

Use of organic exudates from two polar diatoms by bacterial isolates from the Arctic Ocean

Lucas Tisserand, Laëtitia Dadaglio, Laurent Intertaglia, Philippe Catala, Christos Panagiotopoulos, Ingrid Obernosterer, Fabien Joux

▶ **To cite this version:**

Lucas Tisserand, Laëtitia Dadaglio, Laurent Intertaglia, Philippe Catala, Christos Panagiotopoulos, et al.. Use of organic exudates from two polar diatoms by bacterial isolates from the Arctic Ocean. Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences, 2020, 378, pp.20190356. 10.1098/rsta.2019.0356 . hal-02916320

HAL Id: hal-02916320
https://hal.science/hal-02916320

Submitted on 17 Aug 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Use of organic exudates from two polar diatoms by bacterial isolates from the Arctic Ocean

Lucas Tisserand[1], Laëtitia Dadaglio[1], Laurent Intertaglia[2], Philippe Catala[1], Christos Panagiotopoulos[3], Ingrid Obernosterer[1] and Fabien Joux[1*]

[1] *Sorbonne Université, CNRS, Laboratoire d'Océanographie Microbienne (LOMIC), Observatoire Océanologique de Banyuls, 66650 Banyuls/mer, France.*
[2] *Sorbonne Université, CNRS, FR3724, Observatoire Océanologique, 66650 Banyuls/Mer, France.*
[3] *Aix Marseille Université, Université de Toulon, CNRS, IRD, MIO UM 110, 13288, Marseille, France*

*: corresponding author: fabien.joux@obs-banyuls.fr

Abstract

Global warming affects primary producers in the Arctic, with potential consequences on the bacterial community composition through the consumption of microalgae-derived dissolved organic matter. To determine the degree of specificity in the use of an exudate by bacterial taxa, we used simple microalgae-bacteria model systems. We isolated 92 bacterial strains from the sea ice bottom and the water column in spring-summer in the Baffin Bay (Arctic Ocean). The isolates were grouped into 42 species belonging to Proteobacteria, Bacteroidetes, Actinobacteria and Firmicutes. 40 strains were tested for their capacity to grow on the exudate from two Arctic diatoms. Most of the strains tested (78 %) were able to grow on the exudate from the pelagic diatom *Chaetoceros neogracilis* and 33 % were able to use the exudate from the sea ice diatom *Fragilariopsis cylindrus*. 17.5% of the strains were not able to grow with any exudate while 27.5 % of the strains were able to use both types of exudates. All strains belonging to Flavobacteriia (n = 10) were able to use the DOM provided by *C. neogracilis*, and this exudate sustained a growth capacity of up to 100 times higher than diluted marine broth medium, of two *Pseudomonas* sp. strains and one *Sulfitobacter* strain. The variable bioavailability of exudates to bacterial strains highlights the potential role of microalgae in shaping the bacterial community composition.

Keywords: Arctic Ocean; diatoms; Dissolved organic exudates; Biodegradation; Bacterial isolation; Bacterial diversity.

1. Background

Phytoplankton are major contributors to the dissolved organic matter (DOM) pool in marine environments by different processes: grazing by zooplankton, viral lysis, autolysis and exudation [1].

Dissolved organic exudates from phytoplankton are considered as labile and semi labile molecules composed of sugars (monosaccharides, oligosaccharides and polysaccharides), nitrogen compounds (amino acids, polypeptides or proteins), lipids (fatty acids) and organic acids (vitamins) [2]. On average, DOM exudation accounts for 10-20 % of total primary production in the marine environment and for 2-10% (average 5 %) for exponentially growing cells [1]. However, different environmental factors may increase the percentage extracellular release (PER), such as suboptimal light intensity and temperature, nutrient limitation and high pCO_2 [2–4].

Phytoplankton primary production and PER are both affected by the unprecedented changes occurring in the Arctic Ocean over the past several decades due to climate variations and human activities. The Arctic air temperatures have increased by 2.7°C on the annual scale over the past 47 years (1971-2017), which is twice as fast as in the rest of the Northern Hemisphere [5]. This global warming led to dramatic modifications in the Arctic sea ice, both in the rates and the magnitude of change in extent, area, thickness, and spatial distribution [5]. This results in a greater transmission of light through the ice and into newly formed open ocean areas [6]. It is expected that the increase in light intensity in the water column will promote phytoplankton primary production and biological productivity throughout the Arctic Ocean [6,7]. In addition, while phytoplankton blooms were until recently considered negligible in the water column under the ice pack [8,9], recent studies have shown the existence of blooms under the sea ice in the marginal ice zone [10–13]. Diatoms are an important component of the primary production in both pelagic and under sea ice environments during spring blooms in Artic Ocean [14–17]. However, measurements of PER in the Arctic Ocean are scarce. Engel et al. [3] measured PER values between 11 % and 23 % during mesocosm experiments conducted from June to July in Kongsfjorden, Svalbard.

Bacteria are key organisms in carbon cycling in aquatic ecosystems, acting as a sink (mineralization of dissolved organic carbon to CO_2) or as a link (production of biomass which can be transferred through the microbial food web) [18]. Roughly 50% of carbon fixed by primary production in the ocean is passing through bacteria [19]. The quality of the DOM produced by phytoplankton constitutes an important regulator of both the metabolism and composition of bacterial communities [20]. Interactions between heterotrophic bacteria and diatoms are complex [21]. On the one hand bacteria exert positive (e.g., production of vitamins) or negative effects (e.g., production of algicidal metabolites) on diatom growth [22,23] and can also modify the composition of the diatom exudates [24]. These effects appear to be diatom species-specific, resulting in compositional shifts of diatom communities when different diatom species were grown together [25]. On other hand, DOM released during a diatom bloom can reshape the bacterial community by favoring some bacterial groups like Roseobacter, Sulfitobacter and Flavobacteriaceae, that are more adapted to the rapid use of substrates released by diatoms [20]. Consequently, the modification of the primary producers in the Arctic Ocean induced by the global

warming have potential consequences on the bacterial community composition through the consumption of microalgae-derived dissolved organic matter [26]. Some experimental studies have shown that bacterial community composition changes are dependent on microalgae species [27], whereas other studies observed a weak bacterial selectivity of exudates produced by specific algae species [28,29]. However, extrapolation of these results is complicated by temporal [30] and spatial [31] changes in the bacterial response to the same DOM exudate. Additionally, these different studies have been performed on natural bacterial communities where complex interactions can occur (e.g., competition, co-metabolism, antibiosis). By contrast, the capacity of distinct bacterial strains to use the exudates from phytoplankton is not well known. Only a simplified approach, combining one bacterial strain with the excretion product of one phytoplankton species allows to decipher more precisely the intrinsic capacity of bacteria to use diatom DOM. This type of study has thus far not been carried out and it complements those with natural microbial consortia.

To determine the degree of specificity in the use of an exudate by bacterial taxa, we used simple microalgae-bacteria model systems. We first identified different bacterial strains isolated from the sea ice bottom and water column during the spring phytoplankton bloom in the Baffin Bay. The field work for the isolation of the bacterial strains was carried out as part of the Green Edge project (http://greenedge-expeditions.com/) with its main objective to study the phytoplankton development in spring [32]. The study site, which is located in a marginal sea (360 m depth) of the Baffin Bay, is covered by a seasonally changing layer of ice. The ecological relevance of the bacterial strains isolated was evaluated by comparing them with the environmental 16S rRNA sequences retrieved during the same sampling period [33]. Then, we followed the capacity of the bacterial strains to grow on the exudates produced by two Arctic diatoms, *Chaetoceros neogracilis* and *Fragilariopsis cylindrus*, characteristic of planktonic and sea ice environments, respectively [17,34,35]. This experimental design allowed us to study the link between the phylogeny of isolated bacteria as well as their origin of their isolation and their capacity to degrade each type of exudate.

2. Methods

2.1. Sampling

A sampling campaign was conducted from April 20th to July 27th in 2016, on an ice camp located near Qikiqtarjuaq (Nunavut), in the Canadian Arctic at 67°28.784' N, 063°47.372' W (Fig. 1). This period was chosen in order to capture the dynamics of the sea-ice algae and phytoplankton spring bloom from initiation to termination. Water sampling was carried out through a 1x1 m hole in the ice pack shielded by a tent. Water samples were collected every week at 2 m and 40 m (or 60 m) depths using a Niskin bottle. The bottom of the first-year sea ice (first 10 cm) was subsampled from sea ice cores collected using a manual ice corer and melted at 4°C.

2.2. Bacterial strains isolation and identification

An aliquot of each sample (0.5 ml) was placed in cryotubes containing 500 µL of 70 % sterile glycerol and stored at –80°C before isolation at the laboratory. After thawing, 100 µL of each sample were spread in triplicate on Marine Agar (MA) medium ([36], Supplementary Table S1) and the petri dishes were incubated in the dark at 4°C to allow the development of aerobic heterotrophic psychrotolerant marine bacteria. At regular intervals (1, 2 and 3 weeks), the colonies were counted and categorized based on their morphological characteristics (morphotype). Representatives of each morphotype were selected for isolation by repeated streaking. Finally, we isolated 92 bacterial strains in total.

After isolation and purification, each strain was cultivated in Marine Broth (MB) medium ([36], Supplementary Table S1) at 4°C under agitation and darkness to identify the strains by partial sequencing of the 16S rRNA. Bacterial cells corresponding to each strain were recovered by centrifugation (3 min at 14000 g), from 2 mL of MB culture. The DNA was then extracted using the Wizard® Genomic DNA Purification kit (Promega) following the manufacturer's recommendations. The DNA was amplified by PCR using the primer pair 27f/1492r to target the 16S rRNA gene [37,38]. The complete PCR mix used contained ultrapure water (3.2 µL), KAPA2G mix (5 µL), forward primer (0.4 µM final concentration), reverse primer (0.4 µM final concentration) and DNA template (1 µL) for a total reaction volume of 10 µL. The PCR amplification conditions used were as follows: 5 min at 95°C; 35 cycles of 15s at 95°C, 15s at 50°C and 15s at 72°C; 5 min at 72°C and finally holding at 4°C in a VeritiTM Thermal Cycler (Applied Biosystems). The PCR products, previously controlled by electrophoresis, were then purified using the AmpliCleanTM Magnetic Bead-Based PCR Cleanup kit (Nimagen) according to the manufacturer's instructions. DNA was then sequenced by the Sanger method [39]. To do this, a sequence reaction was performed on the samples using the 907r primer [40]. The complete PCR mix used contained ultrapure water (5.75 µL), BDT buffer (1.75 µL), BigDye Terminator v3.1 kit (0.5 µL), primer (3.2 µM, 1 µL) and DNA matrix (1 µL) for a total reaction volume of 10 µL. The PCR amplification conditions used were as follows: 40 cycles of 10 s at 95°C, 5 s at 50°C and 2.5 min at 60°C in a VeritiTM Thermal Cycler (Applied Biosystems). The PCR reaction products were cleaned with the D-pure DyeTerminator Clean-up kit (Nimagen) before being sequenced using a Sanger 16 capillary sequencer AB3130XL (Applied Biosystems).

2.3. Sequences analysis

Partial 16S rRNA gene sequences were trimmed , quality controlled and dereplicated using the package Staden-GAP4 [41]. For bacterial strain identification, each FASTA file was uploaded in Ez Taxon-e [42] and compared with the cultured bacterial strain database using Basic Local Alignment Search Tool (BLAST). The sequences were aligned using the MUSCLE multiple alignment method [43]. A hierarchical Likelihood Ratio Test (hLRTs) was performed to determine the most appropriate substitution model for

our dataset. We used default parameters for these different tools. Finally, a phylogenetic tree was constructed from the model used according to the Maximum Likelihood (ML) criterion. To study the robustness of the tree nodes, a bootstrap analysis was performed with 1000 repetitions. All sequence processing was performed using MEGA X v10.0.1 software [44]. Sequences were deposited in Genbank (NCBI) under the following numbers: MK 224724-224815 for the 92 bacterial strains isolated during this study and MK 217878-217881 for the four bacterial strains isolated in August 2009 at 3 m depth in the Beaufort Sea and used in the microplate growth assay (see below). The strains were registered in the Banyuls Bacterial Culture Collection (BBCC) (https://collection.obs-banyuls.fr/index.php).

2.4. Culture of arctic microalgae and recovery of exuded dissolved organic matter

Two diatoms from the Roscoff Culture Collection (RCC) of the Roscoff Biological Station (http://roscoff-culture-collection.org/) were used: the pelagic strain RCC 2278 *Chaetoceros neogracilis* (Mediophyceae, [45]) and the ice strain RCC 4289 *Fragilariopsis cylindrus* (Bacillariophyceae, Grunow ex Cleve). Both strains were isolated from Arctic Ocean. Cultures were not axenic. These diatoms were cultured at 4°C with a continuous white light intensity of 10 µE in K/2 medium+Si [46] for *C. neogracilis* and L1 medium [47] for *F. cylindrus*. The composition of these different media is given on the website of the RCC (http://roscoff-culture-collection.org/). The diatoms were then transferred to a modified K culture medium in which (1) tris(hydroxymethyl)aminomethane [Tris-Base], Na_2-Glycerophosphate [$C_3H_7O_6PNa_2$, 5 to 6 H_2O], and ethylene diamine tetra acetic [EDTA] as organic molecules were removed, (2) ammonium was removed to reduce bacterial growth during culture and (3) iron concentration was reduced to 11.7 µM to limit iron precipitation due to the elimination of EDTA. The culture flasks containing 200 mL of modified K medium were incubated under the same conditions as before. Cell growth was measured by flow cytometry (BD Accuri C6 Plus, Becton Dickinson). The samples were fixed with glutaraldehyde (0.25 % final) and stored at –20°C before analysis. The diatoms were detected by chlorophyll fluorescence and side angle light scattering properties using blue laser (488 nm). Maximum growth rates (µmax) in exponential phase were calculated using cell counts according to the equation $\mu_{max} = \ln (N_2/N_1) / (t_2–t_1)$, where µ = doublings d^{-1}; N = algal abundance ml^{-1}; and t = time, d^{-1}. Bacteria were also counted after staining with SYBR Green (Invitrogen, 0.05 % final) for 10 min in the dark before to be run by flow cytometry. The bacteria were detected by green fluorescence and side angle light scattering properties using blue laser (488 nm). Flow cytometric results were processed using the BD CSamplerTM C6 v1.0.241.21 software (Becton Dickinson). Results were analyzed with the FlowJo v7.6.1 (FlowJo LLC) software.

