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Biological transformation of Arctic dissolved organic matter in a NE Greenland fjord

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Abstract

Arctic waters are often enriched with terrestrial dissolved organic matter (DOM) characterised by having elevated visible wavelength fluorescence (commonly termed humic-like). Here we have identified the sources of fluorescent DOM (FDOM) in a high Arctic fjord (Young Sound, NE Greenland) influenced by glacial meltwater. The biological transformation of FDOM was further investigated using plankton community size-fractionation experiments. The intensity of ultraviolet fluorescence (commonly termed amino acid-like) was highly variable and positively correlated to bacterial production and mesozooplankton grazing. The overall distribution of visible FDOM in the fjord was hydrographically driven by the high-signal intrusion of Arctic terrestrial DOM from shelf waters and dilution with glacial runoff in the surface waters. However, the high-intensity visible FDOM that accumulated in subsurface waters in summer was not solely linked to allochthonous sources. Our data indicate that microbial activity, in particular, protist bacterivory, to be a source. A decrease in visible FDOM in subsurface waters was concurrent with an increase in bacterial abundance, indicating an active bacterial uptake or modification of this DOM fraction. This was confirmed by net-loss of visible FDOM in experiments during summer when bacterial activity was high. The degradation of visible FDOM appeared to be associated with bacteria belonging to the order Alteromonadales mainly the genus *Glaciecola* and the SAR92 clade. The findings provide new insight into the character of Arctic terrestrial DOM and the biological production and degradation of both visible and UV wavelength organic matter in the coastal Arctic.

Introduction

Microorganisms produce, transform and consume dissolved organic matter (DOM) and as a result, all aquatic environments contain a complex mixture of organic molecules that vary greatly in chemical characteristics and size. This results in a considerable analytical challenge for resolving the production, turnover and fate of carbon, nitrogen and phosphorus bound as organic matter. The most common approach to quantify DOM is to measure its carbon content (dissolved organic carbon, DOC), however, this provides no information on DOM characteristics, which ultimately impacts its fate. Other measures such as bioavailability (BDOC) (Søndergaard and Middelboe 1995), and optical properties of the organic matter (Stedmon and Nelson 2015), offer insight into the DOM character. Fluorescent DOM (FDOM) signal can be separated into underlying components which group into broad visible wavelength "humic-like" fluorescence (henceforth termed visible fluorescence) and ultraviolet wavelength fluorescence (henceforth termed UV fluorescence) which is typical for simpler structures such free or combined amino acids or benzoic acid derivatives (Wünsch et al. 2015).

Arctic waters are characterised by having elevated visible fluorescence and this is linked to the high terrestrial input of organic matter (Amon et al. 2003; Walker et al. 2013), which have been used to trace large-scale water mass distribution of Arctic water (Amon et al. 2003; Gonçalves-Araujo et al. 2016). The rapid warming of the Arctic cryosphere is increasing riverine discharge and thus the land to ocean transport of organic carbon (Holmes et al. 2008; Feng et al. 2013). In the glacial fjords of Greenland, the rate of ice loss from the Greenland Ice Sheet has doubled in the last decade (Kjeldsen et al. 2015). Glacial meltwater from the ice sheet contains a significant fraction of bioavailable DOM (Lawson et al. 2014; Paulsen et al. 2017), which potentially constitutes an important carbon source for coastal and marine food webs. This is particularly relevant in low productive Arctic systems characterised by a short ice-free summer, stratification and low light conditions due to riverine freshwater and inorganic particle input. Increases in stratification limit inorganic nutrient replenishment from deeper waters and thus we can expect that local primary production is more dependent on allochthonous inputs and local mineralisation. Young Sound in North East Greenland (Fig. 1) is typical for such an Arctic system. It is influenced by melt-water from the Greenland Ice Sheet via land-terminating glaciers, while the marine end-member of the fjord originates from the East Greenland Current stemming from the Arctic. Local conditions are changing and this is evident as the average

salinity from 2003 to 2015, has decreased in Young Sound by 0.12 per year indicating an increased influence of freshwater (Sejr et al. 2017).

Young Sound is considered to be low productive (annual pelagic primary productivity of 10.3 g C m^{-2} yr^{-1}; Rysgaard et al. 1999), due to the short sea ice-free season allowing for only 30 % of the yearly PAR flux to reach the water column. Further, the silty glacial runoff drastically reduces the euphotic depth. The effects of the glacial runoff on the distribution of micro- and mesozooplankton (Arendt et al. 2016; Middelbo et al. 2018), marine ecosystem productivity (Meire et al. 2017), coloured DOM (CDOM) absorption (Murray et al. 2015) and the carbon availability for bacteria (Paulsen et al. 2017), have previously been described for Young Sound. Small phytoplankton (< 2 μm) dominate the murky inner fjord and contribute on average 89 % of chl *a* compared to 59 % at the mouth of the fjord. At the same time copepod grazing is considerably less in the inner fjord (Middelbo et al. 2018), while protist grazing is enhanced (Arendt et al. 2016). Copepods and protists generally dominate the grazer biomass in Young Sound, although the pelagic gastropod *Limacina helicina* is abundant particularly in autumn (Middelbo et al. 2018).

The three major sources of organic carbon in Young Sound are 1) the local phytoplankton production, 2) runoff from land-terminating glaciers and lowland rivers, and 3) inflow from the East Greenland Current waters on the shelf. The fraction of bioavailable DOC (%BDOC) is highest in the glacial runoff (30-35 %) and lowest in the subsurface fjord water (5-7 %) (Paulsen et al. 2017). However, as DOC concentration in the glacial runoff is low, absolute BDOC concentrations for both are similar (15 ± 8 μM) (Paulsen et al. 2017). BDOC is difficult logistically to measure at high temporal and spatial resolution. Further BDOC measurements do not reflect the degradation potential by the representative *in situ* bacterial communities when carried out in long-term (weeks to months) bottle experiments. FDOM components, instead, can be measured at high resolution and related to: changes in biological activity in the fjord; the *in situ* bacterial community composition; and changes occurring in short-term (days) incubations.

While FDOM has been used as a water mass tracer, little is known about how the biological processes in marine waters may transform the FDOM signature (i.e. cause breakage or production of fluorescent molecular structures) and thus alter its terrestrial character in Arctic waters. Several recent studies have aimed to link the spatial and vertical distribution of FDOM components to biological standing-stock parameters such as bacterial abundance (Catalá et al.

2016) or chlorophyll *a* fluorescence (Lønborg et al. 2014; Gonçalves-Araujo et al. 2016; Sa and Kim 2017), but not to biological processes and activity. Bacteria are often considered to be the sole transformers of DOM and can consume UV FDOM and produce visible FDOM (Guillemette and del Giorgio 2014; Lønborg et al. 2014). The latter is therefore considered to be less bioavailable and correlates negatively to bacterial growth efficiency and BDOC (Asmala et al. 2013). The accumulation of visible FDOM in the deep ocean is attributed to aphotic bacterial transformation of organic matter (Yamashita and Tanoue 2008; Jørgensen et al. 2011; Aparicio et al. 2015). However, DOM is produced at all levels of the food web (Jiao et al. 2010; Lønborg et al. 2013; Stedmon and Cory 2014) and there is also evidence that protist grazing of bacteria produces high molecular weight DOM with a visible FDOM signature (Nagata and Kirchman 1992; Baña et al. 2014). As protist grazing is an important process in the deep ocean (Rocke et al. 2015), this process can contribute to the production of this FDOM signal in the deep sea, as well as in the epipelagic ocean.

