $\mu {\rm m}$	3-20 $\mu {\rm m}$	$>20~\mu{\rm m}$
UI	40	35	40
MIZ	18	28	34
OW	16	5	18

Table 3: Number of ASVs by phytoplankton genera present in each sector; only genera with more than 2 ASVs in the whole dataset were taken into account. Note that taxa not assigned to the genus level might contain more than one genus.

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Class	Genus	UI	MIZ	OW	Total
Bacillariophyta	Bacillaria	7	7	3	9
Bacillariophyta	Chaetoceros	19	26	22	35
Bacillariophyta	Cylindrotheca	2	3	1	5
Bacillariophyta	Ditylum	3	1	0	3
Bacillariophyta	Entomoneis	6	2	1	6
Bacillariophyta	Fragilaria	3	3	1	3
Bacillariophyta	Fragilariops is	3	3	2	3
Bacillariophyta	Melosira	3	4	1	5
Bacillariophyta	Navicula	3	2	2	3
Bacillariophyta	Naviculales	5	2	1	5
Bacillariophyta	Pleurosigma	3	1	0	3
Bacillariophyta	Pseudogomphonema	3	1	0	3
Bacillariophyta	Pseudo-nitzschia	2	4	1	6
Bacillariophyta	Raphid-pennate X	6	6	0	6
Bacillariophyta	Stauroneis	2	3	0	3
Bolidophyceae	Parmales env 1 X	4	3	1	5
Bolidophyceae	Parmales env 2 X	5	1	0	6
Bolidophyceae	Parmales env 3 X	2	1	0	3
Bolidophyceae	Triparma	3	3	2	6
Cryptophyceae	Falcomonas	5	3	1	5
Cryptophyceae	Goniomonadales XX	3	0	1	4
Cryptophyceae	Plagioselmis	1	3	1	3
Cryptophyceae	Rhodomonas	3	3	2	4
Cryptophyceae	Teleaulax	3	1	1	3
Dictyochophyceae	Pseudochattonella	6	4	1	6
Haptophyta Clade HAP4	Haptophyta Clade HAP4 XXX	3	0	0	3
Haptophyta X	Haptophyta XXXX	3	2	0	3
Mamiellophyceae	Dolichomastigaceae-B	14	12	11	29
Mamiellophyceae	Micromonas	5	6	3	7
MOCH-1	MOCH-1 XXX	3	1	0	3
MOCH-2	MOCH-2 XXX	5	4	0	6

Class	Genus	UI	MIZ	OW	Total
Pyramimonadophyceae	Pyramimonadales XXX	4	4	2	4
Pyramimonadophyceae	Pterosperma	3	1	1	4
Pyramimonadophyceae	Pyramimonas	7	6	3	8

Table 3: (continued)

Table 4: Indicator ASVs with their taxonomic assignation for each sector or group of sectors, divided by size fraction. "A" represents the positive predictive power of the ASV, or the probability of a sampling site being a member of the sector or group of sectors when the ASV appears in that site. "B" represents how often one ASV is found in sampling sites of the sector or group of sectors. The value of the correlation (stat) and the statistical significance of the association (*p*-value) are also shown.