The diatom DOM was harvested after 40-44 days of cultivation, corresponding to a prolonged stationary phase. This time period was chosen to assure the collection of a sufficient amount of organic exudates for the subsequent bioassay experiments. Therefore, triplicate culture flasks for each strain were pooled

and then centrifuged for 15 min at 5166 g at 4°C. The supernatant was then filtered through two GF/F filters (0.7 µm, 47 mm, Whatman), using a glass vacuum flask. To avoid any organic contamination, the filters and glassware were previously combusted at 450°C for 6 h. The filtrate of each strain was stored at –20°C in Nalgene vials, previously washed with 10% hydrochloric acid (HCl) and then rinsed with Milli-Q® water. Inorganic nutrients and dissolved organic carbon (DOC) were analyzed at the beginning and at the end of the culture for each diatom strain (see below). Particulate organic carbon (POC) and dissolved and total saccharides were analyzed at end of the culture (see below).

2.5. Chemical analyses

Samples for POC (10 ml aliquots of culture in duplicate) were filtered onto pre-combusted (450°C for 6 h) GF/F filters, which were then stored at −20°C. Before analysis, filters were placed in a desiccator for 48 h at room temperature. Samples were analysed with a Carlo Erba Instruments EA1108 elemental analyser using an acetanilide standard as reference. Samples (10 ml aliquots of culture in duplicate) for nitrate (NO_3^-), phosphate (PO_4^{3-}) and silicate ($Si(OH)_4$) were stored at −20°C before analysis on a nutrient autoanalyzer (SEAL Analytical AA3HR). DOC samples (20 ml aliquots of culture in duplicate) were filtered through two overlaid combusted (450°C, 6 h) 25 mm GF/F filters. The filtrate was transferred into combusted glass tubes, poisoned with 85% H_3PO_4, closed with Teflon-lined screw caps and stored in the dark at room temperature until analysis. Samples (65 ml) for dissolved and total saccharides analyses were stored at −20°C.

Carbohydrates were determined in the filtrates of each strain by the TPTZ method [48,49]. This method detects the following categories of monosaccharides: hexoses (fructose, galactose, glucose, and mannose), pentoses (ribose, arabinose, and xylose), deoxy-sugars (fucose and rhamnose), and uronic acids (glucuronic, galacturonic, and mannuronic acids). Dissolved free monosaccharides (DFCHO) were determined without acid hydrolysis. Total dissolved monosaccharides (TDCHO) were determined after acid hydrolysis using 1 M HCl (final concentration) at 100°C for 20h [50]. Hydrolysis was stopped after placing the tubes in an ice bath for 5 min. Combined monosaccharides (i.e., dissolved polysaccharides or DPCHO) were then calculated as the difference between TDCHO and DFCHO. A standard calibration curve was obtained by the analysis of five glucose standards spanning a concentration 0.2 to 2 $mg.L^{-1}$. The response was linear over the above concentration range (R^2 = 0.999) and monosaccharides concentrations were converted to C-equivalents by using a molar conversion factor of six.

2.6. Microplate assay to measure bacterial growth with microalgae exudates

We studied the ability of 40 different bacterial strains, each corresponding to a different species, to degrade the DOM exuded by the two Arctic diatom strains. Among these bacterial strains, 36 were selected from the 92 bacterial strains isolated within the Green Edge project and 4 additional strains,

isolated in the Beaufort Sea at 3 m depth in August 2009 [51], were also selected. Bacterial strains were cultured in a Marine Broth at 4°C in the dark for 3 to 5 days, then 2 mL of culture were centrifuged at 8000 *g* for 5 min at 4°C. The cell pellets were washed 3 times with sterile artificial seawater [52], with a centrifugation cycle between each wash as before, in order to remove the DOM contained in the culture medium. The inoculum of each strain was resuspended in artificial seawater and the cell concentration was determined by flow cytometry as described above (Cytoflex, Beckman & Coulter).

Bacterial growth assays were conducted in 24-well microplates. Each well contained 2 ml of bacterial suspension adjusted to $2x10^5$ cell.mL^{-1} in artificial seawater. Dissolved organic exudates were added in triplicate at a final concentration of 375 µM DOC. NO_3^- and PO_4^{3-} were adjusted at 184 µM and 16 µM final concentrations, respectively, to avoid any effect of inorganic nutrients concentrations differences between the two exudates tested. Positive controls were prepared in triplicate for each strain by adding diluted MB (1/560) at the same DOC concentration than for exudates. Negative controls were also prepared in triplicate for each strain by adding a volume of artificial seawater equivalent to those of exudates and diluted MB. Microplates were incubated à 4°C in the dark with a slight agitation. Bacterial growth was monitored every 2 days for 6 days by flow cytometry using the same protocol described above, taking 50 or 100 µL samples in each well. Preliminary assays were performed with different MB dilutions to confirm that bacterial growth was measurable at this time scale of incubation with a concentration of 375 µM DOC (Fig. S1).

To estimate the growth capacity of the bacterial strains, we used a first index that is the ratio of the maximum cell abundance to the initial cell abundance: $\frac{[B]max-[B]T0}{[B]T0}$. $[B]_{T0}$ corresponds the initial cell concentration and $[B]_{max}$ to the maximum cell concentration. We considered that growth was positive when this index was greater than or equal to 4, which corresponds to two cell divisions.

In order to specify the growth capacity of the strains to use exudates comparatively to the MB, a second index was calculated that considers the intrinsic growth of each strain. For this purpose, we reported the growth obtained with exudates compared to that obtained with diluted MB (positive control). The mathematical formula for this index was: $\frac{\frac{[B]\max exudate-[B]T0\ exudate}{[B]T0\ exudate}}{\frac{[B]\max MB-[B]T0\ MB}{[B]T0\ MB}}$. With $[B]_{T0}$ exudate the initial cell concentration in the exudate, $[B]_{max\ exudate}$ the maximum cell concentration with the exudate, $[B]_{T0\ MB}$ the initial cell concentration with the diluted Marine Broth and $[B]_{max\ MB}$ the maximum cell concentration obtained with the diluted Marine Broth. This index was calculated only for strains showing positive growth with index 1.

3. Results

3.1. Viable counts and cultivable bacterial diversity

Percentages of cultivability varied between 0.002 % and 4.3 % (Table 1). The percentages of cultivability were not significantly different between the different habitats even if the sea ice samples were characterized by much higher concentrations of chlorophyll *a* compared to the samples from the water column (Table 1). No temporal trend was observed in the percentages of cultivability.

Sequence analysis of the 92 isolated bacterial strains allowed identification of 42 putatively different species, according to similarity criterion ≥ 99 % (1 % divergence) for the 16SrRNA gene sequence, belonging to 4 major phyla (Fig. 2, electronic supplementary material, figure S2A). The percentages of similarity of the 16S rRNA gene between the isolated strains and the closest reference sequences were between 95.72 and 100 %. The bacterial strains were mostly similar to species previously isolated from polar environments. They belong primarily to Proteobacteria (70 % of the 92 sequences identified) and more particularly to Gammaproteobacteria, which represented 53 % of all the sequences (electronic supplementary material, figure S2). The remaining Proteobacteria were Alphaproteobacteria (16 % of the total sequences). The two other phyla were Bacteroidetes and Actinobacteria, representing 16 % and 13 % of the sequences, respectively. Finally, one bacterial strain belonging to the Firmicutes phylum was isolated.

When the phylogeny of the bacterial strains was analyzed according to the sampling habitat, we observed only slight modifications in the relative proportion of each group (electronic supplementary material, figure S2B). Among Proteobacteria, Alphaproteobacteria were more present in sea ice (25 %) compared to the water column (13 % and 12 % at 5 m and 40-60 m, respectively). Inversely, the proportion of Flavobacteriia was higher in the water column (21 % and 15% at 2 m and 40 m, respectively) as compared to the sea ice (11 %). Twenty-nine bacterial species (69 %) were specific to a given environment. Only 5 bacterial isolates (12 %) were found in both the sea ice and the water column at both depths, with the closest relatives being *Alteromonas stellipolaris* (Gammaproteobacteria) [53], *Paraglaciecola chatamensis* (Gammaproteobacteria) [54,55], *Psychrobacter aquimaris* (Gammaproteobacteria) [56], *Leeuwenhoekiella aequorea* (Bacteroidetes) [57] and *Rhodococcus cerastii* (Actinobacteria) [58].

3.2. Growth of Arctic microalgae and characterization of the dissolved organic exudates

The two Arctic diatoms, *C. neogracilis* and *F. cylindrus,* were characterized by similar growth rates (0.25 ± 0.02 d^{-1} and 0.30 ± 0.002 d^{-1}, respectively) and reached stationary phase after 12 and 24 days,

265 respectively. Inorganic nutrient analyses showed that both diatoms cultures were limited mainly by
266 $Si(OH)_4$ in the stationary phase (Table 2).
267 The exudates were recovered from the cultures after 40 days of cultivation for *C. neogracilis* and after
268 44 days for *F. cylindrus*, corresponding to a stationary phase of 32 days for *C. neogracilis* and 20 days
269 for *F. cylindrus* (Fig. 3). In terms of diatom cell abundance, the stationary phase was stable for each strain
270 until this date, suggesting that cell lysis and the consequent release of DOM by this process were of
271 minor importance. DOC concentrations were 234 µM and 109 µM for *C. neogracilis* and *F. cylindrus*,
272 respectively, at the start of the cultures and they were significantly higher at the end of the experiment
273 due to DOM exudation (Table 2). This exudation ($DOC_{final} - DOC_{initial}$) represented ≈1800 µM for *C.*
274 *neogracilis* and ≈ 870 µM for *F. cylindrus*. The DOC exuded represented 45 % of the sum of POC and
275 DOC for *C. neogracilis* and 61 % for *F. cylindrus*. Carbohydrates accounted for 4 to 18 % of the DOC and
276 were dominated by polysaccharides in the *C. neogracilis* exudates (Table 2).

277 The diatom cultures were not axenic, and an increase in heterotrophic bacterial abundance over time
278 was observed in the cultures (electronic supplementary material, figure S3). We estimated the bacterial
279 consumption of DOC considering a carbon conversion factor of 20 fg C $cell^{-1}$ [59] and a bacterial growth
280 efficiency of 50 % for bacteria growing under high primary productivity conditions [60]. Integrated over
281 the 40-44 days, heterotrophic bacteria accounted for the processing of 0.01 % (0.26 µM DOC) and 6 %
282 (56 µM DOC) of the DOC produced by *C. neogracilis* and *F. cylindrus*, respectively. These results indicate
283 that DOM present in the diatom cultures after 44 days can be considered predominantly diatom-derived
284 and weakly reshuffled by bacteria.

285 ### 3.3. Bioavailability of dissolved organic exudates for the different bacterial strains

286 We observed different growth patterns among the strains, indicative for their capacity to use the
287 exudates (Fig. 4). According to the first index, we confirmed the lack of growth in the negative controls
288 (Artificial Sea Water (ASW) without DOM addition). Surprisingly, only 60 % of the strains were able to
289 grow in the diluted MB used as a positive control. When the exudates were used as growth substrates,
290 78 % of bacterial strains (31 out of 40) responded positively to the DOM from *C. neogracilis,* and 33 %
291 to the *F. cylindrus* exudates. The Venn diagram based on these growth capacities shows that only 9
292 strains (23%) were able to grow in all different media (i.e., diluted MB and the two exudates) (Fig. 5).
293 These strains belonged to the phyla Proteobacteria, Bacteroidetes and Actinobacteria. If we focus on the
294 use of exudates, we found that 55% of the strains were able to use only a single exudate and 27.5 %
295 grew on the two exudates. Finally, 17.5% of the strains tested did not grow in any of the two exudates
296 with the majority of bacteria belonging to the Gammaproteobacteria class. We did not find specific
297 relationships between the habitat of the bacterial strains (sea ice bottom versus water column) and their
298 capacity to use the different exudates. For instance, among the 13 bacterial strains able to grow on the

exudate of the ice diatom *F. cylindrus*, only 3 were isolated from the sea ice. Venn diagrams for each type of habitat are available in supplementary data, figure S4.

Several isolates belonging to the same genus, such as *Rhodococcus*, *Maribacter* and *Pseudoalteromonas*, had different growth patterns on the same type of exudate (Table 3). All Flavobacteriia strains succeeded in degrading the exudate of *C. neogracilis*. One third of the bacterial strains obtained an index higher than two using the exudate of *C. neogracilis* while this was observed for only 13 % of the strains for the *F. cylindrus* exudate. Index 2 highlights the large variability in the amplitude of growth on exudates relative to a common reference (diluted MB). The highest values (up to 100 times higher than in diluted MB medium) were measured with *C. neogracilis* exudates during the growth of two *Pseudomonas* sp. strains and one *Sulfitobacter* strain (Table 2).

4. Discussion

4.1. Cultivable bacterial diversity

Isolation of bacterial strains by culturing techniques is key for studying their physiology and functional capabilities. The environmental relevance of isolated strains remains, however, an important issue. Cultivation on a medium rich in organic matter leads to a well-known bias by selecting copiotrophic species that are not necessarily abundant in the marine environment, except during episodes of higher productivity or significant organic matter input [61–63]. Gammaproteobacteria are generally overrepresented in the cultivable fraction compared to the natural community [64]. In our case, they represented 53 % of the isolates, whereas *in situ* bacterial community composition determined by Illumina sequencing showed that the relative abundance of Gammaproteobacteria was 47 % in sea ice and 31 % in the water column [33]. Strains belonging to the Flavobacteriaceae family were well represented among the isolated strains (n=16; 17 % of the total strains isolated). Interestingly, the survey of the bacterial community composition by metabarcoding underlined the importance of this family during the phytoplankton bloom in this region [33]. Indeed, Flavobacteriaceae were well represented in the total *in-situ* bacterial community with 16% of the total DNA sequences. Furthermore, they reflected 19% of the sequences in the sea ice bottom and 16% of the sequences in the water column. Rhodobaceteraceae bacterial family was well represented in the isolates with 10 bacterial strains. As for Flavobacteriaceae, Rhodobaceteraceae members are frequently associated with phytoplankton blooms in marine ecosystems [20].

In the sea ice bottom, the cultivable genera belonging to *Paraglaciecola* (Gammaproteobacteria) represented 12*%* of the sequences obtained by Illumina sequencing from the *in-situ* community at the same period, *Polaribacter* (Flavobacteriia) represented 8%, *Pseudoalteromonas* (Gammaproteobacteria)

represented 6% and *Colwellia* (Gammaproteobacteria) 1% [33]. In the water column, the cultivable genera with the highest *in situ* abundance were *Polaribacter* (Flavobacteriia) with 7%, *Pseudoalteromonas* (Gammaproteobacteria) with 3 %, *Paraglaciecola* (Gammaproteobacteria) with 2%, *Rhodococcus* (Actinobacetria) with 2 % and *Pseudomonas* (Gammaproteobacteria) with 1% of total sequences. This is a rough estimate, because each genus may contain many different species, of which only a few representatives have been isolated. However, these results underline the fact that the isolated strains were overall representative of the *in situ* bacterial community, especially in the sea ice bottom.