Here we evaluate the sources of FDOM in the Young Sound fjord system and further study the biological transformation of DOM in short-term (days) incubation experiments designed to contain a representative *in situ* microbial community composition. While considering the FDOM signature from mesozooplankton grazers (copepods and pteropods) and different size classes of phytoplankton, the main focus is on the effect that bacteria and heterotrophic nanoflagellate (HNF) grazing activity have on the FDOM signal. Three central questions were addressed: 1) Can FDOM be used as a tracer in the fjord to distinguish between different DOM sources, 2) What imprint does the open water productivity period leave on the FDOM signal, and 3) Is the fjord microbial community capable of modifying visible- and UV FDOM?

Material and methods

Study site and sampling

The study was conducted in the Tyroler fjord-Young Sound system, Northeast Greenland (74.2-74.3 °N, 19.7-21.9 °W) (Fig. 1). The system is 90 km long, 2-7 km wide and covers an area of 390 km^2, with a maximum depth of 360 m. One 45-m sill is situated in the inner part of the system at the mouth of Tyroler fjord, and a second sill separates Young Sound from the East Greenland shelf waters (Fig. 2). Sampling was conducted at four stations located along the freshwater gradient from the inner fjord to the shelf (St. 1-4), and in the three major rivers (R1-R3) (Fig. 1). The fjord stations 1, 2, 3, and 4 are located according to stations monitored yearly by the Greenland Ecosystem Monitoring (GEM) MarinBasis Zackenberg program

named Tyro 05, YS 3.18, Standard St. and GH 05, respectively. The fjord is influenced by runoff from June to September with an accumulated amount of ca. 0.9 -1.4 km^3 per year (Bendtsen et al. 2014). Land-terminating glaciers contribute on average 50-80 % of the runoff, mainly in the inner part of the fjord (Citterio et al. 2017).

A Seabird SBE 19+ CTD profiler was deployed at every sampling occasion and recorded vertical profiles of temperature (° C), salinity (practical salinity unit), oxygen (µmol kg^{-1}), chlorophyll *a* fluorescence (flu_{chl}, relative; no units), turbidity (FTU), and photosynthetically active radiation (PAR, µmol m^{-2} s^{-1}). Discrete water samples were taken at 6 depths (1, 10, 20, 30, 40 and 100 m) and additionally at the chlorophyll *a* maximum/maxima with a 12 bottle, 1.2 L Niskin mini-rosette. Location of the deep chlorophyll max (DCM) was determined just prior to every sampling occasion using a Satlantic Free-falling Optical Profiler. Each month a longitudinal transect with CTD stations every 5 km (25 CTD in total) were performed to obtain high-resolution coverage of the fjord hydrography (Fig. 2). Three of the major rivers discharging into the fjord were sampled as long as the water was flowing (the last sampling was on September 10). The meltwater in the Tyroler river (R1) and Clay Bay river (R2) flows from glaciers through rocky sediment basins with very little vegetation and a distance of ca. 0.5 km and 2 km before they reach the fjord. Zackenberg river (R3) is different from the two others as the water has a longer residence time in two lakes and flow through the vegetated Zackenberg Valley before entering the fjord. As a result, DOC concentration in R3 is approximately 50 % higher than R1 and R2 (Paulsen et al. 2017). A model study estimated the residence time of river water in the fjord to be about 2 weeks in July and up to a month in August (Bendtsen et al. 2014).

Water samples were kept in the dark in 10 L opaque high-density polyethylene (HDPE) plastic containers and transported back to the Daneborg Marine Station (near St. 3) for further analysis. Chlorophyll *a* (chl *a*) was analysed according to Jespersen and Christoffersen (1987). Samples for dissolved organic carbon (DOC) and total nitrogen (TN) concentrations were collected in 30 mL acid-washed HDPE bottles and stored at -20 ˚C until analysis. Concentrations were determined by high-temperature combustion (720 ˚C) using a Shimadzu TOC-V CPH-TN carbon and nitrogen analyser. Samples were acidified to pH 2 using hydrochloric acid. The instrument was calibrated using acetanilide (Cauwet 1999) and carbon determination was referenced to the community deep-sea reference (Hansell laboratory, Miami). Bacterial production (BP; µg C L^{-1} d^{-1}) was estimated from the incorporation of ^{3}H-thymidine in 10 mL samples in triplicate (Riemann et al. 1982). The specific BP (µg C L^{-1} d^{-1}

cell^{-1}) was calculated as BP/bacterial abundance (cells L^{-1}). Oxidised nitrogen (NO_2^-+NO_3^-), phosphate (PO_4^{3-}) and silicic acid (H_4SiO_4) were measured on a Smartchem200 (by AMS Alliance) autoanalyser following procedures as outlined in Wood et al. (1967) for NO_3^-+NO_2^-, Murphy and Riley (1962) for PO_4^{3-}, Holmes et al. (1999) for NH_4^+ and Koroleff (1983) for the determination of H_4SiO_4. Water for DNA and RNA extraction was collected from the rivers and at 1 m and the DCM in the fjord, and water for size-fractionated chl *a* and micro-sized protists were collected only at 1 m and the DCM in the fjord.

Dissolved organic matter fluorescence (FDOM)

Samples for DOM fluorescence from the fjord and experiments were filtered through 0.2 µm syringe filters (Acrodisc® ion chromatography) into acid cleaned and pre-combusted amber glass bottles and kept at 4 °C until measured within two months. The logistics of sampling in North East Greenland across four expeditions hindered sample measurements on site and the measurements can potentially be influenced by microbial regrowth and organic matter degradation during storage despite 0.2 µm filtration. 7 samples were checked for bacterial regrowth during storage by 3 months and results showed a regrowth from < 200 cells mL^{-1} to 11.000 ± 7.500 cells mL^{-1}. No optimal sample storage procedure exists for FDOM, as the addition of preservatives and freezing can influence fluorescence more than sterile filtration alone (Schneider-Zapp et al. 2013). Samples were acclimated to room temperature before measurement on a Horiba Aqualog spectrofluorometer within two months. The instrument measured fluorescence intensity across emission wavelengths 300–600 nm at excitation wavelengths from 250 to 450 nm in a 1 cm quartz cuvette. Excitation-Emission Matrix (EEM) were merged into a three-dimensional matrix and analysed via the multivariate data analysis technique Parallel Factor Analysis (PARAFAC) (Murphy et al. 2013). FDOM signal was split into 5 components (Fig. 3) and they are named according to the wavelength at their emission maximum, and the 'Coble's peaks' from Coble (1996) that each component resemble are displayed. Three components had emission maxima at visible wavelengths (C_{417}, C_{498}, C_{405}) and two at UV wavelengths (C_{340}, C_{310}). The fluorescence intensities reported here are at the excitation and emission maximum in Raman units, nm^{-1} (Lawaetz and Stedmon 2009).

To better reveal how DOM properties varied between different sources, samples were grouped by each river, and the water types defined as "river plume" (S < 25), "fjord surface waters" (S = 25–32.5 and T > -1 °C), "subsurface waters" (S < 32.5 and T < -1 °C) and "coastal shelf waters" (S > 32.5) as in Paulsen et al. (2017). The fluorescence intensity of the 5 components was averaged within each water type for each season (Fig. 5). The high salinity "coastal shelf

water" was encountered only at St. 4, at 100 m (Fig. 2) at few sampling occasions, and FDOM was only sampled from this water type on three occasions. Therefore, our FDOM description of this end member is likely weaker than for the rivers.