Size fraction	Sectors	ASVs	Class	Species	А	В	Stat	p.value	Sign
0.2 -3 μm	UI	asv_023_00009	Bacillariophyta	Melosira arctica	0.98	0.7	0.83	1e-04	***
0.2-3 $\mu{\rm m}$	UI	asv_023_00015	Bacillariophyta	Fragilariopsis cylindrus	0.93	0.75	0.83	1e-04	***
0.2-3 $\mu{\rm m}$	UI	asv_023_00104	Mamiellophyceae	Mantoniella squamata	1	0.48	0.69	2e-04	***
0.2-3 $\mu{\rm m}$	UI	asv_023_00125	Prymnesiophyceae	Phaeocystis sp.	0.93	0.75	0.84	1e-04	***
0.2-3 $\mu{\rm m}$	UI	asv_023_00171	Bacillariophyta	Bacillaria paxillifer	0.97	0.68	0.81	1e-04	***
0.2-3 $\mu{\rm m}$	UI	asv_023_00244	Pyramimonadales	Pterosperma sp.	1	0.42	0.65	5e-04	***
0.2-3 $\mu{\rm m}$	UI	asv_023_00311	Pelagophyceae	Ankylochrysis sp.	0.96	0.48	0.67	4e-04	***
0.2-3 $\mu{\rm m}$	UI	asv_023_00384	Mamiellophyceae	Dolichomastigaceae-B sp.	1	0.32	0.57	0.0031	**
0.2-3 $\mu{\rm m}$	UI	asv_023_00239	Prymnesiophyceae	Chrysochromulina sp.	1	0.22	0.47	0.0189	*
0.2-3 $\mu{\rm m}$	UI	asv_023_00381	Haptophyta_Clade_HAP4	Haptophyta Clade HAP4 XXX sp. $$	1	0.28	0.52	0.0107	*
0.2-3 $\mu{\rm m}$	MIZ	asv_023_00008	Bacillariophyta	Thalassiosira antarctica	0.52	0.78	0.63	0.0186	*
0.2-3 $\mu{\rm m}$	MIZ	asv_023_00049	Bacillariophyta	Navicula sp.	0.74	0.39	0.54	0.0067	**
0.2-3 $\mu {\rm m}$	OW	asv_023_00421	Mamiellophyceae	Dolichomastigaceae-B sp.	0.89	0.44	0.62	2e-04	***
0.2-3 $\mu {\rm m}$	OW	asv_023_00469	Dictyochophyceae	Pedinellales X sp.	0.98	0.81	0.89	1e-04	***
0.2-3 $\mu {\rm m}$	OW	asv_023_00593	Dictyochophyceae	Pedinellales X sp.	1	0.5	0.71	1e-04	***
0.2-3 $\mu{\rm m}$	OW	asv_023_00731	Dictyochophyceae	Pedinellales X sp.	1	0.31	0.56	3e-04	***
0.2-3 $\mu{\rm m}$	OW	asv_023_00223	Prymnesiophyceae	Prymnesiophyceae Clade F XX sp.	0.89	0.19	0.41	0.0149	*
0.2-3 $\mu{\rm m}$	OW	asv_023_00949	Mamiellophyceae	Dolichomastigaceae-B sp.	1	0.12	0.35	0.0447	*
0.2-3 $\mu{\rm m}$	MIZ+UI	asv_023_00086	Prymnesiophyceae	Chrysochromulina sp.	1	0.33	0.57	0.0262	*
0.2-3 $\mu{\rm m}$	MIZ+UI	asv_023_00041	Cryptophyceae	Falcomonas daucoides	0.95	0.91	0.93	1e-04	***
0.2-3 $\mu{\rm m}$	MIZ+UI	asv_023_00046	Bacillariophyta	Pseudo-nitzschia seriata	1	0.59	0.77	2e-04	***
0.2-3 $\mu{\rm m}$	MIZ+UI	asv_023_00048	Bacillariophyta	Chaetoceros neogracilis	0.97	0.79	0.88	1e-04	***
0.2-3 $\mu{\rm m}$	MIZ+UI	asv_023_00055	Cryptophyceae	Falcomonas daucoides	1	0.57	0.75	8e-04	***
0.2-3 $\mu{\rm m}$	MIZ+UI	asv_023_00061	MOCH-2	MOCH-2 XXX sp.	1	0.78	0.88	1e-04	***
0.2-3 $\mu{\rm m}$	MIZ+UI	asv_023_00073	Bolidophyceae	Triparma laevis clade	0.97	0.76	0.86	2e-04	***
0.2-3 $\mu{\rm m}$	MIZ+UI	asv_023_00075	Dictyochophyceae	Dictyocha sp.eculum	1	0.62	0.79	2e-04	***
0.2-3 $\mu{\rm m}$	MIZ+UI	asv_023_00081	Mamiellophyceae	Bathycoccus prasinos	0.96	0.91	0.94	1e-04	***
0.2-3 $\mu{\rm m}$	MIZ+UI	asv_023_00192	Prymnesiophyceae	Haptolina sp.	0.94	0.45	0.65	0.0444	*
0.2-3 $\mu{\rm m}$	MIZ+UI	asv_023_00105	Prymnesiophyceae	Phaeocystis cordata	1	0.5	0.71	0.0013	**
0.2-3 $\mu {\rm m}$	MIZ+UI	asv_023_00114	Dictyochophyceae	Florenciellales X sp.	0.98	0.66	0.8	2e-04	***
0.2-3 $\mu{\rm m}$	MIZ+UI	asv_023_00133	Pelagophyceae	Pelagomonas calceolata	0.98	0.83	0.9	1e-04	***
0.2-3 $\mu{\rm m}$	MIZ+UI	asv_023_00151	Dictyochophyceae	Florenciella parvula	0.97	0.83	0.9	1e-04	***
0.2-3 $\mu{\rm m}$	MIZ+UI	asv_023_00267	Mamiellophyceae	Dolichomastigaceae-B sp.	1	0.29	0.54	0.0393	*
0.2-3 $\mu {\rm m}$	MIZ+UI	asv_023_00154	Mamiellophyceae	Micromonas polaris	1	0.48	0.7	0.0017	**
0.2-3 $\mu{\rm m}$	MIZ+UI	asv_023_00235	Mamiellophyceae	Micromonas commoda A2	0.96	0.9	0.93	1e-04	***
0.2-3 $\mu{\rm m}$	MIZ+UI	asv_023_00236	Dictyochophyceae	Pseudochattonella sp.	1	0.76	0.87	1e-04	***
0.2-3 $\mu{\rm m}$	MIZ+OW	asv_023_00016	Bacillariophyta	Porosira glacialis	0.87	0.53	0.68	9e-04	***
0.2-3 $\mu{\rm m}$	MIZ+OW	asv_023_00136	Bacillariophyta	Chaetoceros decipiens	0.91	0.88	0.9	1e-04	***
0.2-3 $\mu {\rm m}$	MIZ+OW	asv_023_00247	Prymnesiophyceae	Prymnesiophyceae Clade E XX sp.	0.93	0.5	0.68	5e-04	***
3-20 $\mu {\rm m}$	UI	asv_023_00171	Bacillariophyta	Bacillaria paxillifer	0.94	0.6	0.75	0.0031	**
3-20 $\mu {\rm m}$	UI	asv_023_00244	Pyramimonadales	Pterosperma sp.	1	0.49	0.7	0.0095	**
3-20 $\mu {\rm m}$	UI	asv_023_00104	Mamiellophyceae	Mantoniella squamata	0.94	0.46	0.66	0.0175	*
3-20 $\mu {\rm m}$	UI	asv_023_00281	Cryptophyceae	Cryptomonadales XX sp.	0.87	0.57	0.71	0.0251	*
3-20 $\mu {\rm m}$	UI	asv_023_00239	Prymnesiophyceae	Chrysochromulina sp.	0.94	0.4	0.61	0.0327	*
3-20 $\mu {\rm m}$	UI	asv_023_00311	Pelagophyceae	Ankylochrysis sp.	0.86	0.46	0.63	0.0421	*
3-20 $\mu {\rm m}$	MIZ	asv_023_00064	Bacillariophyta	Fragilaria sp.	0.89	0.44	0.63	0.0267	*
3-20 $\mu {\rm m}$	MIZ	asv_023_00347	MOCH-2	MOCH-2 XXX sp.	0.89	0.59	0.73	0.0127	*

Table 4: (continued)