Finally, comparison of the sequences of our isolated strains with sequences in the EZBiocloud database revealed that the lowest percentage of similarity (95.72 %) was obtained for *Antarcticibacterium flavum* [65] belonging to the class of Flavobacteriia (Bacteroidetes). This low percentage of similarity suggests the isolation of a new species belonging to the genus *Antarcticibacterium* which can only be confirmed by further genetic analysis.

4.2. Biodegradability of the microalgae exudates

To assess how phytoplanktonic blooms can shape bacterial community composition, we performed a biodegradation assay to identify the capacity of several isolated bacterial strains to use the DOM produced by two polar diatoms, *C. neogracilis* and *F. cylindrus.* The exudates used in the present study originated from non-axenic diatom cultures. We estimated that heterotrophic bacteria consumed up to 6 % of the DOC over the course of culturing period, and a fraction of this organic carbon could have been released by bacteria as DOM with a chemical composition different to the consumed compounds [66,67]. Therefore, part of the readily available substrates specific for each diatom species was likely utilized or transformed prior to the biodegradation experiments. Given the overall low fraction of bacterially processed organic carbon and exudation being a continuous process throughout the culturing period, we consider the DOM used here representative for the two diatoms. This idea is further supported by our biodegradation assays that revealed a preference of the bacterial strains for the use of DOM from *C. neogracilis*, the diatom with the longer stationary phase, as compared to *F. cylindrus*.

We investigated carbohydrates, major components of phytoplankton exudates to explore differences in the chemical composition of the two DOM sources. The relative abundance of carbohydrates in phytoplankton exudates appears variable among phytoplankton species (26-80% [68] ; 6-13% [28]) and tends to increase in the stationary phase [68]. These two facts can explain why *F. cylindrus* exudates had a lower contribution of carbohydrates to the DOM (4 %) as compared to *C. neogracilis* (18 %). Polymeric and monomeric carbohydrates were consistently shown to be utilized in short-term (days) biodegradation experiments [69,70]. The lower content of this labile source of organic carbon in the exudate of the sea ice diatom as compared to the water column diatom could explain the lower number

of bacterial strains growing on this DOM. Carbohydrates are present in high concentrations (80-1300 µMC) in sea-ice as compared to the water column in the Arctic ocean [71,72]. The high similarity observed in other studies between the carbohydrate composition of sea ice and the carbohydrates produced by sea ice diatoms, including *F. cylindrus,* confirm the microalgal origin of these compounds [72].

Furthermore, we did not find a specific relationship between the habitat of bacterial strains and their capacity to use the different exudates. As explained earlier, among the 13 bacterial strains able to grow on the *F. cylindrus* exudate, only 3 strains have been isolated from sea ice samples. This may indicate that a co-metabolim is important to degrade such exudates in sea ice environment. Indeed, some bacterial strains could be able to degrade the primary energy source given by the *F. cylindrus* DOM in the ice, producing secondary compounds which in turn would be used by other bacterial strains as potentially the ones which did not grow in our biodegradation assay. Thus, our results could complement previous observations with mixed communities where cross-feeding among taxa can occur [73]. However, 6 strains out of 13 (46%) which grew on this DOM were isolated at 2m and 3m depth. Thus, it means that 69% of the strains growing on *F. cylindrus* DOM were isolated in the ice or in the first meters of the water column. This is relevant with the fact that some interactions happen between the sea ice bottom and the water column. The microalgae living in the ice excrete DOM which will be used as a source of carbon by bacteria in the first few meters of the water column. Moreover, these interactions are reinforced as spring progresses with the beginning of the sea ice melt causing the release of a significant amount of DOM into the water column, which will serve as a source of energy and carbon for bacteria [33].

The growth of bacterial strains on the diatom exudates is in part linked to their capacity to produce extracellular enzymes to degrade polymers. In the present study, polysaccharides constituted a lower fraction of the carbohydrates of the *F. cylindrus* exudate (42 %) as compared to the *C. neogracilis* exudate (68 %) (Table 2). The incubation of phylogenetically different bacterial strains with a given DOM source allowed us to determine that the genetic potential to produce extracellular enzymes, more or less specific to DOM compounds, was a selective mechanism for the use of a given exudate. Phytoplankton-derived polysaccharide composition is highly diverse, may fluctuate between species [74] and is influenced by external factors such as nutrients, light and salinity stress [75]. Jain and Krishnan [76] showed that 52 % of a total of 215 cold-adapted heterotrophic bacteria (all belonging to Gammaproteobacteria) isolated in an open glacial fjord in the Arctic Ocean were able to produce extracellular polysaccharide enzymes at 4°C. Interestingly, these authors observed high diversity in terms of enzyme activities among strains belonging to a same genus and/or species. This result can be compared to the observation we made in the heterogeneity of the growth response within the same

399 genus for the same type of exudate. Whether a DOM source is biologically labile might therefore depend
400 on the bacterial taxa and their respective functional repertoire.

401 The commonly observed rapid utilization of phytoplankton exudates by mixed microbial communities is
402 likely due to the activity of the most successful taxa. In this context, it was interesting to note that the
403 highest growth was observed for one *Sulfitobacter* strain on the *C. neogracilis* exudate. Two *Sulfitobacter*
404 Operational Taxonomic Units (OTUs) were identified as most responsive among a Southern Ocean
405 natural bacterial community to the exudate of *Chaetoceros debilis* [77]. This bacterial group is known
406 for its capacity to use organic sulfur compounds that could be the basis for this distinct diatom-bacteria
407 association. *Sulfitobacter* could have responded positively to the dimethylsulfide produced in the *C.*
408 *neogracilis* culture, even if this diatom has been shown to emit this compound at a lower rate as
409 compared to *Emiliania huxleyi* [78].

410 All Flavobacteriia, including a representative of the genus *Polaribacter*, had the capacity to use the *C.*
411 *neogracilis* exudate. Flavobacteriia and more precisely the genus *Polaribacter* was identified as a
412 bacterial group responding positively to diatom blooms in polar regions [30,33]. Recently, we confirmed
413 the responsiveness of *Polaribacter* after the addition of *C. neogracilis* exudates to a natural bacterial
414 community present in the Baffin Bay at two ice zone stations [31]. Marine Flavobacteriia are known as
415 efficient degraders of biopolymers, such as proteins and polysaccharides [79].
416 Over the last decade, next generation sequencing (NGS) technologies have enabled the emergence of
417 adetailed analysis of the response of several cultivable bacterial strains, representative of
418 Flavobacteriia, to organic matter, in particular through proteomic and transcriptomic approaches [80].
419 This approach was used to explore the metabolic pathways of two *Polaribacter* strains isolated in the
420 North Sea during their growth with various models of organic molecules like carbohydrates and
421 polysaccharides [80]. This study showed that both *Polaribacter* strains were able to degrade algal
422 polysaccharides while they each occupy different ecologic niches. However, they observed that
423 one strain was feeding on proteins and a small subset of algal polysaccharides while the other was able
424 to degrade a wider range of polysaccharides, making it a more flexible strain [80]. More recently,
425 proteomic approaches have also been used to explore the response of *Formosa* strains
426 (Flavobacteriaceae) isolated in the North Sea to laminarin as a model of polysaccharides [81]. The authors
427 observed that laminarin was used as a major source of energy, and as signal molecule, which induced
428 transporters and digestive enzymes to use also other compounds released from the lysis of diatom cells.
429 These studies confirm the link between Flavobacteria and microalgal blooms with their capacity to
430 degrade and use algal DOM. It's consistent with the fact that all the bacterial strains belonging to
431 Flavobacteria tested in our biodegradation assay were able to grow
432 on the pelagic microalgae *C. neogracilis* exudate. However, depending on their genetic

material, bacterial strains differ in their ability to degrade DOM according to its composition. It implies the occurrence of different ecological niches in which bacterial strains use the energy source for which they are the most adapted to.

Even though environmental relevance of isolated strains remains an important issue, our study underlines the fact that the isolated strains from the ice camp were overall representative of the *in situ* bacterial community, especially in the sea ice bottom. We showed through a biodegradation experiment a preference for the DOM degradation from the pelagic diatom *Chaetoceros neogracilis* among 40 different bacterial strains isolated from ice and several depths. Indeed, most of the strains tested (78 %) were able to grow on the exudate from the pelagic diatom *C. neogracilis* and 33 % were able to use the exudate from the sea ice diatom *F. cylindrus*. 17.5% of the strains were not able to grow with any exudate while 27.5% of the strains were able to use both types of exudates. Nevertheless, we observed highly diverse response patterns among the bacterial strains even between strains with the same genus. We did not find specific relationships between the habitat of the bacterial strains (sea ice bottom versus water column) and their capacity to use the different exudates. One hypothesis for this lack of relationship between microbial habitat and microalgal DOM could be cross-feeding, meaning the production of secondary compounds based on the degradation of microalgal DOM by specific bacterial strains which allows less specific strains to use these secondary compounds for their growth. All strains belonging to Flavobacteriia (n = 10) were able to use the DOM provided by *C. neogracilis*, and this exudate sustained a growth capacity of up to 100 times higher than diluted marine broth medium, of two *Pseudomonas* sp. strains and one *Sulfitobacter* strain.

In conclusion, using a simple model of interaction (one microalgal exudate / one bacterial strain) to avoid complex biotic interactions which occur in microbial communities, we were able to confirm that dissolved exudates from different microalgae differed in their bioavailability to bacterial strains. Our results reinforce the fact that DOM can shape the bacterial community composition by selecting the most responsive species having the right genetic material to degrade the DOM at their disposal in their specific environment.

Additional Information

Acknowledgments

We thank the Roscoff Culture Collection (RCC) for proving us the microalgae strains. We would like to thank J. Caparros for DOC and POC analyses, O. Crispi for inorganic nutrients analyses, D. Vaulot, D. Marie and M. Tragin for bacterial counts by flow cytometry, J. Ras and C. Dimier for chlorophyll a measurments by HPLC. We are grateful to the BIO2MAR and the BIOPIC platforms (http://bio2mar.obsbanyuls.fr) for providing technical support and access to instrumentation. The field

campaign would not have been possible without the support of the Hamlet of Qikiqtarjuaq and the members of the community as well as the Inuksuit School and its Principal, Jacqueline Arsenault. The field campaign was successful thanks to the contribution of J. Ferland, G. Bécu, C. Marec, J. Lagunas, F. Bruyant, J. Larivière, E. Rehm, S. Lambert-Girard, C. Aubry, C. Lalande, A. LeBaron, C. Marty, J. Sansoulet, D. Christiansen-Stowe, A. Wells, M. Benoît-Gagné, E. Devred and M.-H. Forget from the Takuvik laboratory, C.J. Mundy and V. Galindo from University of Manitoba & F. Pinczon du Sel and E. Brossier from Vagabond. We also thank Michel Gosselin, Québec-Océan, the CCGS Amundsen and the Polar Continental Shelf Program for their in-kind contribution in terms of polar logistics and scientific equipment.

Funding Statement

This work was supported by LEFE-CYBER CNRS program (EXPERT project) and by the following French and Canadian programs and agencies (Green Edge project): ANR (Contract #111112), ArcticNet, CERC on Remote sensing of Canada's new Arctic frontier, CNES (project #131425), French Arctic Initiative, Fondation Total, CSA, LEFE and IPEV (project #1164). This latest project was conducted under the scientific coordination of the Canada Excellence Research Chair on Remote sensing of Canada's new Arctic frontier and the CNRS & Université Laval Takuvik Joint International Laboratory (UMI3376). L.D. and L.T. were supported by PhD grants from Sorbonne Université.

Data Accessibility

All DNA sequences were deposited in Genbank (NCBI) with accession nos.: MK 224724-224815 for bacterial strains isolated during this study and MK 217878-217881 for four bacterial strains isolated in the Beaufort Sea. Additional data are available within the electronic supplementary material.

Competing Interests

We have no competing interests.

Authors' Contributions

F.J. and L.T. conceived and designed the research, L.T., L.D., L.I., P.C., C.P. performed the experimental work, L.T., L.D., L.I., P.C., C.P., I.O., F.J. contributed to the interpretation of the data and the discussion of the results presented in the manuscript. F.J. wrote the first draft of the manuscript and all the authors made comments and amendments, and approved the final version.

References

1. Nagata T. 2000 Production mechanisms of dissolved organic matter. In *Microbial Ecology of the*

497 *Oceans* (ed DL Kirchman), pp. 121–152. New York: Wiley-Liss.

498 2. Thornton DCO. 2014 Dissolved organic matter (DOM) release by phytoplankton in the
499 contemporary and future ocean. *Eur. J. Phycol.* **49**, 20–46. (doi:10.1080/09670262.2013.875596)

500 3. Engel A, Borchard C, Piontek J, Schulz KG, Riebesell U, Bellerby R. 2013 CO2 increases 14C primary
501 production in an Arctic plankton community. *Biogeosciences* **10**, 1291–1308. (doi:10.5194/bg-
502 10-1291-2013)

503 4. Obernosterer I, Herndl GJ. 1995 Phytoplankton extracellular release and bacterial growth:
504 Dependence on the inorganic N:P ratio. *Mar. Ecol. Prog. Ser.* **116**, 247–257.