Enumeration of microorganisms

The abundance of bacteria, heterotrophic nanoflagellates (HNF) and small phytoplankton were determined on an Attune® Acoustic Focusing Flow Cytometer (Applied Biosystems by Life Technologies) with a syringe-based fluidic system and a 20 mW 488 nm (blue) laser. (Paulsen et al. 2016)(Paulsen et al. 2016)(Paulsen et al. 2016)(Paulsen et al. 2016)(Paulsen et al. 2016)(Paulsen et al. 2016)(Paulsen et al. 2016)(Paulsen et al. 2016)Samples for heterotrophic bacteria and nanoflagellates were fixed with glutaraldehyde (0.5 % final conc.) and kept dark at 4 °C until analysis within 12 hours. Phytoplankton samples were enumerated from fresh samples and the populations of pico- and nano-sized phytoplankton were grouped based on their pigmentation on biplots of green *vs.* red fluorescence as in Paulsen et al. (2016). Samples for heterotrophic prokaryotes (hereafter bacteria) and HNF were stained with SYBR Green I (Molecular Probes, Eugene, Oregon, USA) for minimum 1 h. Bacteria were analysed at a low flow rate (25 µL min^{-1}) following the protocol of Marie et al. (1999). HNF were measured at a high flow rate according to Zubkov et al. (2007) and subdivided into two different size groups of ca. 3-5 µm diameter (hereafter small HNF) and ca. 5-10 µm diameter (hereafter large HNF) by filtering parallel samples through 3, 5 and 10 µm polycarbonate filters and counting the filtrate and adjusting gates. The ratio of small HNF to bacteria is used here as an indicator of bacterial grazing pressure as in other studies (Sanders et al. 1992). Samples for the larger micro-sized protists (ciliates, heterotrophic dinoflagellates and micro-phytoplankton) were fixed in acid Lugol's solution (2 % final conc.) and stored cold and dark until analyses. 50 mL were examined after 24 h sedimentation in Utermöhl chambers. The protists were enumerated and identified to species/morphotype level using an inverted microscope (magnification: 200-400x). While only heterotrophic dinoflagellates were enumerated by microscope, chloroplast 16s rRNA gene analysis additionally detected autotrophic dinoflagellates.

DNA and RNA extraction, 16S rRNA sequencing and data analysis

Samples for molecular analysis were collected by filtering onto 0.22 µm Sterivex filters (2 L filtered from environmental samples and 4 L from experiments). DNA and RNA was extracted simultaneously from the filters using the AllPrep DNA/RNA Mini Kit (Qiagen, Hilden, Germany). DNA from experimental samples and RNA from environmental samples was used

for the analysis of the bacterial community. RNA was treated with the DNA-free DNA Removal kit (Invitrogen, CA, USA), and reverse transcribed using the SuperScript III First-Strand Synthesis System for RT-PCR (Invitrogen). Amplification of cDNA and DNA was performed using a two-step nested PCR approach with primers 519F and 806R targeting both the archaeal and the bacterial 16S rRNA gene V4 hypervariable region. Details regarding extraction, amplification and amplicon library preparation can be found in Wilson et al. (2017). Libraries were sequenced at the Norwegian Sequencing Centre (Oslo, Norway) using their MiSeq platform (MiSeq Reagent Kit v2, Illumina, CA, USA). Sequencing data is available at "The European Bioinformatics Institute" under study accession number **PRJEB16067**. (http://www.ebi.ac.uk).

Paired-end sequences were processed using different bioinformatic tools incorporated on a qiime-processing platform (Caporaso et al. 2011) as described in Paulsen et al. (2016). FASTQ files were quality end-trimmed, merged and prokaryotic OTUs (operational taxonomic unit) were selected at a sequence similarity threshold of 97 %. Taxonomy was assigned using the Greengenes reference database (DeSantis et al. 2006). The eukaryotic plastidial sequences were taxonomical assigned using the Phytoref database of the plastidial 16S rRNA gene of photosynthetic eukaryotes (Decelle et al. 2015).

Plankton community size-fractionation experiments

Three plankton community fractionation experiments were performed; *Experiment 1* was initiated while the central fjord was still ice-covered (on July 11), *Experiment 2* was initiated 4 days after the fjord became ice-free (July 19), and *Experiment 3* was initiated during autumn (September 16). We chose to collect water for the experiments from St. 3, as this was most accessible from Daneborg field station during ice-cover and at the same time with its central location it is representable for the fjord system as a whole. For each experiment, water (70-100 L) was collected at the chl *a* maximum at St. 3 and directly gently syphoned into dark carboys. Prior to the setup, bottles and carboys were acid-washed and then rinsed in Milli-Q water. The treatments (hereafter: <0.8, <3, <10 and <90) were prepared by screening the water through either a 0.8 µm polycarbonate filter or a 3, 10 or 90 µm mesh filter by gentle reverse filtration in order to successively exclude protists of increasing sizes. Water for each treatment was gently transferred into triplicate 5 L transparent foldable politainers (®RPC Promens) by staggered filling using silicone tubing. To mirror the seasonal change in mesozooplankton biomass in the fjord (Middelbo et al. 2018), *Exp. 2* and *3* included additional treatments where mesozooplankton were added to <90 µm filtered water. During *Exp. 1* there were relatively

few copepods present in the fjord (a biomass of <0.5 mg C m^{-3}), therefore a treatment with copepod addition was not included. After the ice broke up copepod abundance increased up to 5 mg C m^{-3} (Middelbo et al. 2018) and a 'copepod treatment' was included both in *Exp. 2* and *3*. As pelagic pteropods (snails) became abundant in autumn (up to 2 mg C m^{-3}), an additional treatment was included only in *Exp. 3*. In both *Exp. 2* and *3* copepods (*Calanus hyperboreus* CVI) were added to a final abundance of 1 copepod L^{-1}. In *Exp. 3* pteropods (*Limacina helicina*) were added to a final abundance of 2 individuals per 5 L carboy. Hereafter the treatments are referred to as "Copepod" and "Pteropod" ("Co" and "Pt" in Fig. 7). All individuals were alive after the 8-9 days of incubation.

The experimental carboys were incubated on a pier by the fjord in a 1000 L PVC tank submerged in a flow-through water bath pumping water from the shore (1-3 m depth depending on the tide) to keep the temperature close to *in situ* surface temperature. The bottles were wrapped in dark nylon mesh, reducing the irradiance to ~30 % of surface PAR, similar to the light conditions at the depth at which they were collected. The bottles were rotated twice per day by hand. Every day, 50 mL sample (1 % of total volume) was removed for the quantification of bacteria, small phytoplankton and HNF. Every second day 200 mL were additionally removed to measure bacterial production, FDOM, DOC, and inorganic nutrients. Further chl *a* (>0.7 µm (total), 2-10 µm and >10 µm) and samples for enumeration of micro-sized protists were collected initially (T0), after 3 days and at the end of each experiment. Samples for 16S rRNA gene sequencing were collected from the <90 treatment initially from *Exp. 1* and *Exp. 3* and from all treatments at the end of each experiment by filtering the remaining water onto 0.22 µm Sterivex filter (ca. 4 L) to enable comparison between the starting community and the effect of treatments by the end. The initial community from the <90 treatment in *Exp. 2* was lost and we, therefore, can only compare to the unfiltered *in situ* sample collected along with the experimental water. *Exp. 1* was terminated after 5 days and *Exp. 2* after 7.8 days and *Exp. 3* after 9 days.