Size fraction	Sectors	ASVs	Class	Species	Α	В	Stat	p.value	Sign
3-20 μm	MIZ	asv_023_00016	Bacillariophyta	Porosira glacialis	0.82	0.74	0.78	0.0047	**
3-20 $\mu {\rm m}$	MIZ	asv_023_00277	Bacillariophyta	Naviculales sp.	0.93	0.37	0.59	0.0488	*
3-20 $\mu {\rm m}$	MIZ	asv_023_00663	Filosa-Imbricatea	Novel-clade-2 X sp.	1	0.19	0.43	0.0438	*
3-20 $\mu {\rm m}$	MIZ	asv_023_00008	Bacillariophyta	Thalassiosira antarctica	0.77	0.74	0.76	0.0166	*
3-20 $\mu {\rm m}$	MIZ	asv_023_00049	Bacillariophyta	Navicula sp.	0.82	0.89	0.85	6e-04	***
3-20 $\mu {\rm m}$	OW	asv_023_00320	Bacillariophyta	Navicula sp.	0.54	0.8	0.66	0.0141	*
3-20 $\mu {\rm m}$	OW	asv_023_00057	Bacillariophyta	Thalassiosira sp.	0.92	0.8	0.86	1e-04	***
3-20 $\mu {\rm m}$	OW	asv_023_00177	Bacillariophyta	Chaetoceros rostratus	0.83	1	0.91	1e-04	***
3-20 $\mu {\rm m}$	$_{\rm MIZ+UI}$	asv_023_00009	Bacillariophyta	Melosira arctica	1	0.69	0.83	0.0045	**
3-20 $\mu {\rm m}$	$_{\rm MIZ+UI}$	asv_023_00015	Bacillariophyta	Fragilariopsis cylindrus	1	0.98	0.99	1e-04	***
3-20 $\mu {\rm m}$	$_{\rm MIZ+UI}$	asv_023_00041	Cryptophyceae	Falcomonas daucoides	1	0.81	0.9	8e-04	***
3-20 $\mu {\rm m}$	MIZ+UI	asv_023_00046	Bacillariophyta	Pseudo-nitzschia seriata	1	0.87	0.93	2e-04	***
3-20 $\mu {\rm m}$	$_{\rm MIZ+UI}$	asv_023_00048	Bacillariophyta	Chaetoceros neogracilis	0.99	0.98	0.99	1e-04	***
3-20 $\mu {\rm m}$	MIZ+UI	asv_023_00022	Bacillariophyta	Actinocyclus curvatulus	0.98	0.77	0.87	0.0126	*
3-20 $\mu {\rm m}$	MIZ+UI	asv_023_00099	Bacillariophyta	Cylindrotheca closterium	1	0.65	0.8	0.0143	*
3-20 $\mu {\rm m}$	MIZ+UI	asv_023_00061	MOCH-2	MOCH-2 XXX sp.	1	0.94	0.97	2e-04	***
3-20 $\mu {\rm m}$	MIZ+UI	asv_023_00073	Bolidophyceae	Triparma laevis clade	1	0.89	0.94	1e-04	***
3-20 $\mu {\rm m}$	MIZ+UI	asv_023_00075	Dictyochophyceae	Dictyocha speculum	1	0.79	0.89	9e-04	***
3-20 $\mu{\rm m}$	MIZ+UI	asv_023_00109	Bacillariophyta	Fragilariopsis sublineata	1	0.61	0.78	0.0192	*
3-20 $\mu{\rm m}$	MIZ+UI	asv_023_00003	Mamiellophyceae	Micromonas polaris	1	0.61	0.78	0.0189	*
3-20 $\mu{\rm m}$	MIZ+UI	asv_023_00114	Dictyochophyceae	Florenciellales X sp.	1	0.73	0.85	0.0046	**
3-20 $\mu{\rm m}$	MIZ+UI	asv_023_00105	Prymnesiophyceae	Phaeocystis cordata	1	0.58	0.76	0.0289	*
3-20 $\mu{\rm m}$	MIZ+UI	asv_023_00125	Prymnesiophyceae	Phaeocystis sp.	1	0.65	0.8	0.0215	*
3-20 μm	MIZ+UI	asv_023_00149	Cryptophyceae	Plagioselmis prolonga	0.99	0.56	0.75	0.0364	*
3-20 μm	MIZ+OW	asv_023_00079	Bacillariophyta	Eucampia sp.	0.93	0.75	0.83	5e-04	***
3-20 $\mu{\rm m}$	MIZ+OW	asv_023_00136	Bacillariophyta	Chaetoceros decipiens	0.92	0.78	0.85	0.0011	**
3-20 μm	MIZ+OW	asv_023_00225	Pelagophyceae	Ankylochrysis sp.	0.96	0.53	0.72	0.0116	*
3-20 $\mu{\rm m}$	MIZ+OW	asv_023_00283	Bacillariophyta	Attheya septentrionalis	0.92	0.34	0.56	0.0476	*
3-20 $\mu {\rm m}$	MIZ+OW	asv_023_00218	Bacillariophyta	Chaetoceros danicus	0.92	0.69	0.8	0.0028	**
3-20 μm	MIZ+OW	asv_023_00223	Prymnesiophyceae	Prymnesiophyceae Clade F XX sp.	0.9	0.5	0.67	0.0302	*
3-20 μm	MIZ+OW	asv_023_00013	Bacillariophyta	Thalassiosira rotula	0.97	0.31	0.55	0.0398	*
$> 20 \ \mu {\rm m}$	UI	asv_023_00086	Prymnesiophyceae	Chrysochromulina sp.	0.96	0.17	0.41	0.017	*
$> 20 \ \mu {\rm m}$	UI	asv_023_00046	Bacillariophyta	Pseudo-nitzschia seriata	0.79	0.85	0.82	1e-04	***
$> 20 \ \mu m$	UI	asv_023_00105	Prymnesiophyceae	Phaeocystis cordata	0.76	0.45	0.58	0.0019	**
$> 20 \ \mu m$	MIZ	asv_023_00259	Bacillariophyta	Entomoneis ornata	0.83	0.62	0.72	2e-04	***
$> 20 \ \mu m$	MIZ	asv_023_00265	Bacillariophyta	Pauliella toeniata	0.69	0.68	0.68	0.0046	**
$> 20 \ \mu m$	OW	asv_023_00334	Bacillariophyta	Chaetoceros contortus	0.72	0.83	0.77	1e-04	***
$> 20 \ \mu m$	OW	asv_023_00407	Bacillariophyta	Chaetoceros diadema 1			0.74	1e-04	***
$> 20 \ \mu m$	MIZ+UI	asv_023_00009	Bacillariophyta	Melosira arctica	1	1	1	1e-04	***
$> 20 \ \mu m$	MIZ+UI	asv_023_00025	Bacillariophyta	Melosira arctica	1	0.81	0.9	1e-04	***
$> 20 \ \mu m$	MIZ+UI	asv_023_00038	Cryptophyceae	Teleaulax gracilis	0.97	0.51	0.71	9e-04	***
$> 20 \ \mu m$	MIZ+UI	asv 023 00049		Navicula sp.	0.97	0.84	0.9	1e-04	***
$> 20 \ \mu m$	MIZ+UI	asv 023 00064	Bacillariophyta	Fragilaria sp.		0.73		1e-04	***
$> 20 \ \mu m$	MIZ+UI	asv 023 00073	Bolidophyceae	Triparma laevis clade	0.99	0.61	0.78	1e-04	***
$> 20 \ \mu m$ $> 20 \ \mu m$			Dictyochophyceae	Dictyocha speculum	1		0.89	1e-04	***
$> 20 \ \mu \text{m}$ $> 20 \ \mu \text{m}$		asv 023 00084		Raphid-pennate X sp.	1	0.81		1e-04	***
$> 20 \ \mu \text{m}$ $> 20 \ \mu \text{m}$		asv_023_00099	* *	Cylindrotheca closterium	1		0.75	1e-04	***
$> 20 \ \mu \text{m}$ $> 20 \ \mu \text{m}$		asv 023 00178		Raphid-pennate X sp.	1			0.0124	*
$> 20 \ \mu \text{m}$ $> 20 \ \mu \text{m}$		asv_023_00173 asv_023_00172	* *	Attheya septentrionalis	1		0.89		***
~ =0 µm			=		-	5.0	0.00	10 01	