505 5. Box JE *et al.* 2019 Key indicators of Arctic climate change: 1971-2017. *Environ. Res. Lett.* **14**,
506 045010. (doi:10.1088/1748-9326/aafc1b)

507 6. Randelhoff A *et al.* 2019 The evolution of light and vertical mixing across a phytoplankton ice-
508 edge bloom. *Elem. Sci. Anthr.* **7**, 20. (doi:10.1525/elementa.357)

509 7. Wassmann P, Reigstad M. 2011 Future Arctic Ocean seasonal ice zones and implications for
510 pelagic-benthic coupling. *Oceanography* **24**, 220–231. (doi:10.5670/oceanog.2011.65)

511 8. Arrigo KR, van Dijken GL. 2011 Secular trends in Arctic Ocean net primary production. *J. Geophys.*
512 *Res. Ocean.* **116**, 1–15. (doi:10.1029/2011JC007151)

513 9. Pabi S, van Dijken GL, Arrigo KR. 2008 Primary production in the Arctic Ocean, 1998-2006. *J.*
514 *Geophys. Res. Ocean.* **113**, 1998–2006. (doi:10.1029/2007JC004578)

515 10. Arrigo KR *et al.* 2012 Massive phytoplankton blooms under arctic sea ice. *Science* **336**, 1408.
516 (doi:10.1126/science.1215065)

517 11. Arrigo KR *et al.* 2014 Phytoplankton blooms beneath the sea ice in the Chukchi sea. *Deep. Res.*
518 *Part II Top. Stud. Oceanogr.* **105**, 1–16. (doi:10.1016/j.dsr2.2014.03.018)

519 12. Lowry KE, van Dijken GL, Arrigo KR. 2014 Evidence of under-ice phytoplankton blooms in the
520 Chukchi Sea from 1998 to 2012. *Deep. Res. Part II Top. Stud. Oceanogr.* **105**, 105–117.
521 (doi:10.1016/j.dsr2.2014.03.013)

522 13. Assmy P *et al.* 2017 Leads in Arctic pack ice enable early phytoplankton blooms below snow-
523 covered sea ice. *Sci. Rep.* **7**, 1–9. (doi:10.1038/srep40850)

524 14. von Quillfeldt CH. 2000 Common diatom species in Arctic spring blooms: Their distribution and
525 abundance. *Bot. Mar.* **43**, 499–516. (doi:10.1515/BOT.2000.050)

526 15. Laney SR, Sosik HM. 2014 Phytoplankton assemblage structure in and around a massive under-
527 ice bloom in the Chukchi Sea. *Deep. Res. Part II Top. Stud. Oceanogr.* **105**, 30–41.
528 (doi:10.1016/j.dsr2.2014.03.012)

529 16. Leu E, Mundy CJ, Assmy P, Campbell K, Gabrielsen TM, Gosselin M, Juul-Pedersen T, Gradinger R.
530 2015 Arctic spring awakening - Steering principles behind the phenology of vernal ice algal
531 blooms. *Prog. Oceanogr.* **139**, 151–170. (doi:10.1016/j.pocean.2015.07.012)

532 17. van Leeuwe MA *et al.* 2018 Microalgal community structure and primary production in Arctic and
533 Antarctic sea ice: A synthesis. *Elem. Sci. Anth.* **6,** 4. (doi:10.1525/elementa.267)

534 18. Cotner JB, Biddanda BA. 2002 Small players, large role: Microbial influence on biogeochemical
535 processes in pelagic aquatic ecosystems. *Ecosystems* **5**, 105–121. (doi:10.1007/s10021-001-0059-

3)

19. Azam F, Fenchel T, Field J, Gray J, Meyer-Reil L, Thingstad F. 1983 The Ecological Role of Water-Column Microbes in the Sea. *Mar. Ecol. Prog. Ser.* **10**, 257–263. (doi:10.3354/meps010257)

20. Buchan A, LeCleir GR, Gulvik CA, González JM. 2014 Master recyclers: features and functions of bacteria associated with phytoplankton blooms. *Nat. Rev. Microbiol.* **12**, 686–698. (doi:10.1038/nrmicro3326)

21. Amin SA, Parker MS, Armbrust E V. 2012 Interactions between Diatoms and Bacteria. *Microbiol. Mol. Biol. Rev.* **76**, 667–684. (doi:10.1128/mmbr.00007-12)

22. Paul C, Pohnert G. 2011 Interactions of the algicidal bacterium Kordia algicida with diatoms: Regulated protease excretion for specific algal lysis. *PLoS One* **6**, e21032. (doi:10.1371/journal.pone.0021032)

23. Durham BP *et al.* 2015 Cryptic carbon and sulfur cycling between surface ocean plankton. *Proc. Natl. Acad. Sci. U. S. A.* **112**, 453–457. (doi:10.1073/pnas.1413137112)

24. Gärdes A, Ramaye Y, Grossart HP, Passow U, Ullrich MS. 2012 Effects of Marinobacter adhaerens HP15 on polymer exudation by Thalassiosira weissflogii at different N:P ratios. *Mar. Ecol. Prog. Ser.* **461**, 1–14. (doi:10.3354/meps09894)

25. Koedooder C, Stock W, Willems A, Mangelinckx S, De Troch M, Vyverman W, Sabbe K. 2019 Diatom-bacteria interactions modulate the composition and productivity of benthic diatom biofilms. *Front. Microbiol.* **10**, 1255. (doi:10.3389/fmicb.2019.01255)

26. Underwood GJC, Michel C, Meisterhans G, Niemi A, Belzile C, Witt M, Dumbrell AJ, Koch BP. 2019 Organic matter from Arctic sea-ice loss alters bacterial community structure and function. *Nat. Clim. Chang.* **9**, 170–176. (doi:10.1038/s41558-018-0391-7)

27. Tada Y, Nakaya R, Goto S, Yamashita Y, Suzuki K. 2017 Distinct bacterial community and diversity shifts after phytoplankton-derived dissolved organic matter addition in a coastal environment. *J. Exp. Mar. Bio. Ecol.* **495**, 119–128. (doi:10.1016/j.jembe.2017.06.006)

28. Landa M *et al.* 2014 Phylogenetic and structural response of heterotrophic bacteria to dissolved organic matter of different chemical composition in a continuous culture study. *Environ. Microbiol.* **16**, 1668–1681. (doi:10.1111/1462-2920.12242)

29. Sarmento H, Morana C, Gasol JM. 2016 Bacterioplankton niche partitioning in the use of phytoplankton-derived dissolved organic carbon: Quantity is more important than quality. *ISME J.* **10**, 2582–2592. (doi:10.1038/ismej.2016.66)

30. Luria CM, Amaral-Zettler LA, Ducklow HW, Rich JJ. 2016 Seasonal Succession of Free-Living Bacterial Communities in Coastal Waters of the Western Antarctic Peninsula. *Front. Microbiol.* **7, 1731**. (doi:10.3389/fmicb.2016.01731)

31. Dadaglio L, Dinasquet J, Obernosterer I, Joux F. 2018 Differential responses of bacteria to diatom-derived dissolved organic matter in the Arctic Ocean. *Aquat. Microb. Ecol.* **82**, 59–72. (doi:10.3354/ame01883)

32. Oziel L *et al.* 2019 Environmental factors influencing the seasonal dynamics of spring algal blooms in and beneath sea ice in western Baffin Bay. *Elem. Sci. Anth.* **7**, 34. (doi:10.1525/elementa.372)

33. Dadaglio L. 2018 Dynamique des communautés bactériennes en réponse au bloom phytoplanctonique dans l'océan Arctique et identification des acteurs microbiens impliqués dans

577 la dégradation de la matière organique. PhD Thesis. Sorbonne Université, Paris, France. 191p.
578 (https://hal.sorbonne-universite.fr/tel-02614103).

579 34. Balzano S, Marie D, Gourvil P, Vaulot D. 2012 Composition of the summer photosynthetic pico
580 and nanoplankton communities in the Beaufort Sea assessed by T-RFLP and sequences of the
581 18S rRNA gene from flow cytometry sorted samples. *ISME J.* **6**, 1480–1498.
582 (doi:10.1038/ismej.2011.213)

583 35. Aslam SN, Strauss J, Thomas DN, Mock T, Underwood GJC. 2018 Identifying metabolic pathways
584 for production of extracellular polymeric substances by the diatom Fragilariopsis cylindrus
585 inhabiting sea ice. *ISME J.* **12,** 1237–1251. (doi:10.1038/s41396-017-0039-z)

586 36. Zobell CE. 1941 Studies on marine bacteria. I. The cultural requirements of heterotrophic aerobes.
587 *J. Mar. Res.* **4**, 42–75.

588 37. Hogg JC, Lehane MJ. 1999 Identification of bacterial species associated with the sheep scab mite
589 (Psoroptes ovis) by using amplified genes coding for 16S rRNA. *Appl. Environ. Microbiol.* **65**,
590 4227–4229.

591 38. Frank JA, Reich CI, Sharma S, Weisbaum JS, Wilson BA, Olsen GJ. 2008 Critical evaluation of two
592 primers commonly used for amplification of bacterial 16S rRNA genes. *Appl. Environ. Microbiol.*
593 **74**, 2461–2470. (doi:10.1128/AEM.02272-07)

594 39. Sanger F, Nicklen S, Coulson AR. 1977 DNA sequencing with chain-terminating inhibitors. *Proc.*
595 *Natl. Acad. Sci.* **74**, 5463–5467. (doi:10.1073/pnas.74.12.5463)

596 40. Morales SE, Holben WE. 2009 Empirical testing of 16S rRNA gene PCR primer pairs reveals
597 variance in target specificity and efficacy not suggested by in silico analysis. *Appl. Environ.*
598 *Microbiol.* **75**, 2677–2683. (doi:10.1128/AEM.02166-08)

599 41. Staden R, Judge DP, Bonfield JK. 2003 Managing Sequencing Projects in the GAP4 Environment.
600 In *Introduction to Bioinformatics* (eds SA Krawetz, DD Womble), pp. 327–344. Totowa, NJ:
601 Humana Press. (doi:10.1007/978-1-59259-335-4_20)

602 42. Kim OS *et al.* 2012 Introducing EzTaxon-e: A prokaryotic 16s rRNA gene sequence database with
603 phylotypes that represent uncultured species. *Int. J. Syst. Evol. Microbiol.* **62**, 716–721.
604 (doi:10.1099/ijs.0.038075-0)

605 43. Edgar RC. 2004 MUSCLE: Multiple sequence alignment with high accuracy and high throughput.
606 *Nucleic Acids Res.* **32**, 1792–1797. (doi:10.1093/nar/gkh340)

607 44. Kumar S, Stecher G, Li M, Knyaz C, Tamura K. 2018 MEGA X: Molecular Evolutionary Genetics
608 Analysis across computing platforms. *Mol. Biol. Evol.* **35**, 1547–1549.
609 (doi:10.1093/molbev/msy096)

610 45. VanLandingham SL. 1968 *Catalogue of the fossil and Recent genera and species of diatoms and*
611 *their synonyms; part II, Bacteriastrum through Coscinodiscus*. Vaduz, Liechtenstein. See
612 https://eurekamag.com/research/018/519/018519603.php.

613 46. Keller MD, Selvin RC, Claus W, Guillard RRL. 1987 Media for the Culture of Oceanic
614 Ultraphytoplankton. *J. Phycol.* **23**, 633–638. (doi:10.1111/j.1529-8817.1987.tb04217.x)

615 47. Guillard RRL, Hargraves PE. 1993 Stichochrysis immobilis is a diatom, not a chrysophyte.
616 *Phycologia* **32**, 234–236. (doi:10.2216/i0031-8884-32-3-234.1)

617 48. Myklestad SM, Skånøy E, Hestmann S. 1997 A sensitive and rapid method for analysis of dissolved

618 mono- and polysaccharides in seawater. *Mar. Chem.* **56**, 279–286. (doi:10.1016/S0304-
619 4203(96)00074-6)

620 49. Panagiotopoulos C, Sempéré R. 2005 Analytical methods for the determination of sugars in
621 marine samples: A historical perspective and future directions. *Limnol. Oceanogr. Methods* **3**,
622 419–454. (doi:10.4319/lom.2005.3.419)

623 50. Panagiotopoulos C, Sempéré R, Jacq V, Charrière B. 2014 Composition and distribution of
624 dissolved carbohydrates in the Beaufort Sea Mackenzie margin (Arctic Ocean). *Mar. Chem.* **166**,
625 92–102. (doi:10.1016/j.marchem.2014.09.004)

626 51. Ortega-Retuerta E, Joux F, Jeffrey WH, Ghiglione JF. 2013 Spatial variability of particle-attached
627 and free-living bacterial diversity in surface waters from the Mackenzie River to the Beaufort Sea
628 (Canadian Arctic). *Biogeosciences* **10**, 2747–2759. (doi:10.5194/bg-10-2747-2013)

629 52. Eguchi M, Nishikawa T, McDonald K, Cavicchioli R, Gottschal JC, Kjelleberg S. 1996 Responses to
630 Stress and Nutrient Availability by the Marine Ultramicrobacterium Sphingomonas sp . Strain
631 RB2256. *Appl. Environ. Microbiol.* **62**, 1287–1294.

632 53. Van Trappen S, Tan TL, Yang J, Mergaert J, Swings J. 2004 Alteromonas stellipolaris sp. nov., a
633 novel, budding, prosthecate bacterium from Antarctic seas, and emended description of the
634 genus Alteromonas. *Int. J. Syst. Evol. Microbiol.* **54**, 1157–1163. (doi:10.1099/ijs.0.02862-0)

635 54. Matsuyama H, Hirabayashi T, Kasahara H, Minami H, Hoshino T, Yumoto I. 2006 Glaciecola
636 chathamensis sp. nov., a novel marine polysaccharide-producing bacterium. *Int. J. Syst. Evol.*
637 *Microbiol.* **56**, 2883–2886. (doi:10.1099/ijs.0.64413-0)

638 55. Shivaji S, Reddy GS. 2014 Phylogenetic analyses of the genus Glaciecola: Emended description of
639 the genus Glaciecola, Transfer of Glaciecola mesophila, G. agarilytica, G. aquimarina, G. arctica, G.
640 chathamensis, G. polaris and g. psychrophila to the genus Paraglaciecola gen. nov. . *Int. J. Syst.*
641 *Evol. Microbiol.* **64**, 3264–3275. (doi:10.1099/ijs.0.065409-0)

642 56. Yoon JH, Lee CH, Yeo SH, Oh TK. 2005 Psychrobacter aquimaris sp. nov. and Psychrobacter
643 namhaensis sp. nov., isolated from sea water of the South Sea in Korea. *Int. J. Syst. Evol. Microbiol.*
644 **55**, 1007–1013. (doi:10.1099/ijs.0.63464-0)

645 57. Nedashkovskaya OI *et al.* 2005 Reclassification of [Cytophaga] marinoflava Reichenbach 1989 as
646 Leeuwenhoekiella marinoflava gen. nov., comb. nov. and description of Leeuwenhoekiella
647 aequorea sp. nov. *Int. J. Syst. Evol. Microbiol.* **55**, 1033–1038. (doi:10.1099/ijs.0.63410-0)

648 58. Kämpfer P, Wellner S, Lohse K, Lodders N, Martin K. 2013 Rhodococcus cerastii sp. nov. and
649 Rhodococcus trifolii sp. nov., two novel species isolated from leaf surfaces. *Int. J. Syst. Evol.*
650 *Microbiol.* **63**, 1024–1029. (doi:10.1099/ijs.0.044958-0)

651 59. Lee S, Fuhrman JA. 1987 Relationships between biovolume and biomass of naturally derived
652 marine bacterioplankton. *Appl. Environmantal Microbiol.* **53**, 1298–1303.