Net-growth rates (μ, d^{-1}) were calculated as the change in cell abundance (N) from the abundance at t_0 (N_0) to the abundance at sample time t_1 (N_1) as:

$$\mu = (\ln N_1 - \ln N_0)/(t_1 - t_0) \quad \text{(Eq. 1)}$$

When protist grazing was reduced in the smaller size-fractions (i.e. <0.8 and <3), prey growth rate was higher ($\mu_{no\ grazer}$) than in the larger size-fractions i.e. <10 and <90 where grazers are present ($\mu_{with\ grazer}$). Protist grazing (g, d^{-1}) could then be estimated by subtracting the two

growth rates as:

$$g = \mu_{no\ grazer} - \mu_{with\ grazer} \quad \text{(Eq. 2)}$$

It should be noted that the <0.8µm-filtration in *Exp. 2* did not successfully exclude all picophytoplankton, small HNF and nanophytoplankton which all multiplied in the <0.8-treatment (Fig. S1). The treatment was however still included in the further analysis as the HNF:Bac ratio was significantly reduced.

In the experiments, the change in FDOM intensity is calculated as:

$$\Delta\ FDOM = FDOM_X / FDOM_0 - 1 \quad \text{(Eq. 3)}$$

where $FDOM_0$ and $FDOM_x$ are the fluorescence intensities of each component averaged for all treatments at *day 0* and the intensity averaged within each treatment at *day X*, respectively.

Statistical Analysis

Redundancy analysis was done using primer-e version 6 (Plymouth, UK) and Canoco 5 (Ter Braak and Šmilaur, 2012). MANOVA (multivariate analysis of variance and of covariance between depended variables, using a general linear model) was used to examine covariance between the 5 fluorescence components both *in situ* and in the experiments using the program R and the package "car" (Fox and Weisberg 2011).

Results

Hydrography, nutrients and plankton

In the summer (July-August), terrestrial runoff created a clear halocline at 5-6 m with a layer of low salinity (< 20) water in the surface and more saline bottom water (> 30) (Fig. 2). In autumn (September-October) the runoff had ceased, and periodic storms followed, mixing the surface layer depth so that the mixed layer depth (MLD) extended to around 40 m and the near-surface water was colder (2 °C). In general, the inner part of the fjord system was more stratified than the coastal shelf waters, but the wind mixing in October was enough to deepen the MLD in the entire fjord (Fig. 2). Phytoplankton chl *a* fluorescence was most intense at 26-35 m depth at the outer fjord stations (3 and 4) in the summer period (up to 3.1 µg chl *a* L^{-1}). At the innermost stations the chlorophyll *a* maximum was shallower (20 m) and concentrations were highest in late autumn (up to 1.6 µg chl *a* L^{-1}) (Fig. 2, S2).

With respect to Redfield, oxidised nitrogen (NO_x) (0.26 ± 0.25 µM) was limiting relative to phosphate (P) (0.41 ± 0.19 µM) during both seasons in the upper mixed layer. Ammonium, was only measured at St. 3 in the fjord and was at low concentrations ranging between 0.05 and 0.4 µM (avg. 0.27 ± 0.17 µM). In the rivers, phosphate was comparably low as in the fjord (0.3 ± 0.2 µM) but NO_x was several fold higher (1.1 ± 0.5 µM). Silicate was elevated in the river water (avg. 17 ± 12 µM, max 46 µM) with increasing concentrations during the runoff period compared to the fjord surface values (2 ± 1.8 µM). The inner part of the fjord became ice-free prior to the central part. During the first sampling July St. 3 was still ice-covered, and there was a reduction in nutrients just below the ice (NO_x = 0.01, P = 0.33, Si =1 µM) compared to deeper waters at 100 m (NO_x = 3.2, P =0.7, Si = 6.4 µM) indicating that a phytoplankton spring bloom had already started in the inner fjord.

The phytoplankton community differed between the inner fjord (St. 1 and 2) and the outer fjord (St. 3 and 4). In the outer part of the fjord, diatoms, mainly *Chaetoceros* sp., and autotrophic dinoflagellates dominated, while picophytoplankton dominated the inner fjord (Middelbo et al. 2018). Large and small heterotrophic nanoflagellates (HNF) also had different distribution patterns with large HNF being most abundant in the inner part of the fjord in autumn (max. 170 cell mL^{-1}, 63 ± 36 cell mL^{-1}), while small HNF generally were more abundant in summer, but without strong spatial variations (250 ± 155 cell mL^{-1}) (Fig. S2). Abundances of both HNF size groups were significantly reduced in the freshwater-influenced surface water compared to the more saline waters below (Fig. S2). Ciliate abundances were also lower (3.4 ± 2.3 cells mL^{-1}) in 1 m samples than in deeper samples (data not shown). This resulted in a general low predator to prey ratio in the surface water during summer stratification (Fig. 4).

DOM distribution in the fjord and rivers

The average concentration of DOC was 100 ± 22 µM in the fjord (Fig. S2) and the rivers had significantly lower DOC concentrations (< 40 µM). Thus, the rivers diluted the upper 5 m of the fjord in terms of DOC. The three visible wavelength FDOM components displayed a similar vertical distribution with maximum intensities at 30-40 m and decreasing above 20 m, illustrated by C_{417} in Fig. 4. From summer to autumn the intensity decreased in the upper 40 m. Visible FDOM signals were also generally lower at the outermost station at the shelf. The two UV FDOM signals exhibited a higher degree of variation and no distinct vertical patterns, as illustrated by C_{340} in Fig. 4, and the highest intensities of UV FDOM were measured in the central fjord (St. 2 and 3) (Fig. 4). When FDOM intensities were averaged within the different water types (Fig. 5), an ANOVA analysis of each component revealed that the visible

fluorescent components were highly significantly different between water types (C_{417}: p = 6.8 x10^{-6}, C_{498}: p = 2.7 x10^{-9}, C_{405}: p = 2.2 x10^{-6}), whereas the UV fluorescent components were only marginally different (C_{340}: p = 0.02, C_{310}: p = 0.04). The seasonal change within water types revealed a significant decrease in C_{417} and C_{498} and UV fluorescent C_{340} from summer to autumn, as well as an increase in the fjord (Fig. 5). The fluorescence signal of the rivers had higher variation than in the fjord. The glacial rivers (R1 and R2) had the lowest intensity of visible fluorescence of all samples (C_{498} = 0.04-0.05 R.U.), and R3 during summer had the highest (C_{498} = 0.13 R.U.).

Links between bacteria and FDOM

In summer bacterial abundances were lower in the fjord (ca. 4x10^5 cell mL^{-1}) than at the shelf (St. 4) (7x10^5 cell mL^{-1}) and peaked at 10 m just below the halocline at all stations (Fig. 4). In the central fjord, abundances increased significantly during the transition to autumn in the upper 40 m, whereas at the shelf station they did not change (Fig. 4 and S2). Similarly, bacterial production (BP) was stable over the study period at the shelf, whereas in the fjord BP rates were higher (up to 2 µg C L^{-1} d^{-1}) in the summer than in autumn (< 0.2 µg C L^{-1} d^{-1}) (Fig. 4). As a result, the specific BP (production per cell) was on average more than twice as high in the fjord (averaged to 5.4 x 10^{-10} µg C d^{-1} cell^{-1}) than on the shelf (1.8 x 10^{-10} µg C d^{-1} cell^{-1}) (Fig. S2).