Size fraction	Sectors	ASVs	Class	Species	А	В	Stat	p.value	Sign
$> 20 \ \mu m$	MIZ+UI	asv_023_00184	Bacillariophyta	Pleurosigma intermedium	1	0.65	0.8	1e-04	***
$>$ 20 $\mu{\rm m}$	MIZ+UI	asv_023_00219	Bacillariophyta	Bacillaria paxillifer	1	0.5	0.71	3e-04	***
$>$ 20 $\mu{\rm m}$	MIZ+UI	asv_023_00268	Bacillariophyta	Stauroneis kriegeri	1	0.49	0.7	0.001	***
$>$ 20 $\mu{\rm m}$	MIZ+UI	asv_023_00277	Bacillariophyta	Naviculales sp.	0.97	0.61	0.77	3e-04	***
$>$ 20 $\mu{\rm m}$	MIZ+UI	asv_023_00308	Bacillariophyta	Synedra hyperborea	1	0.42	0.65	0.0033	**
$>$ 20 $\mu{\rm m}$	MIZ+UI	asv_023_00335	Bacillariophyta	Raphid-pennate X sp.	1	0.61	0.78	1e-04	***
$>$ 20 $\mu{\rm m}$	MIZ+OW	asv_023_00001	Prymnesiophyceae	Phaeocystis pouchetii	0.91	1	0.96	1e-04	***
$>$ 20 $\mu{\rm m}$	MIZ+OW	asv_023_00013	Bacillariophyta	Thalassiosira rotula	0.96	0.96	0.96	1e-04	***
$>$ 20 $\mu{\rm m}$	MIZ+OW	asv_023_00028	Bacillariophyta	Thalassiosira sp.	0.77	0.85	0.81	3e-04	***
$>$ 20 $\mu{\rm m}$	MIZ+OW	asv_023_00057	Bacillariophyta	Thalassiosira sp.	0.93	0.9	0.92	1e-04	***
$>$ 20 $\mu{\rm m}$	MIZ+OW	asv_023_00071	Bacillariophyta	Thalassiosira anguste-lineata	0.97	0.71	0.83	1e-04	***
$>$ 20 $\mu{\rm m}$	MIZ+OW	asv_023_00079	Bacillariophyta	Eucampia sp.	0.94	0.9	0.92	1e-04	***
$>$ 20 $\mu{\rm m}$	MIZ+OW	asv_023_00111	Bacillariophyta	Chaetoceros cinctus	0.89	0.81	0.85	1e-04	***
$>$ 20 $\mu{\rm m}$	MIZ+OW	asv_023_00136	Bacillariophyta	Chaetoceros decipiens	0.87	0.79	0.83	1e-04	***
$>$ 20 $\mu{\rm m}$	MIZ+OW	asv_023_00137	Bacillariophyta	Detonula confervacea	0.9	0.79	0.84	1e-04	***
$>$ 20 $\mu{\rm m}$	MIZ+OW	asv_023_00177	Bacillariophyta	Chaetoceros rostratus	0.89	0.85	0.87	1e-04	***
$>$ 20 $\mu{\rm m}$	MIZ+OW	asv_023_00218	Bacillariophyta	Chaetoceros danicus	0.92	0.73	0.82	1e-04	***

Table 4: (continued)

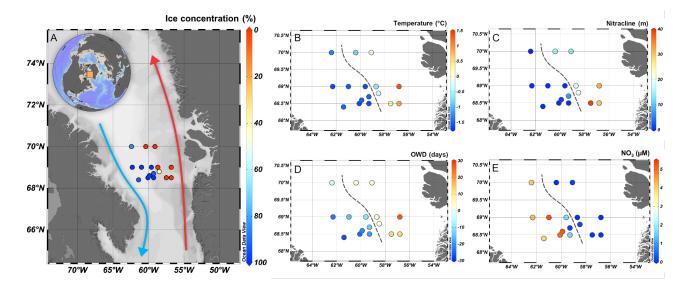


Figure 1: Location of the sampling stations in Baffin Bay and environmental variables. (A) Sampling stations indicating the sea-ice concentration (%); the red arrow represents the warmer West Greenland Current, and the blue arrow represents the Pacific-originated Baffin Current; (B) Temperature (°C) in surface; (C) Depth of the nitracline (meters); (D) Open Water Days: amount of days of open water before (positive values) or after (negative values) the sampling day; (E) Nitrate concentration in surface (μ M). A dashed line separates sampling stations with more (east) and less (west) than 80% sea-ice cover.