653 60. Biddanda B, Opsahl S, Benner R. 1994 Plankton respiration and carbon flux through
654 bacterioplankton on the Louisiana shelf. *Limnol. Oceanogr.* **39**, 1259–1275.
655 (doi:10.4319/lo.1994.39.6.1259)

656 61. Nelson CE, Carlson CA. 2012 Tracking differential incorporation of dissolved organic carbon types
657 among diverse lineages of Sargasso Sea bacterioplankton. *Environ. Microbiol.* **14**, 1500–1516.
658 (doi:10.1111/j.1462-2920.2012.02738.x)

659 62. Blanchet M *et al.* 2015 Changes in bacterial community metabolism and composition during the

degradation of dissolved organic matter from the jellyfish Aurelia aurita in a Mediterranean coastal lagoon. *Environ. Sci. Pollut. Res.* **22**, 13638–13653. (doi:10.1007/s11356-014-3848-x)

63. Mayali X, Stewart B, Mabery S, Weber PK. 2016 Temporal succession in carbon incorporation from macromolecules by particle-attached bacteria in marine microcosms. *Environ. Microbiol. Rep.* **8**, 68–75. (doi:10.1111/1758-2229.12352)

64. Eilers H, Pernthaler J, Glöckner FO, Amann R. 2000 Culturability and In Situ Abundance of Pelagic Bacteria from the North Sea. *Appl. Environ. Microbiol.* **66**, 3044–3051. (doi:10.1128/AEM.66.7.3044-3051.2000)

65. Li A, Lin L, Zhang M, Zhu H. 2018 Antarcticibacterium flavum gen. nov., sp. nov., isolated from marine sediment. *Int. J. Syst. Evol. Microbiol.* **68**, 254–259. (doi:10.1099/ijsem.0.002489)

66. Ogawa H, Amagai Y, Koike I, Kaiser K, Benner R. 2001 Production of refractory dissolved organic matter by bacteria. *Science* **292**, 917–920. (doi:10.1126/science.1057627)

67. Lechtenfeld OJ, Hertkorn N, Shen Y, Witt M, Benner R. 2015 Marine sequestration of carbon in bacterial metabolites. *Nat. Commun.* **6**, 6711. (doi:10.1038/ncomms7711)

68. Biddanda B, Benner R. 1997 Carbon, Nitrogen, and Carbohydrate Fluxes During the Production of Particulate and Dissolved Organic Matter by Marine Phytoplankton. *Limnol. Oceanogr.* **42**, 506–518.

69. Burney CM. 1986 Bacterial utilization of total in situ dissolved carbohydrate in offshore waters. *Limnol. Oceanogr.* **31**, 427–431. (doi:10.4319/lo.1986.31.2.0427)

70. Arnosti C. 2000 Substrate specificity in polysaccharide hydrolysis: Contrasts between bottom water and sediments. *Limnol. Oceanogr.* **45**, 1112–1119. (doi:10.4319/lo.2000.45.5.1112)

71. Underwood GJC, Aslam SN, Michel C, Niemi A, Norman L, Meiners KM, Laybourn-Parry J, Paterson H, Thoma DN. 2013 Broad-scale predictability of carbohydrates and exopolymers in Antarctic and Arctic sea ice. *Proc. Natl. Acad. Sci. U. S. A.* **110**, 15734–15739. (doi:10.1073/pnas.1302870110)

72. Aslam SN, Michel C, Niemi A, Underwood GJC. 2016 Patterns and drivers of carbohydrate budgets in ice algal assemblages from first year Arctic sea ice. *Limnol. Oceanogr.* **61**, 919–937. (doi:10.1002/lno.10260)

73. Beier S, Bertilsson S. 2011 Uncoupling of chitinase activity and uptake of hydrolysis products in freshwater bacterioplankton. *Limnol. Oceanogr.* **56**, 1179–1188. (doi:10.4319/lo.2011.56.4.1179)

74. Mühlenbruch M, Grossart HP, Eigemann F, Voss M. 2018 Mini-review: Phytoplankton-derived polysaccharides in the marine environment and their interactions with heterotrophic bacteria. *Environ. Microbiol.* **20**, 2671–2685. (doi:10.1111/1462-2920.14302)

75. Abdullahi AS, Underwood GJC, Gretz MR. 2006 Extracellular matrix assembly in diatoms (Bacillariophyceae). V. Environmental effects on polysaccharide synthesis in the model diatom, Phaeodactylum tricornutum. *J. Phycol.* **42**, 363–378. (doi:10.1111/j.1529-8817.2006.00193.x)

76. Jain A, Krishnan KP. 2017 A glimpse of the diversity of complex polysaccharide-degrading culturable bacteria from Kongsfjorden, Arctic Ocean. *Ann. Microbiol.* **67**, 203–214. (doi:10.1007/s13213-016-1252-0)

77. Landa M, Blain S, Harmand J, Monchy S, Rapaport A, Obernosterer I. 2018 Major changes in the composition of a Southern Ocean bacterial community in response to diatom-derived dissolved organic matter. *FEMS Microbiol. Ecol.* **94**. (doi:10.1093/femsec/fiy034)

78. Yassaa N, Colomb A, Lochte K, Peeken I, Williams J. 2006 Development and application of a headspace solid-phase microextraction and gas chromatography/mass spectrometry method for the determination of dimethylsulfide emitted by eight marine phytoplankton species. *Limnol. Oceanogr. Methods* **4**, 374–381. (doi:10.4319/lom.2006.4.374)

79. Williams TJ, Wilkins D, Long E, Evans F, DeMaere MZ, Raftery MJ, Cavicchioli R. 2013 The role of planktonic Flavobacteria in processing algal organic matter in coastal East Antarctica revealed using metagenomics and metaproteomics. *Environ. Microbiol.* **15**, 1302–1317. (doi:10.1111/1462-2920.12017)

80. Xing P *et al.* 2015 Niches of two polysaccharide-degrading Polaribacter isolates from the North Sea during a spring diatom bloom. *ISME J.* **9**, 1410–1422. (doi:10.1038/ismej.2014.225)

81. Unfried F *et al.* 2018 Adaptive mechanisms that provide competitive advantages to marine bacteroidetes during microalgal blooms. *ISME J.* **12**, 2894–2906. (doi:10.1038/s41396-018-0243-5)

Tables

Table 1: Cultivable bacteria counts for sea ice bottom and water column samples collected at an ice camp (67°28.784' N, 063°47.372' W) located near Qikiqtarjuaq (Nunavut) in the Baffin Bay. CFU: Colony-Forming Unites, ND: No data.

Table 2: Parameters measured in the microalgae cultures at beginning (T0) and after 44 days (T44d). DOC: dissolved organic carbon; POC: particulate organic carbon; DFCHO-C: dissolved free monosaccharides; DPCHO-C: dissolved polysaccharides; TDCHO-C: total dissolved saccharides. ND: not determined.

Table 3: Indices characterizing the growth of bacterial strains according to the substrate added. (A) Index 1: Distinction between strains which have shown significant growth using different substrates (in red) and those which have not shown visible growth (in blue). (B) Index 2: Results of cell growth on different exudates expressed in relation to those measured in diluted MB. See the material and methods for the explanations of the calculation of the indexes. * Bacterial strains isolated in 2009 in the Beaufort Sea, Arctic Ocean.

Figures

Figure 1. Location of Qikiqtarjuaq Ice Camp (67°28.784' N, 063°47.372' W). The position is shown with a white dot (courtesy of R. Amiraux).

Figure 2. Phylogenetic tree of bacterial strains isolated from ice camp samples and closely related species obtained from GenBank. The codes indicate the environmental Arctic strains isolated (see Table 3). The GenBank accession number follows specific names of the closely related species found in the database. The phylogenetic tree was made using the maximum likelihood method ("Maximum Likelihood", ML). The phylogeny obtained was statistically analyzed by the bootstrap method, with 1000 repetitions (values >0.5 are shown at each node). In red: Gammaproteobacteria ; in orange: Alphaproteobacteria ; in green: Flavobacteriia; in blue: Actinobacteria; in grey: Firmicutes. The *Chloroflexus islandicus* sequence has been used as outgroup to root the tree. Scale bar represents 2% estimated substitutions.

Figure 3. Growth of the microalgae (A) *Chaetoceros neogracilis* and (B) *Fragilariopsis cylindrus*. Values stand for means of triplicate cultures and error bars show ±SD.

Figure 4. Growth of (A) Strain BBCC 770, *Polaribacter filamentus* (3 m depth, Beaufort Sea) ; (B) Strain BBCC 2586, *Idiomarina abyssalis* (40 m depth, Green Edge ice camp) ; (C) Strain BBCC 2589, *Mesonia algae* (40 m depth, Green Edge ice camp) ; (D) Strain BBCC 2637, *Stenotrophomonas chelatiphaga* (sea ice, Green Edge ice camp) ; with different sources of dissolved organic matter (DOM): absence of DOM (ASW); diluted Marine Broth (MB); exudates from *C. neogracilis* and *F. cylindrus*. Values stand for means of triplicate treatments and error bars show ±SD.

Figure 5. Venn diagram showing the number of bacterial strains growing with the different microalgae exudates (*C. neogracilis*, *F. cylindrus*) and diluted Marine Broth (MB).

Supplementary information

Table S1. Marine agar 2216 and Marine broth 2216 composition

Figure S1. Composition of the cultivable bacterial community. (A) Proportion of phyla represented (92 bacterial strains). (B) Proportion of phyla as a function of different habitats (sea ice bottom: 28 strains; water column2 m: 38 strains; water column 40-60 m: 26 strains). For a better representation, the phylum of Proteobacteria was divided into two classes: γ-Proteobacteria and α-Proteobacteria.

Figure S2. Bacterial growth in the (A) *Chaetoceros neogracilis* and (B) *Fragilariopsis cylindrus* cultures. Values stand for means of triplicate cultures and error bars show ±SD.

Figure S3. Venn diagram showing the number of bacterial strains growing with the different microalgae exudates (*C. neogracilis, F. cylindrus*) and diluted Marine Broth (MB). (A) Bacterial strains isolated from sea ice. (B) Bacterial strains isolated at 2-3m depth. (C) Bacterial strains isolated at 40-60m depth.

Figure S4. Bacterial growth of (A) Strain BBCC770, *Polaribacter filamentus* and (B) Strain BBCC808, *Maribacter arcticus* with different dilutions of Marine broth (MB) with or without stirring. The different dilutions of MB contained the following dissolved organic carbon (DOC) concentrations: 1/25 = 8400 µM ; 1/50 = 4200 µM ; 1/100 = 2100 µM ; 1/250 = 840 µM ; 1/500 = 420 µM ; 1/1000 = 210 µM.

Habitat	Sampling date (d/m/y)	Julian day	Temperature (°C)	Salinity (psu)	Chl*a* ($\mu g.L^{-1}$)	CFU ($10^2.mL^{-1}$)	Total bacteria ($10^5.mL^{-1}$)	CFU/Total (%)	Number of isolated strains
Sea ice	09/05/2016	130	ND	ND	30	17.2	1.08	1.59%	8
Sea ice	23/05/2016	144	ND	ND	95.87	8.7	4.87	0.18%	7
Sea ice	30/05/2016	151	ND	ND	164.88	0.1	5.26	0.00%	ND
Sea ice	06/06/2016	158	ND	ND	61.89	0.9	4.6	0.02%	ND
Sea ice	20/06/2016	172	ND	ND	138.01	17.5	ND	ND	8
Sea ice	27/06/2016	179	ND	ND	39.68	27.1	6.24	4.35%	5
2 m	09/05/2016	130	-1.73	32.22	0.06	11.5	2.01	0.57%	7
2 m	16/05/2016	137	-1.74	32.24	ND	20.8	2.62	0.80%	ND
2 m	23/05/2016	144	-1.73	32.22	0.07	32.6	2.64	1.23%	6
2 m	30/05/2016	151	-1.71	32.26	0.16	15.5	2.47	0.63%	ND
2 m	06/06/2016	158	-1.7	32.28	0.88	12.7	2.38	0.53%	ND
2 m	13/06/2016	165	-1.69	32.29	0.36	23.3	2.71	0.86%	6
2 m	20/06/2016	172	-1.62	32.16	0.4	19.5	3.51	0.56%	6
2 m	27/06/2016	179	-1.51	32.1	1.06	14.5	5.09	0.29%	7
2 m	11/07/2016	193	-1.29	31.6	1.44	4.6	6.81	0.07%	6
40 m	09/05/2016	130	-1.67	32.28	0.13	5.7	2.09	0.27%	8
40 m	16/05/2016	137	-1.68	32.35	ND	2.9	2.35	0.12%	ND
40 m	23/05/2016	144	-1.69	32.27	0.06	3	2.43	0.12%	4
40 m	30/05/2016	151	-1.65	32.36	0.05	0.7	2.38	0.03%	ND
40 m	06/06/2016	158	-1.68	32.31	0.08	3.8	2.56	0.15%	ND
40 m	13/06/2016	165	-1.63	32.44	0.06	13.2	2.59	0.51%	5
60 m	27/06/2016	179	-1.58	32.51	0.32	10.5	3.16	0.33%	6
60 m	11/07/2016	193	-1.57	32.38	0.59	1.6	3.62	0.04%	3

Table 1

	C. neogracilis		*F. cylindrus*	
	T0	T44d	T0	T44d
Cells $x10^4.mL^{-1}$	8.7 (± 2.9)	122 (± 13)	0.6 (± 0.2)	31.2 (± 2.2)
NO_3 (µM)	864.9 (± ND)	224.3 (± 118.2)	859.4 (± ND)	674.5 (± 60.2)
PO_4 (µM)	81.5 (± ND)	20.7 (± 8.7)	79.9 (± ND)	62.1 (± 0.8)
$Si(OH)_4$ (µM)	35.2 (± ND)	3.6 (± 0.7)	36.0 (± ND)	2.7 (± 1.2)
DOC (µM)	234.1 (± 0.8)	2007.2 (± 778.4)	108.8 (± 6.8)	977 (± 70.2)
POC (µM)	ND	2500 (± 423)	ND	612 (± ND)
DOC/(POC+DOC) (%)	ND	45	ND	61
DFCHO-C (µM)	ND	118.2	ND	20.2
PCHO-C (µM)	ND	246.4	ND	14.6
TCHO-C (µM)	ND	364.6	ND	34.8
TCHO-C/DOC (%)	ND	18	ND	4