BP rates and several other environmental parameters were tested for correlations with the FDOM using Pearson's correlations (Table 1), in order to identify links between environmental factors and FDOM fluorescence. UV components C_{340} and C_{310} were positively correlated to chl *a* and BP, but C_{417}, C_{498} and C_{405} were strongest correlated to HNF:Bac and salinity and inversely correlated to bacterial abundance (Table 1).

To test the cumulative effect of all environmental parameters on the entire set of FDOM components and to identify the most influential variable, a redundancy analysis was performed separately for the two seasons with FDOM components as the dependent variables and environmental parameters as the explanatory variables (Fig. 6). In summer the environmental parameters explained 53 % of the total FDOM variation, with "HNF:Bac" (18 %, p=0.002) and "chl *a*" (11 %, p=0.008) explaining most. In autumn 42 % of the FDOM variation could be explained, with "Salinity" (14 %, p=0.008) and the water type "Shelf water" (9 %, p=0.004) explaining most (Table S1). When a redundancy analysis was done for the entire data set the

environmental variables were related similarly to FDOM, but with poorer explanatory power (Table S1).

Since bacteria can both produce and consume FDOM, we were further interested in whether FDOM components correlate with the abundance of the bacterial OTUs (Table 2). Several OTUs from different classes correlated both positively (e.g. *Balneatrix* and SAR92 clade) and negatively (e.g. *Litoricola* and SAR86 clade, SAR116 clade) to visible wavelength FDOM components. Only a few OTUs (e.g. *Colwellia* and SAR92 clade) correlated with the two UV FDOM components. The relative contribution (%) of OTUs that correlated positively to visible wavelength FDOM was especially high during summer, such as *Balneatrix* (10 %) and SAR92 clade (11 %). Interestingly, the genera that correlated strongly with visible FDOM signals did not correlate with salinity. The only genera that did correlate negatively with salinity (i.e. *Variovorax* and cyanobacteria) were freshwater taxa. In autumn, however, only a few OTUs correlated positively to visible wavelength FDOM and negative correlations were more common (Table 2).

In order to test whether the FDOM components might explain the changes in the composition of the bacterial community we applied another redundancy analysis. Here the OTUs were the dependent variables and the FDOM components are the explanatory variables (Fig. S4). However, this analysis showed the FDOM components do not explain well the changes in the bacterial community composition. The only significant relationship on community level was found for UV FDOM component C_{340} in July (p=0.024), where it explained 24.5 % of the bacterial community composition.

Phytoplankton diversity in the experiments

The abundance of different size-classes of phytoplankton were successfully altered as part of the plankton community size fractionation manipulation (Fig. 7, Fig. S1, S3). In the first two experiments, *Chaetoceros* sp. dominated all size fractions larger than 10 µm, with occasionally high contributions of silicoflagellates and chrysophytes (Fig. 7A). The large chl *a* fraction (> 10 µm) increased significantly in the treatments < 90 µm and the treatments with copepod addition, whereas in the treatments < 3 µm and < 10 µm the pico- and nanophytoplankton biomass increased (Fig. 7B). The third experiment (initiated in September) was dominated by pico- and nano-sized phytoplankton groups including silicoflagellates, cryptophytes, prasinophytes and also the contribution of autotrophic dinoflagellates increased in autumn (Fig. 7A). Micro-sized diatoms contributed little to the biomass in *Exp. 3* (maximum 10-20 % in the

treatments with mesozooplankton) despite relatively high SiO_4 concentrations (4 µM), compared to *Exp. 1* and *2,* where silicate was reduced to < 1.7 µM and thus in limiting concentrations according to Egge and Aksnes (1992). NH_4^+ increased only in the mesozooplankton amended treatments in Exp. 3; with a gradual increase from 0.2 µM to 1.7 ± 0.4 µM in the pteropod treatment and an increased from 0.2 µM to 0.5 ± 0.03 µM in the copepod treatment, following a decrease after 5 days (Fig. 7B, Fig. S1). Chl *a* in the 2-10 µm fraction doubled in the treatment with mesozooplankton, while it significantly decreased in the treatments with protists as top predators. Heterotrophic dinoflagellates dominated over ciliates numerically, especially in *Exp. 1* and *2*, during which the diatoms dominated the phytoplankton biomass (Fig. S3).

Bacterial diversity, growth and grazing in experiments

The order Alteromonadales (genera *Glaciecola*, *Colwellia, Pseudoalteromnas* and the SAR92 clade) dominated the bacterial community in *Exp. 1* (46 ± 2 %) and *Exp. 2* (48 ± 10 %)). *Exp. 3* was dominated by the order Oceanospirillales (29 ± 10 %) and was in general more diverse with a higher number of unassigned OTUs than in the two other experiments (27 ± 6%) (Fig. 7 C). The genus *Glacieocola* varied most throughout the season and contributed as much as 33-36 % in the first experiments whereas *Exp. 3* only contained up to 4 % *Glaciecola*. In treatments where mesozooplankton were added the Alteromonadales genera became more abundant with *Colwellia* (22-23 %) and *Pseudoalteromnas* (10-21 %) being most prominent. Oceanospirillales (*Balneatrix, Oleispira* and the SAR86 clade) dominated when protists were the only grazers.

The treatments <3, 10 and 90 µm were grouped into one treatment: “plus protists” in Fig. 8 and 9, as we found no significant differences between the three in regards to FDOM development (Fig. S6) nor in the abundance of bacteria and BP (Fig. S1). Likewise, the treatments with addition of copepods and pelagic pteropods were grouped as "plus mesozooplankton". The 0.8 µm-filtration resulted in a reduction of the bacterial abundance at day 0 (Fig. 8A-C). In summer the abundance was reduced by around 18 % and in *Exp. 3* as much as 40-45 %, indicating that bacteria were larger in autumn than in summer. The abundance of bacteria in the 3, 10 and 90 µm filtered water at the beginning of the experiments were also around 4 times higher in autumn (9 $x10^5$ mL^{-1}) than in the summer experiments (1.9 $x10^5$ and 2.6 $x10^5$ mL^{-1}). Bacterial production increased from 0.5 to 6.3 µg C^{-1} L^{-1} d^{-1} within the first 3 days of incubation in the summer experiments (Fig. 8 D-E), while in autumn (*Exp. 3*) BP remained less than 1.2 µg C^{-1} L^{-1} d^{-1} during the entire experiment. The predator-prey ratio (HNF: Bac $x10^3$ in Fig. 8, see also

HNF numbers in Fig. S1) was reduced to near zero in the fraction with only bacteria, except in *Exp. 2*. The ratio remained between 1- 5 (i.e. 1,000 to 5,000 bacteria per HNF) in treatments with protists and mesozooplankton, except for the end of *Exp. 2* where it increased to 14 in the treatments with protists (Fig. 8 G-I). On the whole, this indicates that the experimental size fractionation successfully released grazing pressure so that we could differentiate between FDOM changes due to bacterial degradation and those due to grazing.

Grazing rates of bacteria (calculated by Eq. 2), picophytoplankton and HNF were highest in summer and very similar between *Exp. 1* and *2* (Table S2). The net-grazing on bacteria correlated strongly to HNF:Bac in all experiments (r^2 =0.82, 0.59 and 0.77 p<0.0001, for *Exp. 1, 2* and *3*, respectively; Fig. S5). We, therefore, consider HNF:Bac to be an appropriate indicator of bacterial grazing in our system.