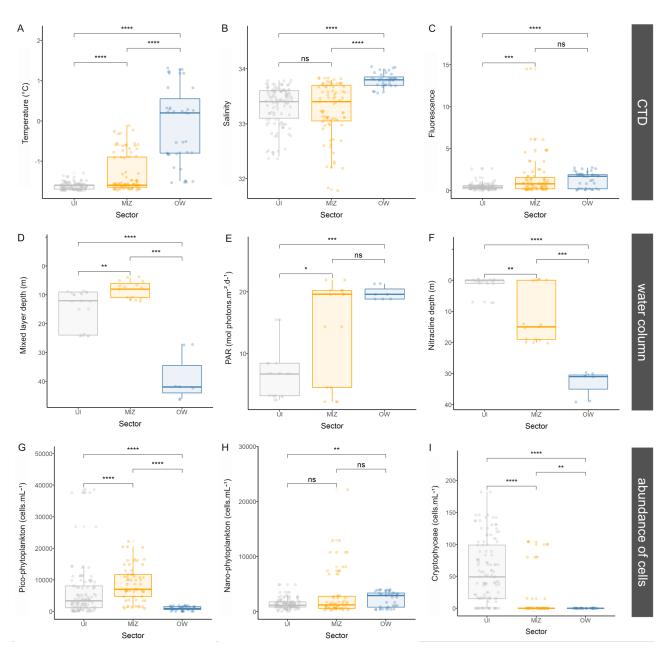


Figure 2: Environmental variables for the three sectors: UI (gray), MIZ (yellow) and OW (blue); (A) temperature (°C); (B) salinity; (C) fluorescence; (D) mixed layer depth (m); (E) Photosynthetically Active Radiation at 3 m (mol photons.m⁻².d⁻¹); (F) nitracline depth (m); (G) pico-phytoplankton abundance (cells.mL⁻¹); (H) nano-phytoplankton abundance (cells.mL⁻¹); (I) Cryptophyceae abundance (cells.mL⁻¹). Number of asterisks represent *p*-value obtained with the Wilcox test as follows: (*) $p \le 0.05$; (**) $p \le 0.01$; (***) $p \le 0.001$; (****) $p \le 0.0001$; "ns" = not significant.

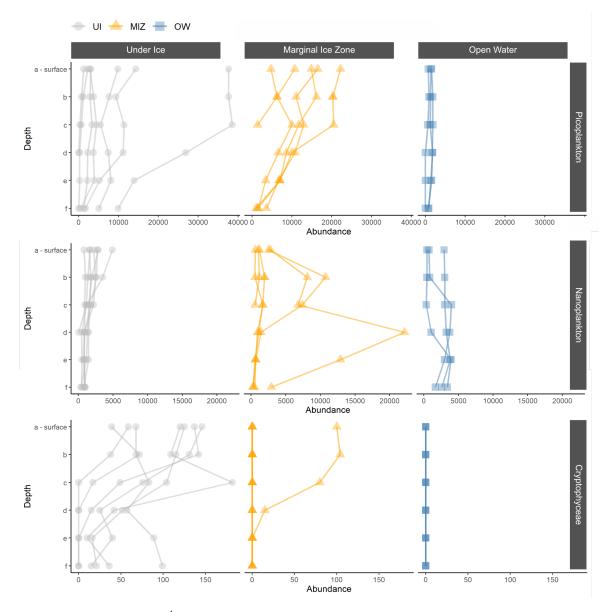


Figure 3: Abundance (cells.mL⁻¹) measured by FCM of pico-phytoplankton (top panels), nano-phytoplankton (middle panels) and Cryptophyceae (lower panels) according to depth, divided between the three sectors: UI (gray), MIZ (yellow) and OW (blue).

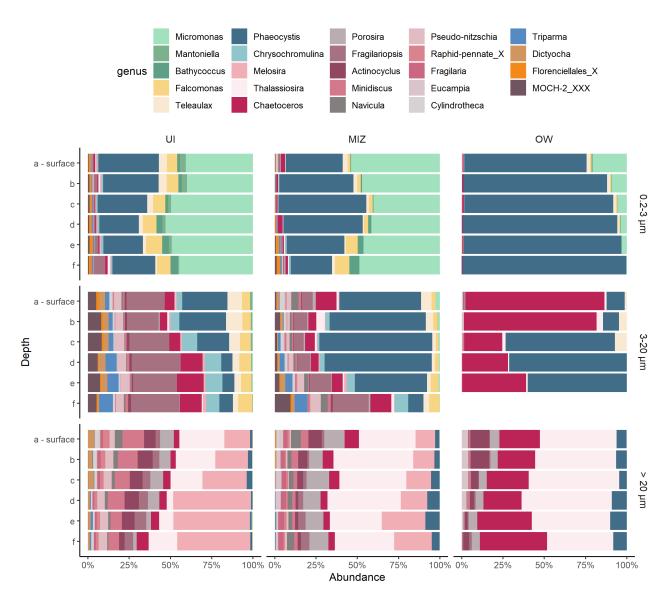


Figure 4: Relative abundance of reads at the genus level between sectors and size fractions. UI: Under Ice; MIZ: Marginal Ice Zone; OW: Open Water; letters on the y-axis refer to the depth level where "a" corresponds to the surface and "f" to the deepest sample depth, usually between 40 m and 60 m depth.

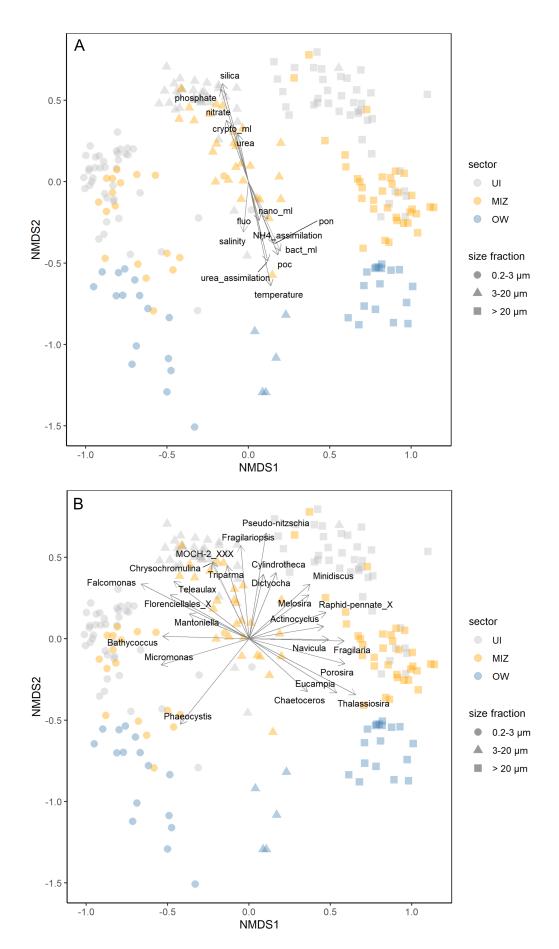


Figure 5: Non-metric multidimensional scaling (NMDS) analysis using Bray-Curtis dissimilarities of the phytoplankton community composition; only statistically significant (A) environmental parameters (p-value = 0.001) and (B) genera (p-value = 0.05) were plotted against ordination. Parameters: ammonium assimilation (NH4_assimilation), bacteria abundance (bact_ml), Cryptophyceae abundance (crypto_ml), fluorescence (fluo), nano-phytoplankton abundance (nano_ml), nitrates, silica, particulate organic carbon (poc), particulate organic nitrogen (pon), phosphate, salinity, temperature, urea, and urea assimilation (urea_assimilation). Stress: 0.11.