Table 2

Habitat	Strain	Class	Family	Closest Relative Species	A. MB	A. *C. neogracilis*	A. *F. cylindrus*	B. *C. neogracilis*/MB	B. *F. cylindrus*/MB
Sea ice	BBCC 2678	Actinobacteria	Microbacteriaceae	*Salinibacterium amurskyense*				0.97	NA
Sea ice	BBCC 2851	Alphaproteobacteria	Erythrobacteraceae	*Porphyrobacter sanguineus*				0.62	NA
Sea ice	BBCC 2680	Alphaproteobacteria	Rhodobacteraceae	*Loktanella salsilacus*				1.58	0.57
Sea ice	BBCC 2856	Gammaproteobacteria	Pseudoalteromonadaceae	*Pseudoalteromonas distincta*				NA	1.76
Sea ice	BBCC 2592	Gammaproteobacteria	Pseudoalteromonadaceae	*Pseudoalteromonas neustonica*				1.81	NA
Sea ice	BBCC 2584	Gammaproteobacteria	Pseudoalteromonadaceae	*Pseudoalteromonas nigrifasciens*				0.47	2.48
Sea ice	BBCC 2635	Gammaproteobacteria	Pseudomonadaceae	*Pseudomonas paralactis*				8.27	NA
Sea ice	BBCC 2597	Gammaproteobacteria	Pseudomonadaceae	*Pseudomonas pelagia*				45.79	NA
Sea ice	BBCC 2637	Gammaproteobacteria	Xanthomonadaceae	*Stenotrophomonas chelatiphaga*				0.40	NA
Sea ice	BBCC 2850	Flavobacteria	Flavobacteriaceae	*Antarticibacterium flavum*				0.35	NA
Sea ice	BBCC 2681	Flavobacteria	Flavobacteriaceae	*Flavobacterium gelidilacus*				0.81	NA
2m	BBCC 2625	Actinobacteria	Microbacteriaceae	*Cryobacterium arcticum*				1.19	NA
2m	BBCC 2611	Actinobacteria	Nocardiaceae	*Rhodococcus fascians*				4.13	13.24
2m	BBCC 2639	Actinobacteria	Nocardiaceae	*Rhodococcus kyotonensis*				7.11	4.22
2m	BBCC 2602	Alphaproteobacteria	Hyphomonadaceae	*Litorimonas haliclonae*				11.06	NA
2m	BBCC 2676	Alphaproteobacteria	Rhodobacteraceae	*Paracoccus hibiscisoli*				NA	NA
3m	BBCC 810*	Alphaproteobacteria	Rhodobacteraceae	*Sulfitobacter marinus*				0.63	0.11
2m	BBCC 2638	Gammaproteobacteria	Alteromonadaceae	*Alteromonas stellipolaris*				2.89	9.17
2m	BBCC 2601	Gammaproteobacteria	Alteromonadaceae	*Paraglaciecola chathamensis*				NA	NA
3m	BBCC 757*	Gammaproteobacteria	Colwelliaceae	*Colwellia polaris*				0.48	1.42
2m	BBCC 2603	Gammaproteobacteria	Moraxellaceae	*Psychrobacter aquimaris*				NA	NA
2m	BBCC 2599	Gammaproteobacteria	Moraxellaceae	*Psychrobacter glaciei*				NA	NA
2m	BBCC 2579	Gammaproteobacteria	Moraxellaceae	*Psychrobacter okhotskensis*				NA	NA
2m	BBCC 2626	Gammaproteobacteria	Pseudoalteromonadaceae	*Pseudoalteromonas translucida*				NA	NA
2m	BBCC 2854	Flavobacteria	Flavobacteriaceae	*Bizionia berychis*				0.93	NA
2m	BBCC 2578	Flavobacteria	Flavobacteriaceae	*Leeuwenhoekiella aequorea*				0.34	NA
2m	BBCC 2613	Flavobacteria	Flavobacteriaceae	*Maribacter dokdonensis*				3.62	NA
2m	BBCC 2624	Flavobacteria	Flavobacteriaceae	*Maribacter orientalis*				0.61	NA
3m	BBCC 808*	Flavobacteria	Flavobacteriaceae	*Maribacter arcticus*				0.82	NA
3m	BBCC 770*	Flavobacteria	Flavobacteriaceae	*Polaribacter filamentus*				1.37	NA
60m	BBCC 2632	Actinobacteria	Nocardiaceae	*Rhodococcus cerastii*				NA	NA
40m	BBCC 2605	Alphaproteobacteria	Rhodobacteraceae	*Paracoccus homiensis*				3.95	0.18
40m	BBCC 2855	Alphaproteobacteria	Rhodobacteraceae	*Sulfitobacter litoralis*				86.19	NA
40m	BBCC 2586	Gammaproteobacteria	Idiomarinaceae	*Idiomarina abyssalis*				0.48	NA
40m	BBCC 2617	Gammaproteobacteria	Moraxellaceae	*Psychrobacter marincola*				7.82	4.49
40m	BBCC 2590	Gammaproteobacteria	Moraxellaceae	*Psychrobacter nivimaris*				NA	NA
40m	BBCC 2848	Gammaproteobacteria	Pseudomonadaceae	*Pseudomonas sabulinigri*				98.61	NA
40m	BBCC 2585	Gammaproteobacteria	Pseudomonadaceae	*Pseudomonas zhaodongensis*				NA	NA
40m	BBCC 2589	Flavobacteria	Flavobacteriaceae	*Mesonia algae*				1.11	0.86
60m	BBCC 2643	Flavobacteria	Flavobacteriaceae	*Gillisia hiemivivida*				0.44	NA

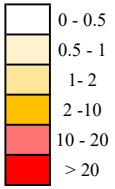


Table 3

Fig. 1

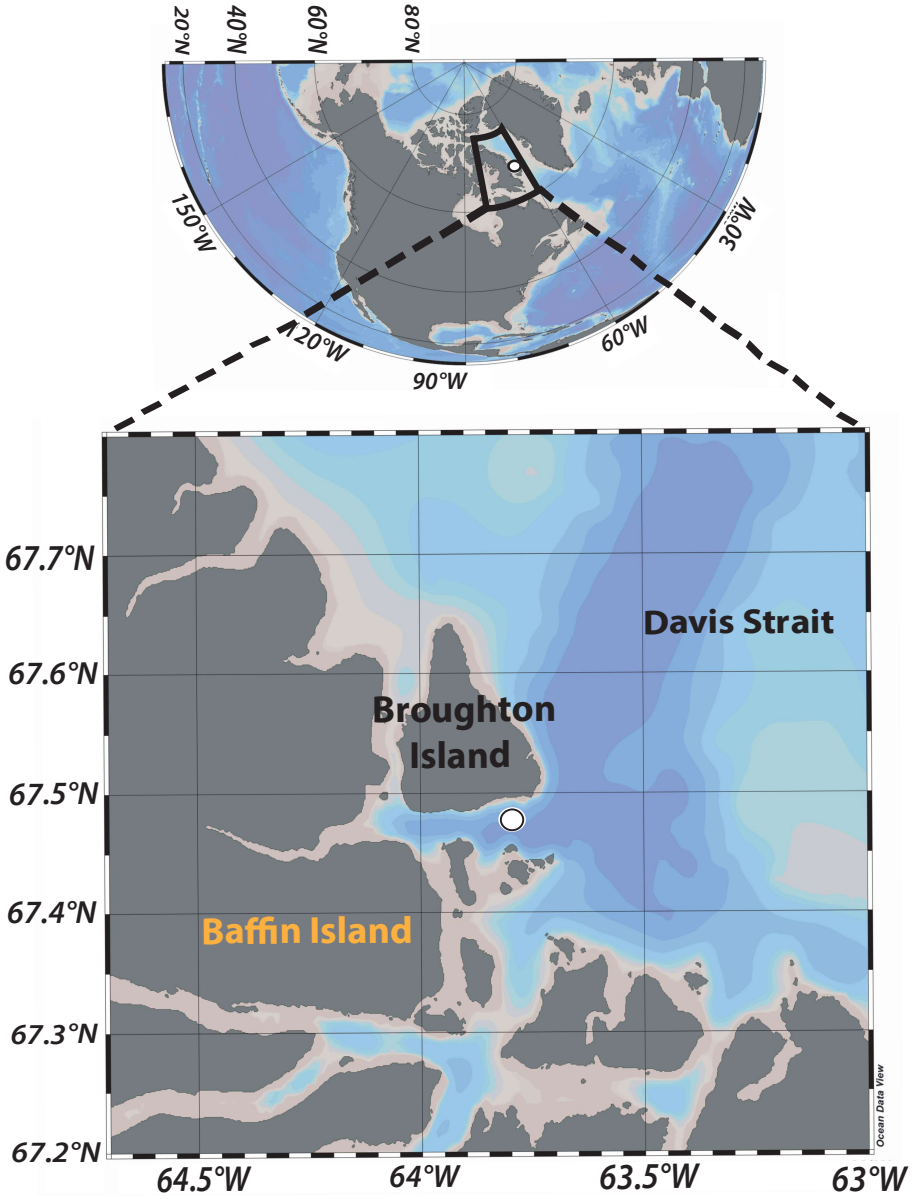

20°N
40°N
60°N
80°N
150°W
30°W
120°W
60°W
90°W
67.7°N
67.6°N
67.5°N
67.4°N
67.3°N
67.2°N
64.5°W
64°W
63.5°W
63°W
Davis Strait
Broughton Island
Baffin Island
Ocean Data View

Fig. 2

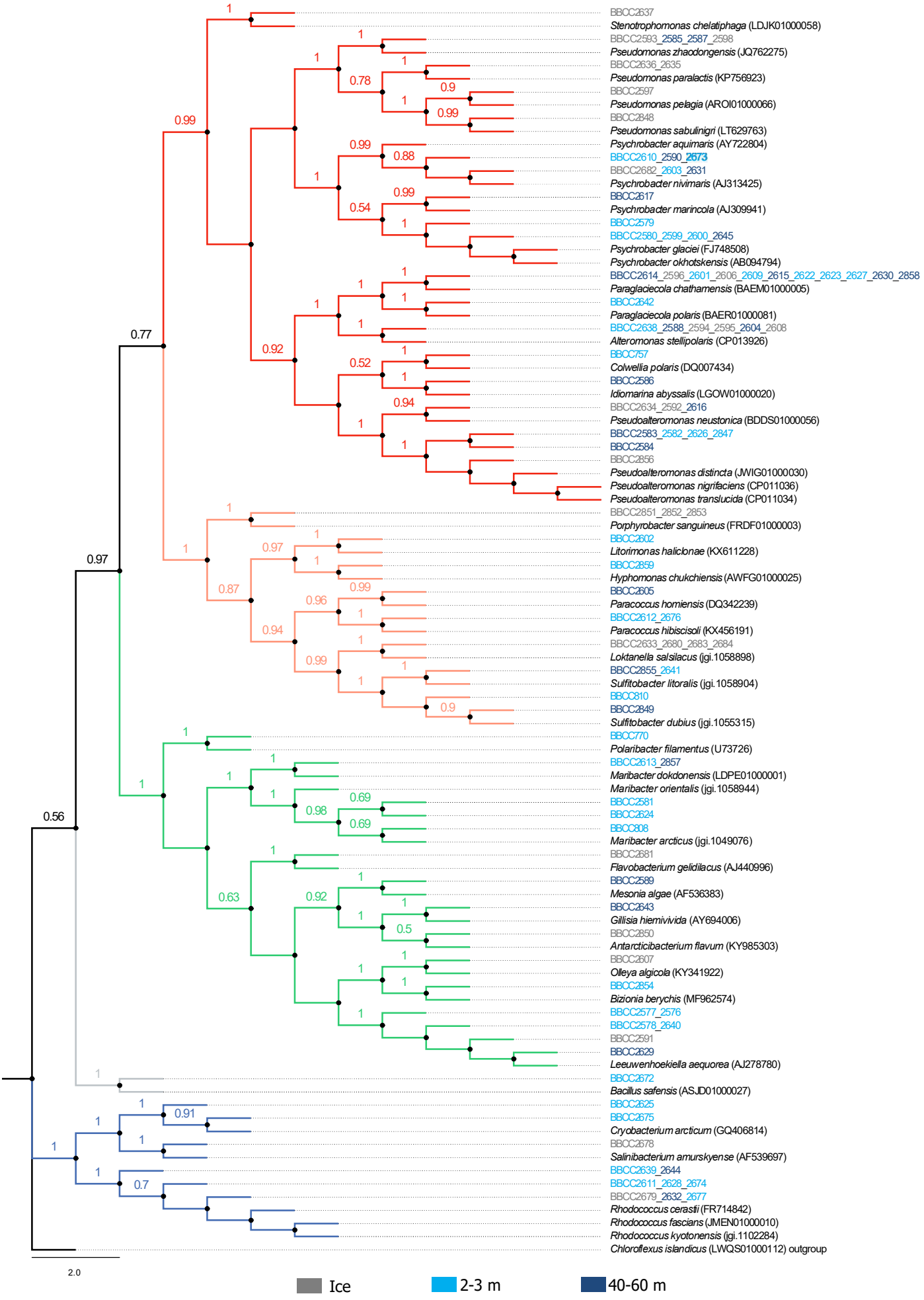

BBCC2637
Stenotrophomonas chelatiphaga (LDJK01000058)
BBCC2593_2585_2587_2598
Pseudomonas zhaodongensis (JQ762275)
BBCC2636_2635
Pseudomonas paralactis (KP756923)
BBCC2597
Pseudomonas pelagia (AROI01000066)
BBCC2848
Pseudomonas sabulinigri (LT629763)
Psychrobacter aquimaris (AY722804)
BBCC2610_2590_2673
BBCC2682_2603_2631
Psychrobacter nivimaris (AJ313425)
BBCC2617
Psychrobacter marincola (AJ309941)
BBCC2579
BBCC2580_2599_2600_2645
Psychrobacter glaciei (FJ748508)
Psychrobacter okhotskensis (AB094794)
BBCC2614_2596_2601_2606_2609_2615_2622_2623_2627_2630_2858
Paraglaciecola chathamensis (BAEM01000005)
BBCC2642
Paraglaciecola polaris (BAER01000081)
BBCC2638_2588_2594_2595_2604_2608
Alteromonas stellipolaris (CP013926)
BBCC757
Colwellia polaris (DQ007434)
BBCC2586
Idiomarina abyssalis (LGOW01000020)
BBCC2634_2592_2616
Pseudoalteromonas neustonica (BDDS01000056)
BBCC2583_2582_2626_2847
BBCC2584
BBCC2856
Pseudoalteromonas distincta (JWIG01000030)
Pseudoalteromonas nigrifaciens (CP011036)
Pseudoalteromonas translucida (CP011034)
BBCC2851_2852_2853
Porphyrobacter sanguineus (FRDF01000003)
BBCC2602
Litorimonas haliclonae (KX611228)
BBCC2859
Hyphomonas chukchiensis (AWFG01000025)
BBCC2605
Paracoccus horniensis (DQ342239)
BBCC2612_2676
Paracoccus hibiscisoli (KX456191)
BBCC2633_2680_2683_2684
Loktanella salsilacus (jgi.1058898)
BBCC2855_2641
Sulfitobacter litoralis (jgi.1058904)
BBCC810
BBCC2849
Sulfitobacter dubius (jgi.1055315)
BBCC770
Polaribacter filamentus (U73726)
BBCC2613_2857
Maribacter dokdonensis (LDPE01000001)
Maribacter orientalis (jgi.1058944)
BBCC2581
BBCC2624
BBCC808
Maribacter arcticus (jgi.1049076)
BBCC2681
Flavobacterium gelidilacus (AJ440996)
BBCC2589
Mesonia algae (AF536383)
BBCC2643
Gillisia hiemivivida (AY694006)
BBCC2850
Antarcticibacterium flavum (KY985303)
BBCC2607
Olleya algicola (KY341922)
BBCC2854
Bizionia berychis (MF962574)
BBCC2577_2576
BBCC2578_2640
BBCC2591
BBCC2629
Leeuwenhoekiella aequorea (AJ278780)
BBCC2672
Bacillus safensis (ASJD01000027)
BBCC2625
BBCC2675
Cryobacterium arcticum (GQ406814)
BBCC2678
Salinibacterium amurskyense (AF539697)
BBCC2639_2644
BBCC2611_2628_2674
BBCC2679_2632_2677
Rhodococcus cerastii (FR714842)
Rhodococcus fascians (JMEN01000010)
Rhodococcus kyotonensis (jgi.1102284)
Chloroflexus islandicus (LWQS01000112) outgroup
2.0
Ice
2-3 m
40-60 m