Consumption and production of FDOM in the experiments

As a result of the changing seasonal conditions in the fjord, the three size-fractionation experiments were initiated with fjord water differing significantly in initial FDOM composition (Two-way ANOVA, P<0.0001) (Fig. 9 Left panel). We observed a strong significant difference in development of FDOM between the experiments (MANOVA: F(2, 122) = 0.55, p<0.00001, partial eta squared = 0.28).

During the incubation, the relative change in intensity (calculated by Eq. 3) differed between the visible and UV wavelength FDOM components (Fig. 9). The UV FDOM increased in all experiments, mainly in *Exp. 2* during which the initial UV FDOM intensity was close to zero. C_{310} was often produced at high rates in the treatment with only bacteria (Fig. 9). Mesozooplankton addition to the incubations resulted in elevated UV FDOM intensities after 3.7 days in *Exp. 2* and by 2.8 days in *Exp. 3*, with the addition of the pteropod *Limacina helicina* having a slightly higher effect than copepods (Fig. S6).

The visible wavelength FDOM components developed differently in the two seasons. In summer (*Exp. 1* and *2*) we observed a gradual decrease (i.e. consumption or transformation) of all components, while in autumn (*Exp. 3*) they were produced. In general, C_{417} was consumed at lower rates and produced at higher rates than C_{498} (Fig. 9). The highest consumption rates were measured in *Exp. 1*. In *Exp. 2*, visible wavelength FDOM decreased the most in the treatment with only bacteria, while the presence of mesozooplankton grazers even stimulated a small net-production of C_{417} and C_{405} during the first 3 days (Fig. 9E). In *Exp. 3* there was no

net-consumption of FDOM, but production rates were almost twice as high in grazer-treatments than in the 'bacteria only' treatments after 7.5 days (Fig. 9 F-K). We observed that the change in visible wavelength FDOM correlated negatively to bacterial net-growth (Eq. 1) in the summer experiments (*Exp. 1*: r^2=0.62, p<0.0001, *Exp. 2*: r^2=0.32, p=0.0008), and a positively to grazing on bacteria in all experiments (*Exp. 1*: r^2=0.45, p=0.0034, *Exp. 2*: r^2=0.43, p=0.0005, *Exp. 3*: r^2=0.19, p=0.017).

Overall, in *Exp. 1* the presence of grazers affected the rate of change in FDOM intensity during the first 3 days, whereas all the different treatments essentially arrived at similar net-change of FDOM intensity after 5 days. In *Exp. 2*, the decrease in visible FDOM was lowest in treatments with grazers whereas the production of UV FDOM was clearly stimulated by their presence. In *Exp. 3,* where bacterial activity was low, visible FDOM was produced in all treatments and the positive effect of grazers on FDOM change remained significant after 7.5 days.

Discussion

FDOM properties have been used as water mass indicator, and especially the "humic-like" FDOM characterized with emission maxima at visible wavelengths is often considered to be refractory and therefore used as a conservative tracer (Catalá et al. 2015). Yet, the imprint that marine microbes have on FDOM remains poorly resolved. The data collected here provides an opportunity to examine the interplay between biological activity and hydrography on the distribution and composition of FDOM. In this light, the FDOM signal can be used as an indicator revealing the dynamics of DOM production, consumption and transformation in the fjord system.

FDOM dilution by glacial meltwater

Surprising and in contrast to most fjord systems, visible wavelength FDOM correlated positively to salinity (Fig. 6) indicating that the marine end-member is the important FDOM source rather than the local runoff. The reduced intensity of visible wavelength FDOM in the freshwater influenced surface layer could potentially also have been caused by photochemical degradation (Aarnos et al.; Ward et al. 2014). However, as the ice in the Young Sound fjord system disappears after the summer solstice, the sun angle is also decreasing rapidly and as a result, the inner fjord system is shaded by surrounding mountains preventing direct exposure. Thus, the likely impact of photochemical degradation is probably limited in Young Sound. In

addition, light penetration is inhibited by the silty runoff that increases turbidity in the fjord (Murray et al. 2015), mainly early in the ice-free period.

The FDOM signal from local terrestrial runoff is difficult to resolve, as FDOM intensity, DOC concentrations and bioavailability can fluctuate (Kroon et al. 2017; Paulsen et al. 2017) in response to episodic input events which are easily be missed when sampling. However, the low fluorescence intensity of riverine FDOM measured 16 times from July to September strongly suggests that the rivers are not a major contributor of carbon or of FDOM in the system but rather dilute FDOM in the fjord. This is in strong contrast to the majority of Arctic rivers, which are important sources of carbon and visible FDOM with as high as 1.8 nm^{-1} (Walker et al. 2013). In comparison, the highest intensity of visible fluorescence sampled in the Young Sound was 0.08 nm^{-1} in the glacial rivers and 0.13 nm^{-1} in R3.

The FDOM signal from the three rivers were directly related to their catchment, with the glacial rivers R1 and R2 supplying similar and low signal, while the tundra and lakes in the R3 catchment supply an elevated and more variable signal. Similar variations in FDOM intensity of large Arctic rivers have been explained by the difference in the vegetation characteristics of the catchment (Walker et al. 2013), further the presence of proglacial lakes results in higher DOC concentrations (340-406 µM C) (Bhatia et al. 2010; Hauptmann et al. 2016). The low carbon content in glacial meltwater in Young Sound is consistent previous observations from the western part of Greenland Ice Sheet with 7-32 µM C, 15-51 µM C and 21-100 µM C found in subglacial, supraglacial discharge and a glacial stream with connection to a proglacial lake, respectively (Bhatia et al. 2010; Lawson et al. 2014; Hauptmann et al. 2016). In terms of carbon concentration and FDOM, the runoff connected to Greenland glaciers thus rather dilutes, than contributes, to the fjord system.

Coastal water as a source of visible FDOM

The shelf water in the East Greenland region is characterised by three general layers (Sejr et al. 2017): 1) *Re-circulating Atlantic water* (T > 0 °C) at depths greater than 200 m (not sampled in the current study) 2) *Polar water* that originates from the Polar halocline transported from the Arctic Ocean in the East Greenland Current (T < 0 °C, S ~ 31-32), and 3) *Surface waters* (S < 25), which are modified locally by the inclusion of meltwater from sea ice and the Greenland Ice Sheet in summer. The overall distribution of visible FDOM was hydrographically driven by the high-signal intrusion of Polar water terrestrial DOM from the marine end-member and dilution by low-signal glacial runoff in the surface.

The fluorescence characteristics of visible FDOM C_{498} reported here is identical to 'C1' described on the Greenland Shelf outside of Young Sound by Gonçalves-Araujo et al., (2016) (Tucker's Congruence Coefficient Em/Ex = 0.96/0.97), who also linked this signal to organic matter in Polar water. The intensity of C_{498} found on the Greenland Shelf (0-300 m) in September ranged from 0 to 0.1 nm^{-1} and is thus not higher than our measurements within the subsurface water in Young Sound in September (range: 0.09-0.16 nm^{-1}, avg.: 0.12 ± 0.02 nm^{-1}, n = 30). This suggests that Polar water is not the only source of the high visible fluorescence signal associated with waters in the depth range of 20-40 m, but rather local biological productivity. It seems that autochthonously produced visible wavelength FDOM is indistinguishable from the allochthonous component of terrestrial FDOM in Polar waters found in the East Greenland Shelf. Thus, the visible wavelength components identified from EEMs cannot serve as a conservative tracer of DOM alone as suggested by Gonçalves-Araujo et al. (2016). Our results indicate that local microbial productivity contributes to altering the signal and thus although behaving conservatively during its passage across the Arctic, microbial productivity at coastal sites stimulates both the production and degradation of visible FDOM.