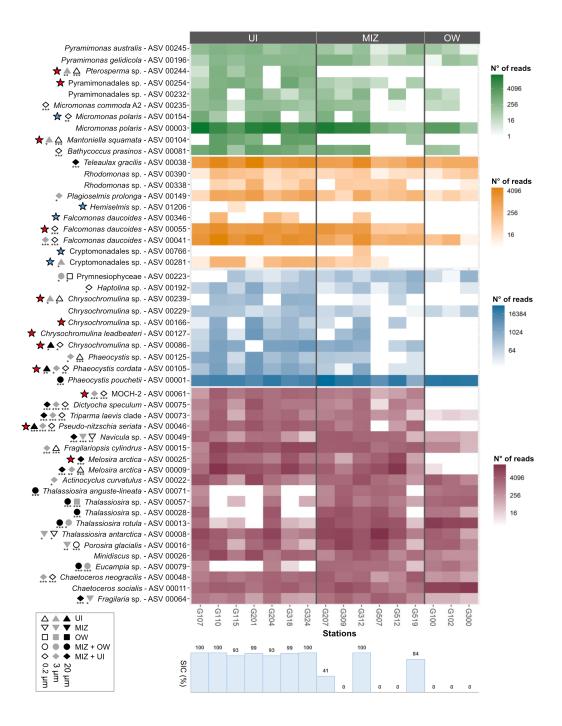


Figure 6: Taxa distribution of the most abundant ASVs for each sector, divided by sampling stations; the top 10 ASVs were selected within Chlorophyta (green), Cryptophyta (orange), Haptophyta (blue), and the top 20 most abundant within the highly diverse Ochrophyta division (red); symbols indicate if a given ASV was reported as indicator ASV for UI (triangles), MIZ (inverted triangles), OW (squares), MIZ+UI (diamonds) or MIZ+OW (circles) sector groups within 0.2-3 μ m (white), 3-20 μ m (grey) or > 20 μ m (black) size fractions; asterisks indicate the *p*-values associated with the indicator ASV: 0 (***), 0.001 (**), and 0.01 (*); red and blue stars indicate if a given ASV was found exclusively in ice-associated sectors, being blue stars not abundant ASVs; SIC = sea-ice concentration on each sampling station.

Arctic phytoplankton spring bloom diversity across the marginal ice zone in Baffin Bay

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¹⁰⁶¹ Supplementary material

All supplementary material is available at https://github.com/catherine-gerikas/GE_Amundsen_18S_metaB_
 supplementary_material

1064 Supplementary Data

- ¹⁰⁶⁵ Supplementary Data S1: Sample dates and environmental data available.
- ¹⁰⁶⁶ Available in: https://github.com/catherine-gerikas/GE_Amundsen_18S_metaB_supplementary_material

¹⁰⁶⁷ Supplementary Tables

Variable	Decription	Unit
sample_code	sample code	
fraction_name	size fraction	
station_id	station ID	
CTD	ID of CTD cast	
transect	cruise transect ID	
bot_depth	bottom depth an a given station	m
depth	depth on each the sample was taken	m
depth_rank	rank of sampling depth in the water column	
sampling_date	sampling date	
julian_day	julian day	
longitude	longitude coordinates	degrees east
latitude	latitude coordinayes	degrees north
OWD	days a given station was ice-free	days
by_OW_minus10_10	classification of sectors based in OWD	sector
$ice_concentration_percent$	ice concentration cover	%
dna_concentration	dna concentration	$ng.\mu L^{-1}$
dna_extraction_kit	dna extraction kit	
n_reads	number of reads after filtering	
reads_total	number of reads obtained from sequencing	
pico_ml	pico-phytoplankton abundance	$\rm cells.mL^{-1}$
nano_ml	nano-phytoplankton abundance	$\rm cells.mL^{-1}$
pico_and_nano_ml	pico- and nano phytoplankton abundance	$\rm cells.mL^{-1}$
crypto_ml	cryptophyceae abundance	$\rm cells.mL^{-1}$
bact	bacteria abundance	$cells.mL^{-1}$
temperature	temperature	degrees Celsius
fluo	fluorescence	
cdom	colored dissolved organic matter	(ppb)
salinity	salinity	
mixed_layer_depth	mixed layer depth	m
$nitracline_depth$	nitracline depth	m
PAR_irradiance	photosynthetically available radiation at 3 m depth	mol photons.m ^{-2} .d ^{-1}

 Table S1: List of variables measured during the Green Edge cruise (see Data Set S1).

Variable	Decription	Unit
primary_production	primary production	$\mu g C. L^{-1}. day^{-1}$
primary production_std_dev	primary production standard deviation	$\mu \rm gC.L^{-1}.day^{-1}$
don_release	dissolved organic nitrogen	$\rm nM.L^{-1}.day^{-1}$
NO3_assimilation	nitrate assimilation	$\mathrm{nM.L^{-1}.day^{-1}}$
NH4_assimilation	ammonium assimilation	$\mathrm{nM.L^{-1}.day^{-1}}$
urea_assimilation	urea assimilation	$\mathrm{nM.L^{-1}.day^{-1}}$
NH4_regeneration	ammonium regeneration	$\mathrm{nM}.\mathrm{L}^{-1}.\mathrm{day}^{-1}$
nitrification	nitrification	$\mathrm{nM}.\mathrm{L}^{-1}.\mathrm{day}^{-1}$
poc	particulate organic carbon	$\mu { m M}$
poc_std_dev	particulate organic carbon standard deviation	$\mu { m M}$
pon	particulate organic nitrogen	$\mu { m M}$
pon_std_dev	particulate organic nitrogen standard deviation	$\mu { m M}$
doc	dissolved organic carbon	$\mu { m M}$
don	dissolved organic nitrogen	$\mu { m M}$
nitrate	nitrate concentration	$\mu { m M}$
nitrite	nitrite concentration	$\mu { m M}$
phosphate	phosphate concentration	$\mu { m M}$
silica	orthosilicic acid concentration	$\mu { m M}$
ammonium	ammonium concentration	$\mu { m M}$
urea	urea concentration	$\mu { m M}$
ratio_NO3_SiOH4	ratio nitrate to silica	
ratio_PO4_NO3	ratio phosphate to nitrate	
ratio_NO3_PO4	ratio nitrate to phosphate	
chlorophyll_a	chlorophyll a concentration	${ m mg.m^{-3}}$
chlorophyll_b	chlorophyll b concentration	${ m mg.m^{-3}}$