Fig. 3

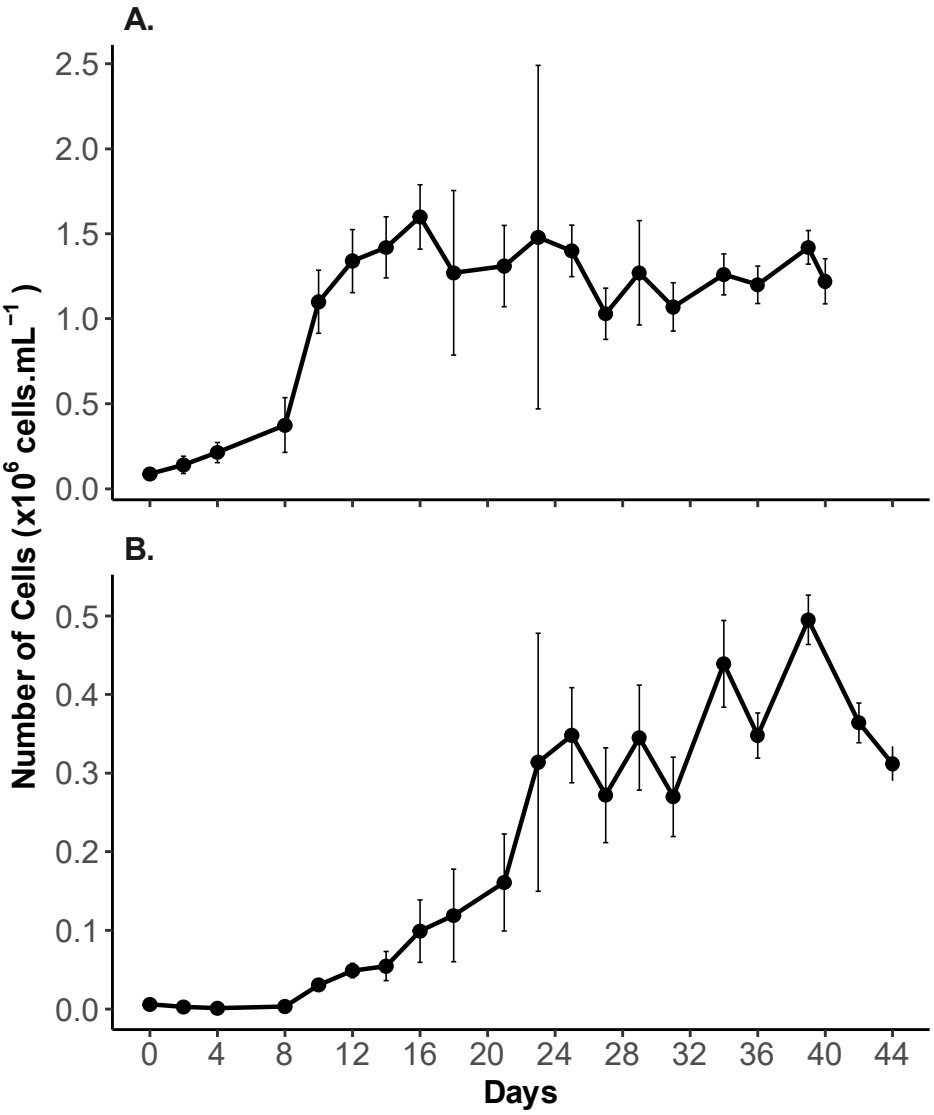

A.
B.
Number of Cells (x10^6 cells.mL^-1)
2.5
2.0
1.5
1.0
0.5
0.0
0.5
0.4
0.3
0.2
0.1
0.0
0
4
8
12
16
20
24
28
32
36
40
44
Days

Fig. 4

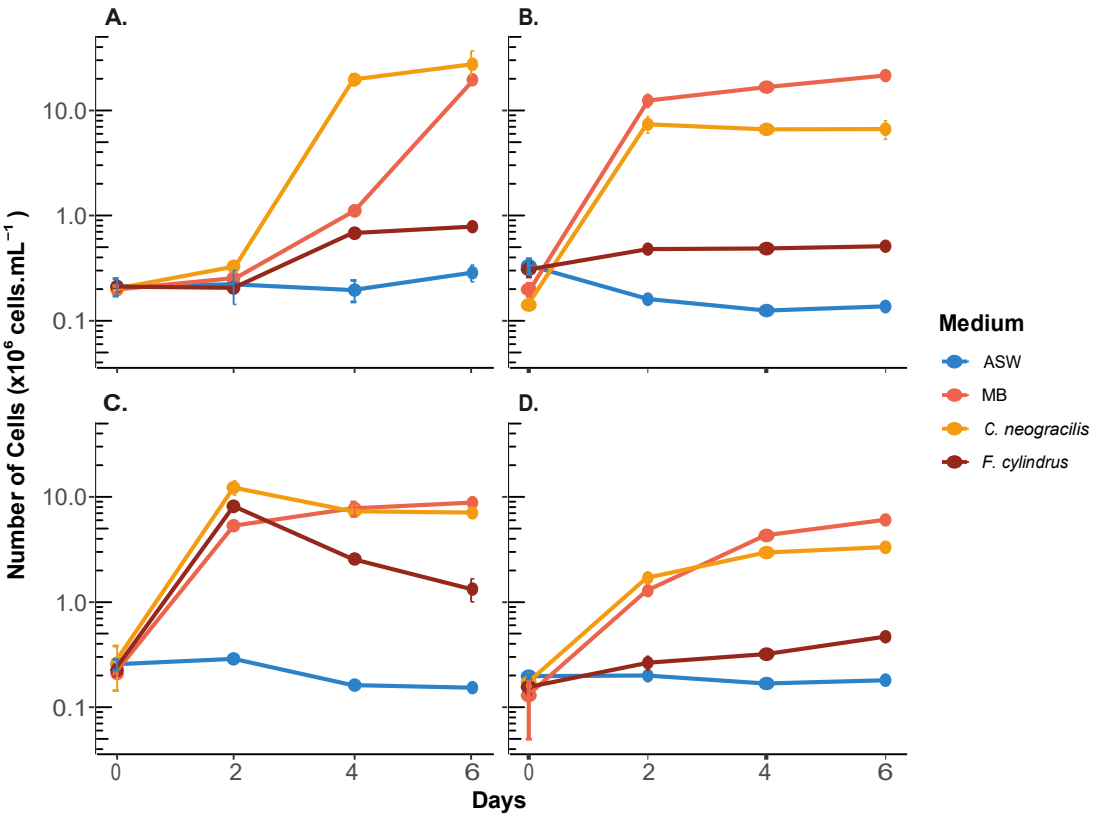

A.
B.
C.
D.
10.0
1.0
0.1
0
2
4
6
Days
Number of Cells (x10^6 cells.mL^-1)
Medium
ASW
MB
C. neogracilis
F. cylindrus

Fig. 5

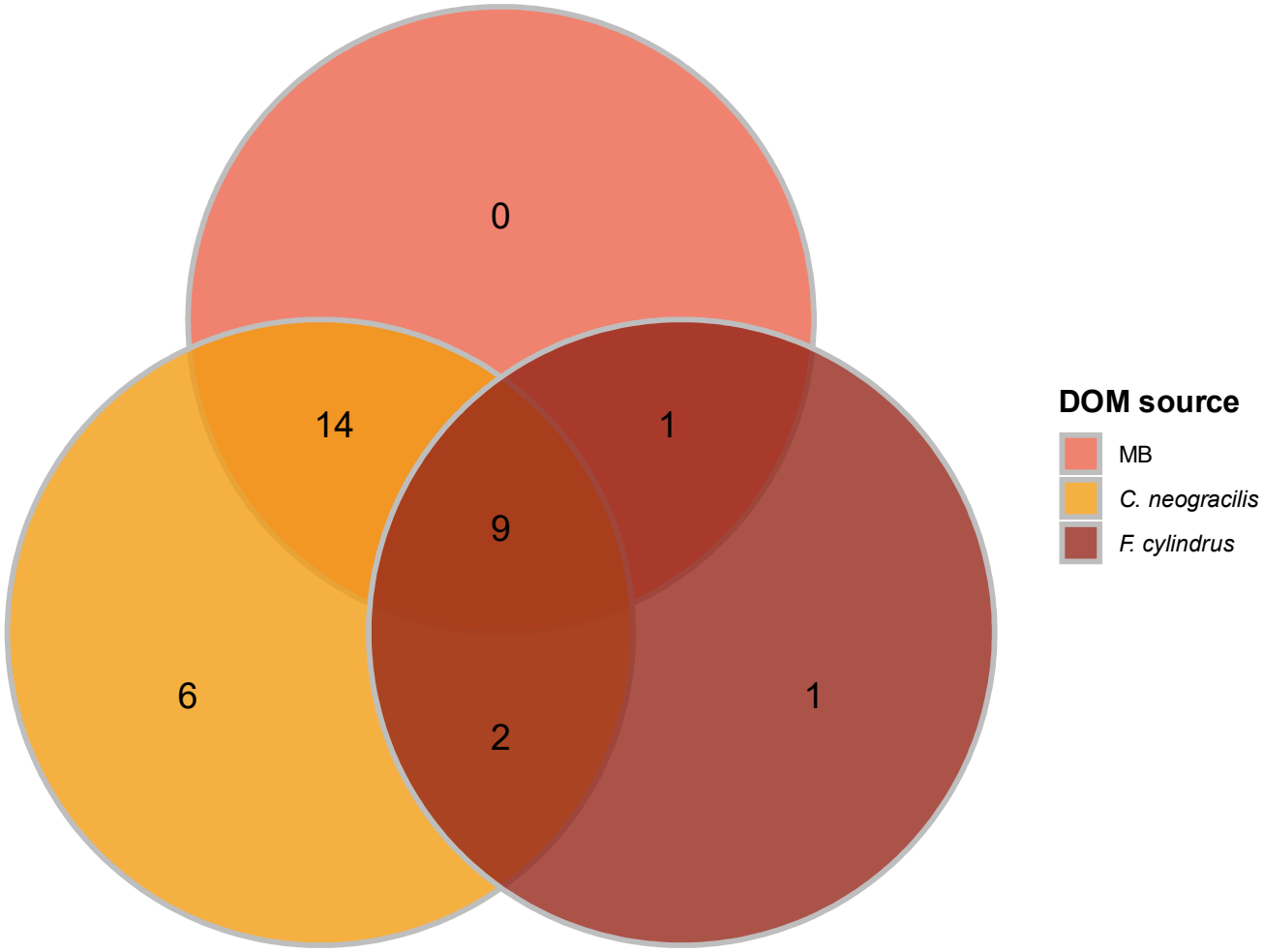


Table S1

Component	Quantity
Peptone	5.0 g
Yeast Extract	1.0 g
Ferrice Citrate	0.1 g
Sodium Chloride	19.45 g
Magnesium Chloride	8.8 g
Sodium Sulfate	3.24 g
Calcium Chloride	1.8 g
Potassium Chloride	0.55 g
Sodium Bicarbonate	0.16 g
Potassium Bromide	0.08 g
Strontium Chloride	34.0 mg
Boric Acid	22.0 mg
Sodium Silicate	4.0 mg
Sodium fluoride	2.4 mg
Ammonium Nitrate	1.6 mg
Disodium Phosphate	8.0 mg
Agar*	15.0 g