Biological production of visible wavelength FDOM

In the fjord, the intensity of the visible wavelength fluorescence signals correlated positively to chl *a* and HNF:Bac in summer and positively to salinity in autumn (Fig. 6, Table 1). This seasonal change may best be explained by the change in biological activity; in summer high primary production, bacterial growth and high grazing rates results in an accumulation of visible wavelength FDOM in the subsurface fjord water. When biological processes were low in autumn, the hydrographical distribution of visible FDOM became more obvious as indicated by the strong positive relationship between salinity and visible FDOM in this period (Table 1). Our experimental results during autumn (*Exp. 3*), together with the previous work by Baña et al., (2014), suggest that that the presence of grazers increase the production of visible wavelength FDOM. We hypothesize that the reason for the increase in *Exp. 3* is that the bacterial growth was so low that the production of visible fluorescence due to bacterial grazing exceeded the bacterial consumption. Also, in *Exp. 3* there were more and larger bacteria (and thus even higher bacterial biomass than suggested by just their numbers) than during the summer experiments (Fig. 8 A-C).

A link between UV FDOM and mesozooplankton

The UV FDOM signals have been linked to phytoplankton abundance (e.g. chl *a*) (Lønborg et al. 2014; Gonçalves-Araujo et al. 2016) as well as to water mass mixing (Catalá et al. 2016). In Young Sound their variability was best explained by productivity related parameters such as chl *a* and BP (Fig. 6, Table 1), although correlations with UV FDOM were weaker than those of visible FDOM (Table 1). The high production of UV FDOM associated with the presence of mesozooplankton in the experiments (Fig. 9) was in agreement with the *in situ* fluorescence intensities being highest in the central fjord (St. 2 and 3), where maximum copepod activity was recorded (Middelbo et al., 2018). When performing linear regression analysis between our UV FDOM intensity and copepod biomass, faecal pellet production and egg production published in Middelbo et al (2018), we found a weak positive correlation between specific faecal pellet production and C_{310} (r^2=0.26, p=0.03, n=19), while there was a stronger correlation when comparing to the community faecal pellet production for both UV components (C_{340}: r^2=0.35, p=0.008, C_{310}: r^2=0.34, p=0.009). However, there was no correlation of UV FDOM to copepod biomass, nor between the visible fluorescent components and any copepod related parameters. Although the correlations with copepod activity were relatively weak, copepod activity relates better to the UV fluorescence than to any other environmental parameter, and we speculate that this is due to sloppy feeding, excretion and leakage from faecal pellets as found in other studies (Poulet et al. 1991; Møller et al. 2003; Urban-Rich et al. 2004; Møller 2007), and possibly, bacterial degradation of organic matter associated with grazing. Our experimental work further demonstrated that the pelagic pteropod *Limacina helicina* could have a similar, or even stronger effects, on FDOM transformations as well as NH_4^+ production.

Bacterial consumption of visible wavelength FDOM

Visible wavelength FDOM decreased markedly in the fjord from summer to autumn (Fig. 4, 5). The deepening of the mixed layer caused by autumn storms can partly account for the reduction in subsurface visible FDOM (Fig. 4). However, if the autumn mixing were the only explanation, a corresponding increase in visible FDOM at the surface (1 m) would be expected, which was not the case. The decrease in visible wavelength FDOM co-occurred with a net-increase in bacterial abundance. This is seen as a negative correlation between visible FDOM and bacterial abundance (Table 1) and indicates a net uptake or transformation of visible fluorescent components by bacteria. This is further supported by relatively higher subsurface bacterial production in the fjord (St. 1-3) in summer when visible wavelength FDOM intensities were high, compared to autumn. Moreover, the incubation experiments demonstrated a decrease in visible FDOM when bacterial growth was high in summer (*Exp. 1*

649 and *2*). The consumption of visible FDOM in these experiments is supported by a similar
650 experiment from the Alaskan Arctic by Sipler et al. (2017), where they found consumption (7
651 % within 4-6 days) of "humic-like" terrestrial derived DOM.

652 As the change in FDOM in the "only bacteria treatment" was similar to the change in treatments
653 with larger organisms, bacteria are likely the main transformers of visible wavelength DOM.
654 Certain bacterial taxa, especially within the class Gammaproteobacteria, are commonly known
655 to degrade a wide range of different carbon sources, including high molecular weight terrestrial
656 DOM (Sosa et al. 2015; Sipler et al. 2017), and can occur at high concentrations in coastal
657 environments. Predominantly taxa from this class, such as *Glaciecola* spp., *Balneatrix* and the
658 SAR92 clade dominated the summer experiments (Fig. 7) and were highly abundant in the
659 fjord in July (Table 2), and thus further supports our finding that Young Sound residing
660 bacterial community was able to degrade humic-like visible wavelength FDOM. Interestingly,
661 however, we found that not all taxa belonging to Gammaproteobacteria showed a positive
662 correlation with visible wavelength FDOM. Especially the order Oceanospirillales was more
663 abundant in autumn and correlated negatively to visible wavelength FDOM as previously
664 observed also in river DOM in Arctic Alaska by Sipler et al. (2017) who further reported there
665 to be no influence of river DOM (positive or negative) on the bacterial community down to the
666 phylogenetic level of 'order'. We saw the same non-coherent tendency with OTUs belonging
667 to the same genus but having different correlation patterns, i.e. most *Glaciecola* OTUs
668 correlated positively with visible wavelength FDOM, but few correlated negatively (Table 2).
669 Such different functional behaviour between clades and strains within the same genus calls for
670 future work focusing on linking bacterial function rather than diversity to DOM turnover.

671 Our study stresses that bacterial community composition and functioning are central for the
672 bioavailability of FDOM and contradict the view that visible wavelength FDOM, in general,
673 is refractory to bacteria. Measurements of %BDOC reveal that the subsurface fjord water had
674 the lowest bioavailability (5.3 ± 1.8 %; Paulsen et al. 2017) and it is tempting to conclude that
675 the low bioavailability is connected to the high contribution of visible FDOM in this water
676 mass. However, we here find a rapid planktonic transformation of visible FDOM from
677 subsurface fjord water during the summer period. Though the loss of FDOM is not a
678 quantitative measure of carbon remineralisation, it can be used as a sensitive indicator of DOM
679 processing occurring at levels below the detection limits of DOC measurements. We therefore
680 speculate that the BDOC method underestimates the *in situ* potential for carbon degradation of
681 visible FDOM. This method relies on long-term incubations and as a result an altered bacterial

community composition (Müller et al. 2018) and function, which as a consequence likely reduces the ability to degrade visible FDOM. In contrast, the method applied here has a bacterial community more representative of natural conditions in the fjord and reveals their potential to degrade visible FDOM. The underestimation of "*in situ* carbon degradation" by the BDOC method would imply that the significant amounts of bioavailable carbon in glacial runoff reported by Hood et al. (2009), Fellman et al. (2010) and Lawson et al. (2014), may, in fact, be negligible compared to the degradation potential of the various autochthonous carbon sources that are already present in the fjord.