Table S1: (continued)

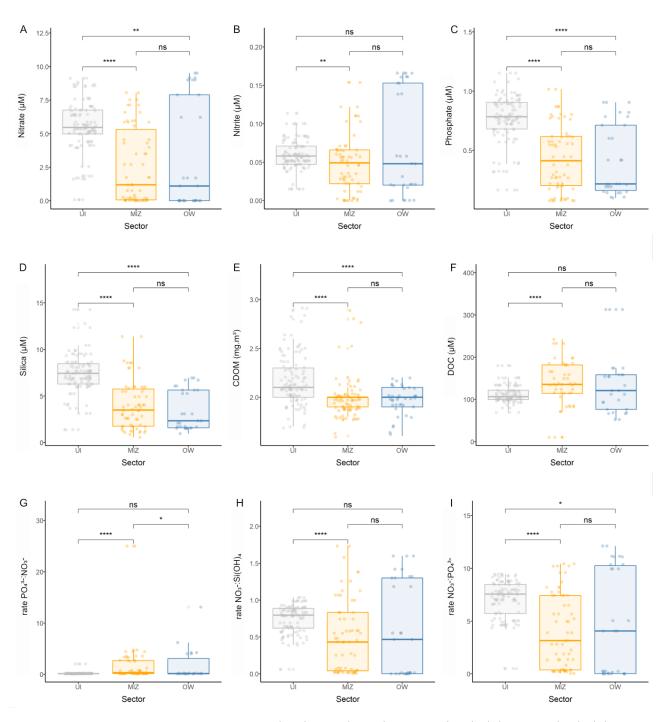


Figure S1: Nutrients for the three sectors: UI (grey), MIZ (yellow) and OW (blue); (A) nitrates (μ M); (B) nitrites (μ M); (C) phosphates (μ M); (D) orthosilicic acid (μ M); (E) colored dissolved organic matter (mg.m³); (F) dissolved organic carbon (μ M); (G) phosphate to nitrate ratio; (H) nitrate to orthosilicic acid ratio; (I) nitrate to phosphate ratio. Number of asterisks represent *p*-value obtained with the Wilcox test as follows: (*) $p \leq 0.05$; (**) $p \leq 0.01$; (***) $p \leq 0.001$; (**) $p \leq 0.001$; (

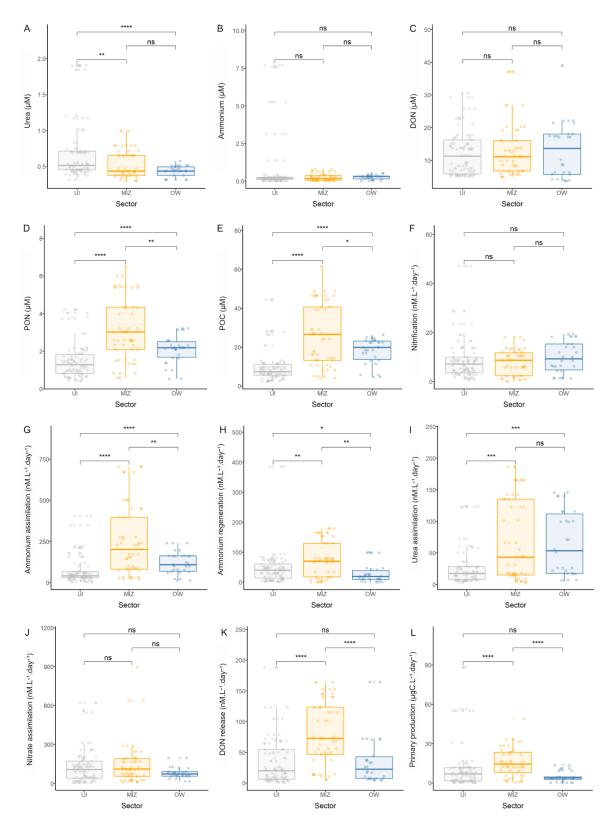


Figure S2: Nutrients and metabolic rates for the three sectors: UI (grey), MIZ (yellow) and OW (blue); (A) urea (μ M); (B) ammonium (μ M); (C) dissolved organic nitrogen (μ M); (D) particulate organic nitrogen (μ M); (E) particulate organic carbon (mg.m³); (F) nitrification (μ M); (G) ammonium assimilation (nM.L⁻¹.day⁻¹); (H) ammonium regeneration (nM.L⁻¹.day⁻¹); (I) urea assimilation (nM.L⁻¹.day⁻¹); (J) nitrate assimilation; (K) dissolved organic nitrogen (μ M); (L) primary production (μ gC.L⁻¹.day⁻¹). Number of asterisks represent *p*-value obtained with the Wilcox test as follows: (*) $p \leq 0.05$; (**) $p \leq 0.01$; (***) $p \leq 0.001$; (****) $p \leq 0.0001$; "ns" = not significant.

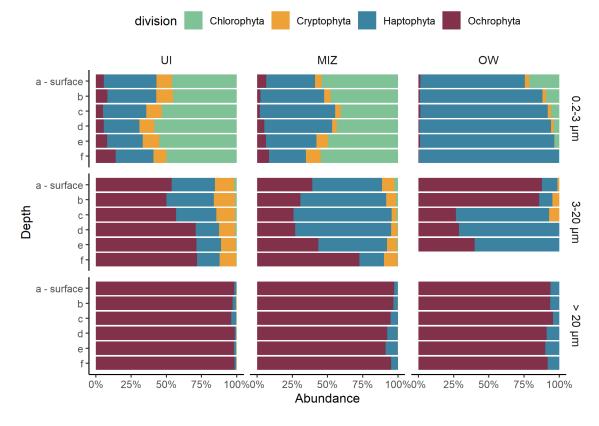


Figure S3: Relative abundance of reads at the division level between sectors and size fractions. UI: Under Ice; MIZ: Marginal Ice Zone; OW: Open Water; letters on the y-axis refer to the depth level where "a" corresponds to the surface and "f" to the deepest sampled depth, usually between 40 m and 60 m.