* Omit Agar for Broth medium

Fig. S1

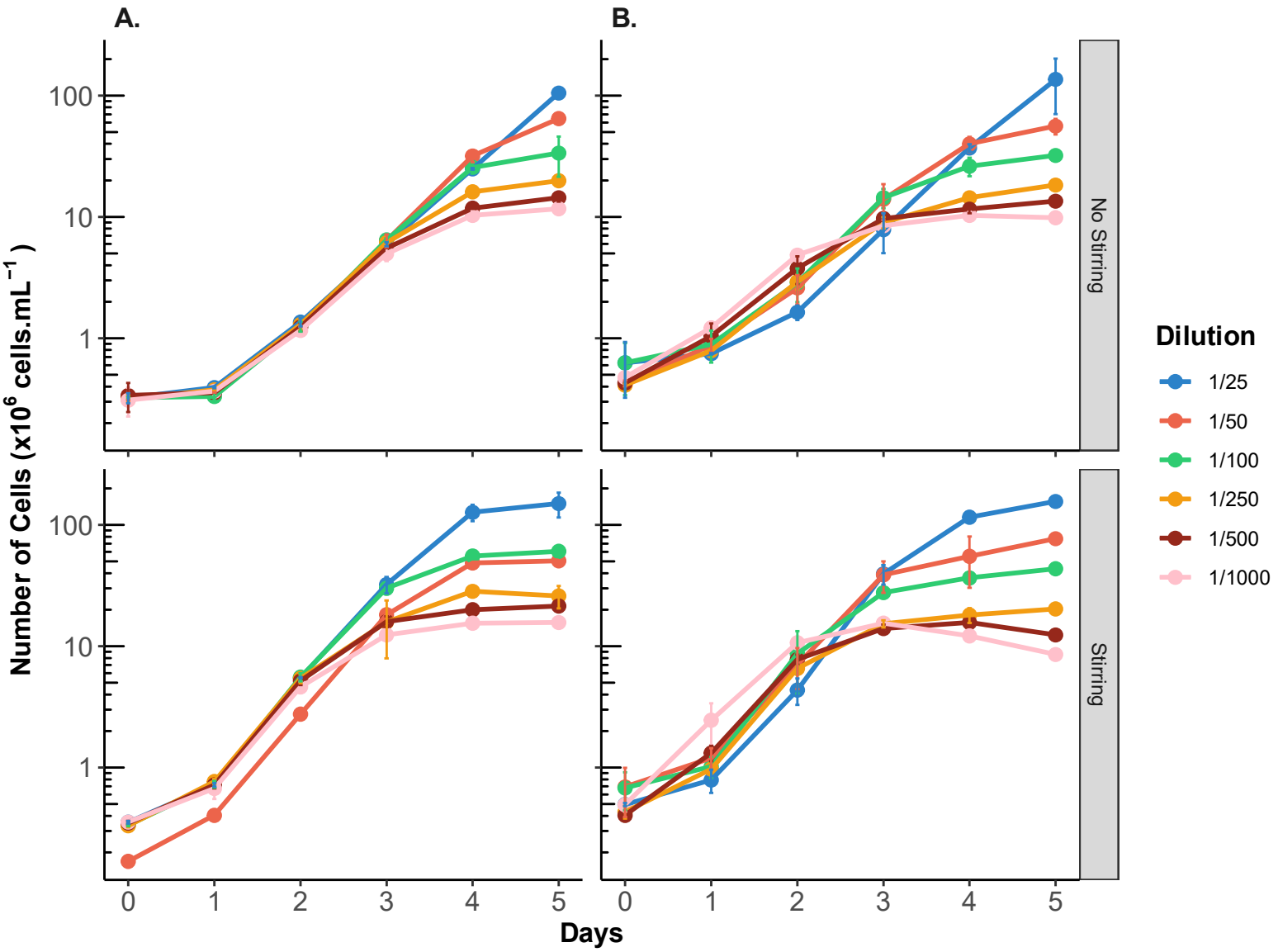

A.
B.
100
10
1
No Stirring
Stirring
Number of Cells (x10^6 cells.mL^-1)
0
1
2
3
4
5
Days
Dilution
1/25
1/50
1/100
1/250
1/500
1/1000

Fig. S2

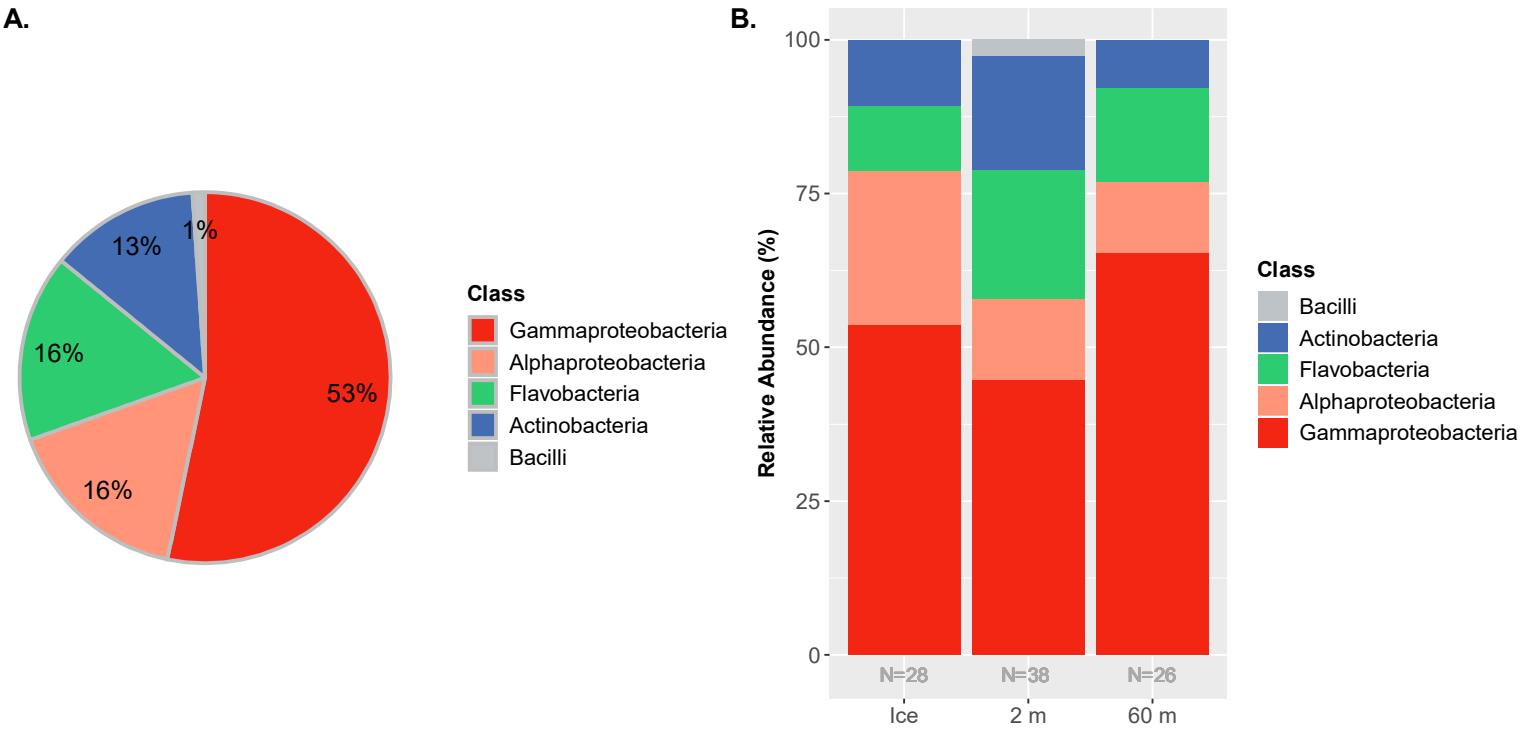

A.
1%
13%
16%
53%
16%
Class
Gammaproteobacteria
Alphaproteobacteria
Flavobacteria
Actinobacteria
Bacilli
B.
Relative Abundance (%)
100
75
50
25
0
N=28
N=38
N=26
Ice
2 m
60 m
Class
Bacilli
Actinobacteria
Flavobacteria
Alphaproteobacteria
Gammaproteobacteria

Fig. S3

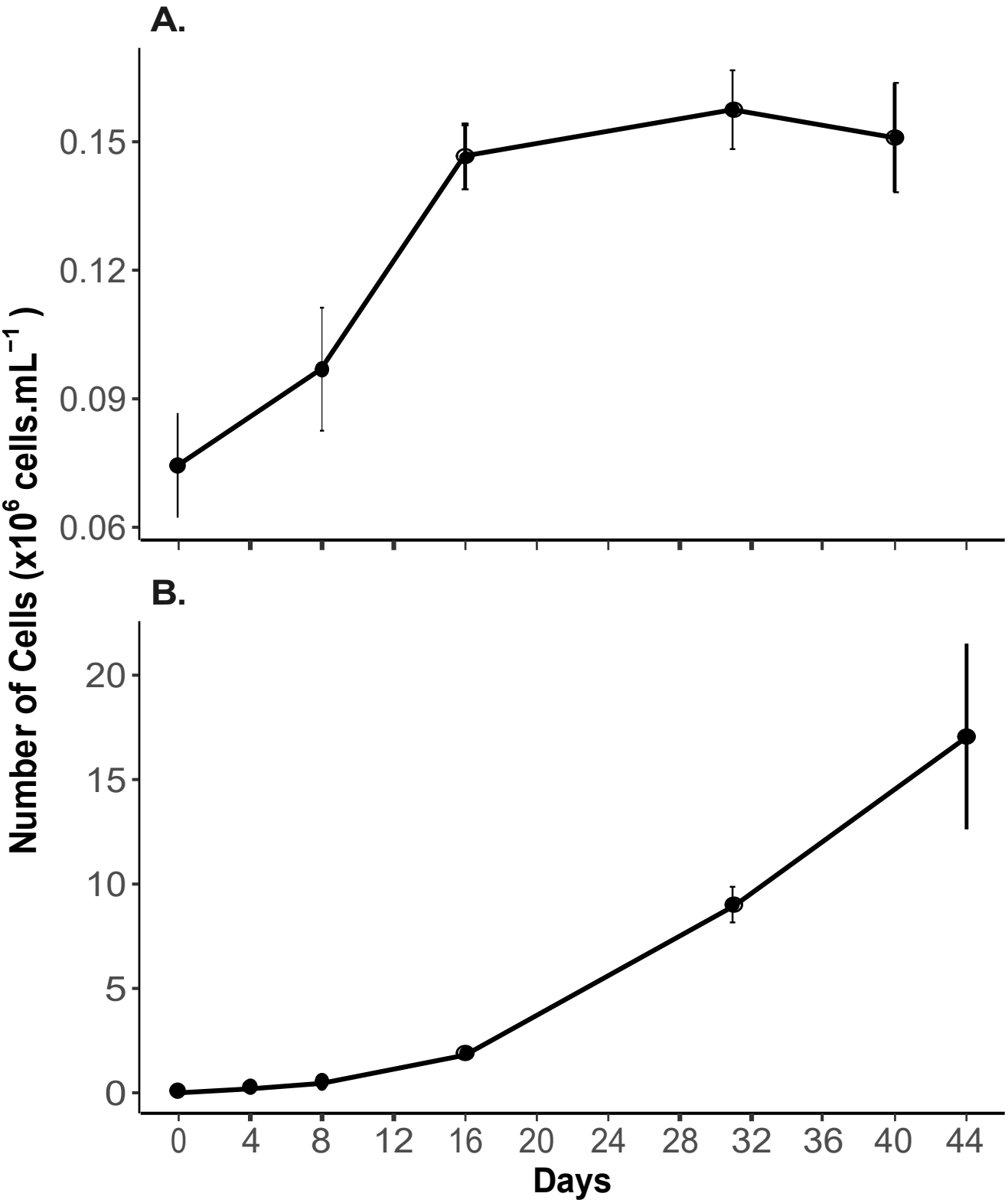
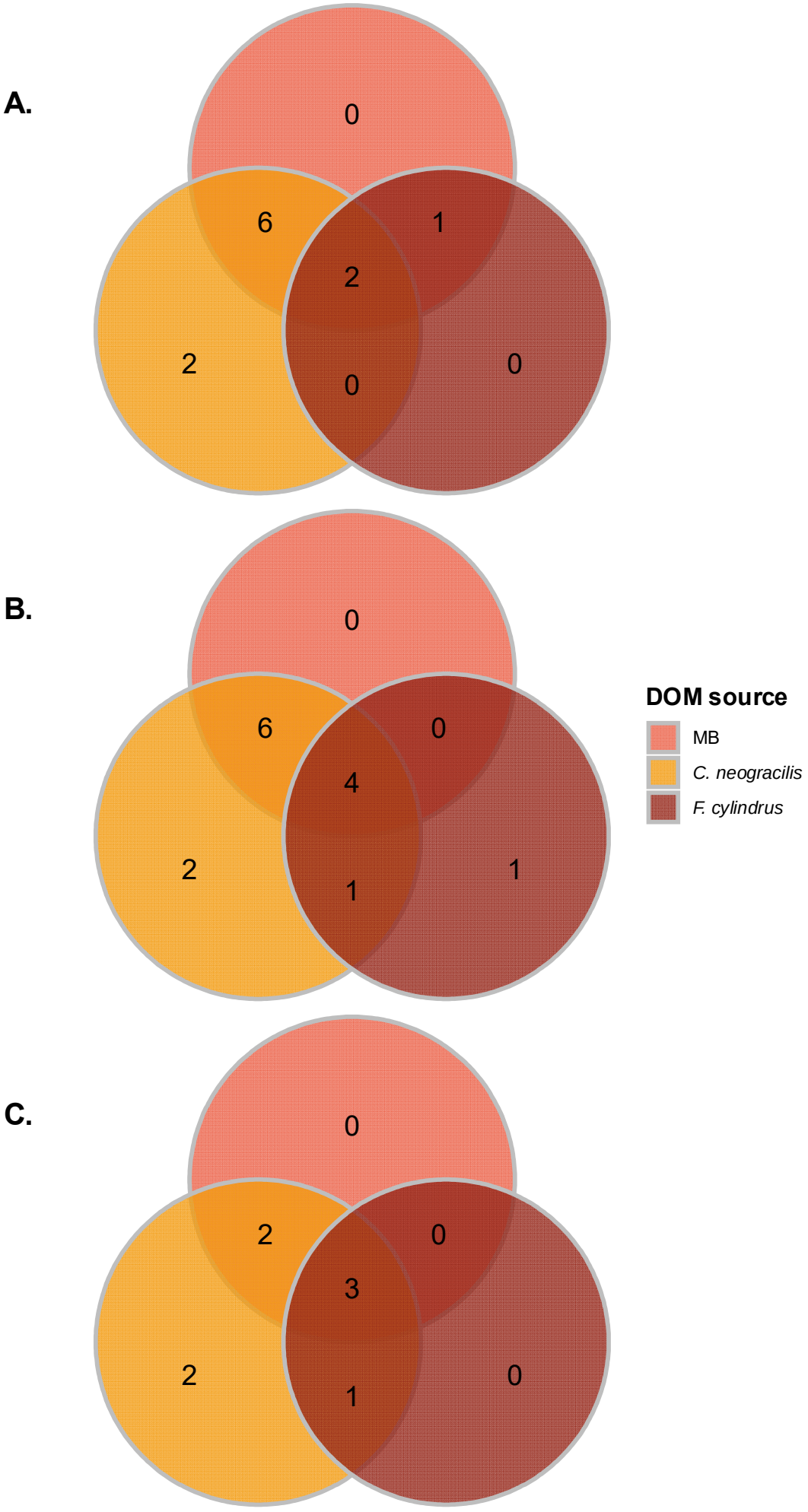

A.
0.15
0.12
0.09
0.06
B.
20
15
10
5
0
0
4
8
12
16
20
24
28
32
36
40
44
Days
Number of Cells (x10^6 cells.mL^-1)

Fig. S4


A.
0
6
1
2
2
0
0
B.
0
6
0
4
2
1
1
DOM source
MB
C. neogracilis
F. cylindrus
C.
0
2
0
3
2
1
0