Conclusions

The low visible FDOM signal of the glacial runoff indicated that the rivers contributed to a seasonal dilution of DOM and FDOM in the surface waters, whereas the more saline coastal water (transported from the Arctic Ocean) had a higher content of visible FDOM. In this light, the NE Greenland fjord systems are unique in the sense that the dominant source of terrestrial organic matter comes from the marine end-member. The high biological productivity period resulted in an elevated visible FDOM signal in the fjord subsurface. The degradation of visible FDOM appears to be linked to specific bacterial taxa (*Glaciecola* spp., *Balneatrix* and the SAR92 clade) and there is a lack of coherency down to the order level suggesting that clades and strains within the same genus may have different functional behaviour. Although bacteria are the major transformers of FDOM, the dynamics of FDOM depends on grazing at protozoan and metazooplankton levels.

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Table and figure legends

Table 1: Pearson correlations coefficient, r, for the linear association between the FDOM components and environmental and biological variables are given for the two seasons from *in*

situ observations from the 4 fjord stations. Red indicates negative and green positive associations. Significant relationships are marked by *.

Table 2: Pearson correlation coefficient, r, for the positive (green) and negative (red) linear association between selected operational taxonomic units (OTUs) of a bacteria (based on plastidial 16S rRNA sequence data), and the 5 FDOM components and salinity in the entire fjord dataset (not including the rivers). Significant relationships are marked by *. The OTU number, the assigned order and genera/clade are given in the three first columns. The 4th column indicates the relative abundance of each OTU as the sum of reads out of the total (green = high abundance, red = low abundance) separated into summer (July) and autumn (September).

Figure 1: Study sites in North East Greenland. Circles indicate the four sampling stations in Young Sound (St. 1-4) and triangles the three sampled rivers (R1-R3). Satellite image in the bottom left corner illustrates the glacial cover at its minimum in August (available at http://ocean.dmi.dk/arctic/daneborg.uk.php).

Figure 2: Monthly fjord transects of salinity (**A-D**), temperature (**E-H**), chl *a*-fluorescence (**I-L**) in Young Sound covering 25 CTD stations from the inner fjord (0 km) to the Greenland Sea. Dashed lines mark the 4 main stations. Plots were drawn using weighted-average gridding in Ocean Data View (Schlitzer 2016).

Figure 3. The excitation (solid line) and emission (red dashed line) of the 5 FDOM components isolated by PARAFAC. The fluorescence maximum is shown as well as the 'Coble peaks' that each component resembles (Coble 1996). The three-dimensional fluorescence contour plots with emission on the y-axis (300-600 nm) and excitation on the x-axis (250-450 nm).

Figure 4: Profiles of the UV wavelength C_{340} and the visible wavelength C_{405} FDOM components, salinity and temperature (°C), bacterial abundance (cells mL^{-1}), bacterial production (µg L^{-1} d^{-1}) and the grazer to prey ratio (HNF:Bac) in the upper 100 m of the fjord stations; St. 1 (green), St. 2 (yellow), St. 3 (red) and St. 4 (black). Values are shown as average ± SE of 3-4 profiles sampled within the summer (upper panel) and autumn period (bottom

panel). Note different x-axis for salinity and temperature in the two periods.

Figure 5: The contribution of the 3 visible wavelength (grey) and 2 UV wavelength (green) FDOM components in the three rivers and in the fjord water types during **A**) summer (July) and **B**) autumn (September-October), values are shown as averaged ± SE, number of samples (n) given above the bars.

Figure 6: Redundancy analysis biplot summarizing the variation of the 5 FDOM components in summer and autumn from *in situ* samples (dark blue arrows) in response to selected environmental and biological variables (red arrows) and to the water type as a categorical value (red triangles).

Figure 7: The abundance of different size-classes of protists in the three incubation experiments. Initial and final values are given on the left and right-hand side of the dashed line, respectively. Duration was 5, 7.8 and 9 days of *Exp. 1*, *2* and *3*, respectively. **A**) Relative abundance of the most abundant phytoplankton species (phylum (size class); order) based on plastidial 16S rRNA gene sequence data, showing the taxonomic diversity **B**) chl *a* fractions (<2, 2-10 and >10 μm) and initial and end nutrient concentration for all treatments (averaged ± SD) **C**) bacterial community composition of the 15 most abundant taxa at genus level (order; genus) in the three incubation experiments. N.B. there are no initial molecular data from *Exp. 2*.

Figure 8: A-C) The change in bacterial abundance ($x10^5$) mL^{-1}, **D-F)** bacterial production (μg C L^{-1} d^{-1}) and **G-I)** predator to prey ratio HNF:Bac ($x10^3$) during the course of the three experiments.

Figure 9: A-C) the initial intensity of the 3 visible wavelength (grey) and 2 UV wavelength (green) FDOM components in the 3 experiments. **D-K)** the change in FDOM fluorescence in the different treatment "only bacteria", "plus protists" and "plus mesozooplankton" calculated by Eq. 3 for the approx. time intervals 0-3, day 0-5 and day 0-7.

Table S1: Summary of the cumulative explained variation from the redundancy analysis with the 5 FDOM components as dependent variables and the environmental parameters as the explanatory variables. The analysis was performed for *in situ* samples from summer and autumn separately and once for summer and autumn combined.

991

992 **Table S2:** Experimentally estimated grazing mortality rates (g, d^{-1}) of microorganisms
993 calculated as the difference in growth rates (μ, d^{-1})) between the different size fractions
994 treatments (<0.8, <3, <10 and <90 µm) using Eq. 1 and 2. The rates are estimated from day 0
995 to day 4-5 and presented as mean ± SD of the triplicate treatments. N.B. grazing on bacteria in
996 *Exp. 2* could not be estimated as the filtration of <0.8 µm was not successful.

997

998 **Figure S1**: Abundance of microorganisms (cell mL^{-1}) and NH_4^+ concentrations during the three
999 fractionation experiments.

1000

1001 **Figure S2:** Distribution of chlorophyll *a*, DOC, DOC to DON ratio and the intensity of the
1002 visible wavelength C_{417}, C_{405} and the UV wavelength C_{340} FDOM components, bacterial
1003 abundance, bacterial production and specific production (µg L^{-1} d^{-1}), abundance of small and
1004 large HNF and the HNF:Bac ratio, in the upper 100 m in July-August (red) and September-
1005 October (blue). Profiles are shown as average ± SE of 3-4 profiles sampled at each of the four
1006 stations within each period.

1007

1008 **Figure S3:** The community structure in the three experiments show as the initial abundance
1009 (cells mL^{-1}) from Lugol fixed samples of micro-sized plankton i.e. dinoflagellates (purple),
1010 ciliates (orange) and diatoms (green) and after 5, 7 and 9 days of incubation in the treatments
1011 <10µm and <90 µm those with mesozooplankton addition.

1012

1013 **Figure S4:** Redundancy analysis biplot summarizing the variation of the bacterial community
1014 composition in response to the 5 FDOM components as explanatory variables (black arrows)
1015 in summer (orange) and autumn (blue). The size of the symbols relates to the sample richness
1016 at genus level. The water type of each sample is given by the different colour shades; light
1017 (surface samples) and dark (DCM samples).

1018

1019 **Figure S5:** Linear correlation between the bacteria grazing mortality (d^{-1}) estimated from day
1020 0-3, day 3-5 and day 5-7 and the HNF: bacteria ratio $x10^3$ averaged over the same time
1021 intervals.

1022

Figure S6: The measured FDOM fluorescence intensity (R.U.) in the 3 experiments on day 0, 3, 5, 7 and 9. Horizontal lines mark the initial averaged value. Colours indicate the different treatments. N.B. y-axis is different for *Exp. 3* day 7 and 9.