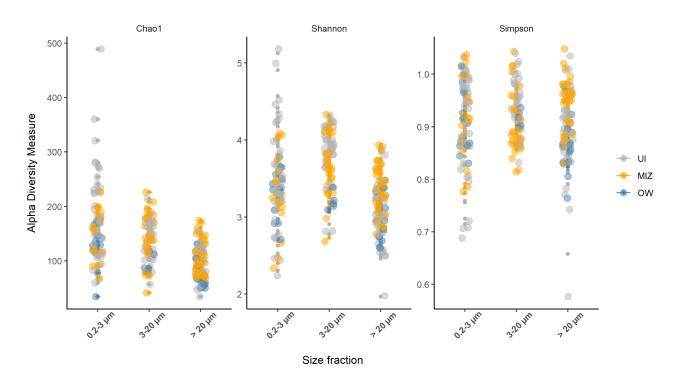


Figure S4: Chao1, Shannon and Simpson alpha diversity indices divided by size fraction; sectors are represented by the colors grey (UI), yellow (MIZ) and blue (OW).

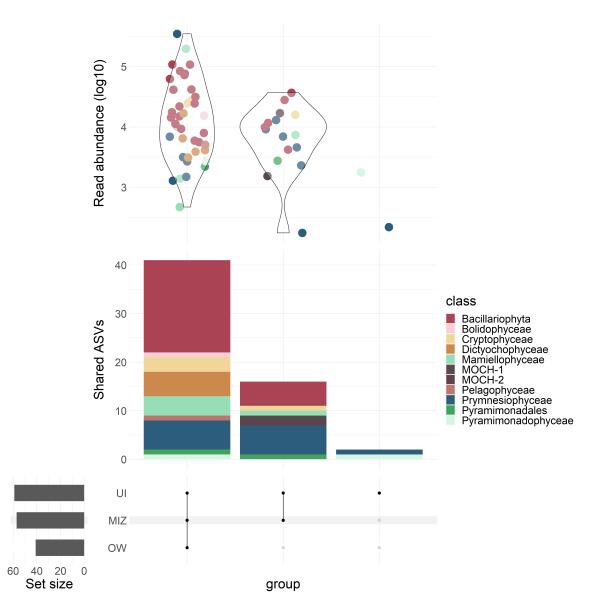


Figure S5: Number of ASVs from the abundant community exclusive from or shared between the sectors UI (under ice), MIZ (marginal ice-zone), and OW (open water); colors represent the class from each ASV; read abundance (in log10) is displayed at the top of each intersection; the names and assignations of the ASVs exclusive from ice-associated sectors are shown in grey panels.

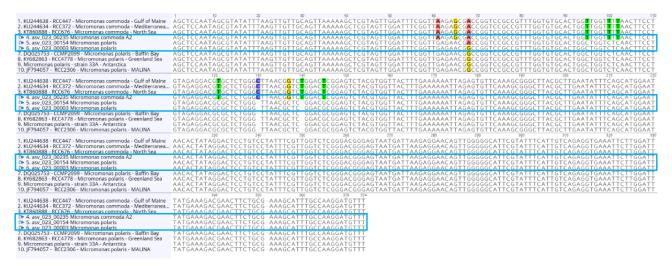


Figure S6: Sequence alignment of the 18S rRNA of *Micromonas* ASVs showing two *M. polaris* ASVs with a single nucleotide difference, and a *M. commoda* A2 ASV.

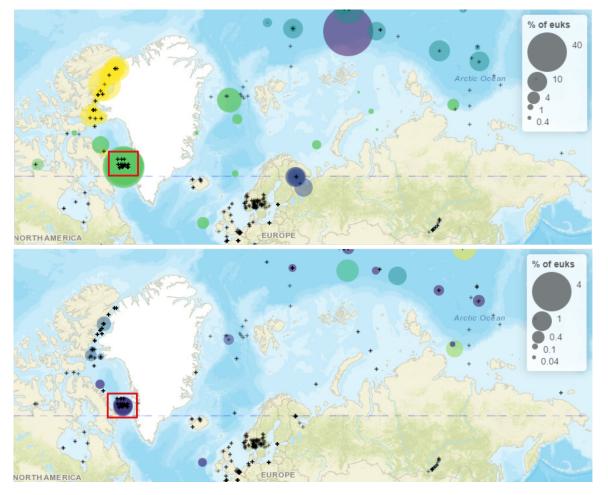


Figure S7: Partial snapshot of M. polaris ASV_0003 (top panel) and ASV_0154 (lower panel) distribution in the metaPR² database showing 100% similar reads from other studies. Colors indicate different sampling campaigns within metaPR². Size of bubbles represent the percentage in relation to other eukaryotes within each station. Note that maximum percentages are distinct between panels to compensate for the lower abundance of ASV_0154.

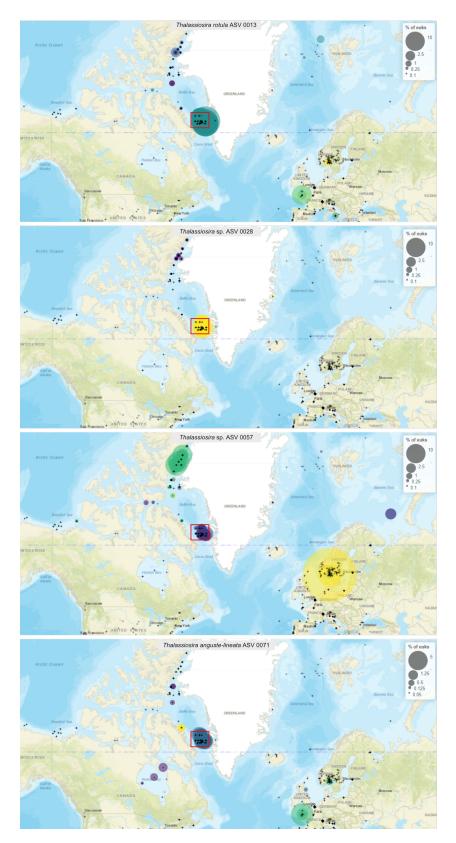


Figure S8: Partial snapshot of *Thalassiosira* ASV_0013 (top panel), ASV_0057 (middle panel), and ASV_0071 (lower panel) distribution in the meta PR^2 database showing 100% similar reads from other studies. Colors indicate different sampling campaigns within meta PR^2 . Size of bubbles represent the percentage in relation to other eukaryotes within each station. Note that maximum percentages are distinct between panels. The approximate region of sampling from the present study is marked by a red square.