

Impacts of meltwater discharge from marine-terminating glaciers on the protist community in Inglefield Bredning, northwestern Greenland

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ABSTRACT: To evaluate the effects of meltwater discharge from marine-terminating glaciers on a fjord protist community in northwestern Greenland during summer, we investigated the distribution, abundance and biomass of the protist community and their relationships with hydrographic parameters. In the standing stock of protists, dinoflagellates (46.4 %) and oligotrich ciliates (39.5 %) were dominant throughout the study region. With respect to vertical distribution, oligotrich ciliates were abundant in the surface layer, mainly due to suitable food conditions (abundance of diatom and nanoflagellates). Near glaciers, relatively high chlorophyll *a* (chl *a*) concentrations were found in the subsurface layers associated with the low-temperature, high-turbidity and slightly high nutrient levels, indicating that the nutrient inputs from the upwelling glacial meltwater plume increased primary production. Large-sized *Protoperidium* spp. were found only at stations near glaciers where nutrients were abundant, and heterotrophic dinoflagellates showed strong relationships with nanoflagellates. These findings suggest that the upwelling associated with subglacial meltwater discharge can stimulate nanoflagellate production, resulting in increases in ciliate and heterotrophic dinoflagellate production.

KEY WORDS: Protist community · Meltwater discharge · Marine-terminating glacier · Ciliates · Dinoflagellates

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1. INTRODUCTION

Recently, tidewater glaciers in Greenland have been thinning and retreating under the influence of atmospheric and oceanic warming (e.g. Howat & Eddy 2011, Cowton et al. 2018). These glaciers flow directly into the ocean, forming important ice–ocean boundaries in glacial fjords. Near the glacier front in a fjord, subglacial discharge upwells cold and high-nutrient deep-water into euphotic zone (Bendtsen et al. 2015, Meire et al. 2017, Kanna et al. 2018), inducing high primary production throughout summer in the fjord (Arendt et al. 2013, Juul-Pedersen et al.

2015, Meire et al. 2017, Kanna et al. 2018). By contrast, this upwelling does not occur in fjords with land-terminating glaciers, which are characterized by lower productivity (Meire et al. 2017, Middelbo et al. 2018). The amount and type of inflow (surface or subsurface) of freshwater into the fjord may influence fjord water circulation, nutrient availability and subsequent productivity (Mortensen et al. 2011, Lydersen et al. 2014).

Ciliates and heterotrophic dinoflagellates (HDFs), which have frequently been observed to ingest bacteria, autotrophic nanoflagellates and diatoms (Gast 1985, Paranjape 1987, Sherr et al. 2003, Calbet et al.

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2011), are abundant in Arctic marine systems during summer (Sherr et al. 1997, Rysgaard et al. 1999, Seuthe et al. 2011). Additionally, heterotrophic nano-flagellates (HNFs) are an essential link from bacteria to the ciliates and HDFs. These heterotrophic organisms are preyed upon by mesozooplankton (Levinsen et al. 2000, Levinsen & Nielsen 2002); thus, they play important roles in the microbial loop (Pomeroy 1974). In Arctic marine waters, the species compositions of the protist communities are typically dominated by athecate dinoflagellates and oligotrich ciliates, whereas thecate dinoflagellates and tintinnids show low abundances (Levinsen & Nielsen 2002, Krawczyk et al. 2015). The biomasses of heterotrophic organisms are influenced by phytoplankton blooms in the Arctic Ocean (Taniguchi 1984, Sherr et al. 1997, Olson & Strom 2002). In Disko Bay, oligotrich ciliates and HDFs have been found to be the dominant members of the protist community during summer (Levinsen et al. 2000, Levinsen & Nielsen 2002). Their biomasses peak during this time due to decreases in top-down effects driven by the absence of large copepods from the euphotic zone in early spring and late summer (Levinsen & Nielsen 2002).

Around Greenland, the features of the protist community have been studied in Disko Bay (Nielsen & Hansen 1995, Levinsen et al. 1999, 2000), Young Sound (Rysgaard et al. 1999, Rysgaard & Nielsen 2006, Krawczyk et al. 2015) and Godthåbsfjord (Arendt et al. 2010, Calbet et al. 2011). However, beyond these regions few studies have been conducted, and no information is available regarding the protist communities in northwestern Greenland. In addition, the impacts of meltwater discharges from glaciers on bacterial production (Paulsen et al. 2017), primary production (Arendt et al. 2013, Juul-Pedersen et al. 2015, Meire et al. 2017) and zooplankton (Arendt et al. 2016) have been reported in Greenland, and the distributions of protist communities in Greenlandic fjords have been studied (e.g. Nielsen & Hansen 1995, Rysgaard et al. 1999). However, the impacts of meltwater discharge on protists are not fully understood.

In this study, we revealed the spatial distributions of protists (diatoms, dinoflagellates, ciliates and nano-flagellates) in Inglefield Bredning, a ~100 km long and ~20 km wide glacial fjord in northwestern Greenland. Recent studies in this region have revealed the importance of meltwater discharge from a marine-terminating glacier for biogeochemical processes in fjords (Kanna et al. 2018, Naito et al. 2019). Inglefield Bredning is fed by retreating marine-terminating glaciers (Sakakibara & Sugiyama 2018) and glacial changes are possibly affecting marine ecosystems.

Based on sampling and hydrographic observations, we evaluated the impacts of meltwater discharges from marine-terminating glaciers on the biomasses of the protist community during summer.

2. MATERIALS AND METHODS

2.1. Field sampling

Boat-based, daytime observations were performed from 13–17 August 2018 in the northeastern section of Inglefield Bredning (Fig. 1). The study area includes regions that are within several km of Sharp and Hart Glaciers, as well as the region ~10 km from Melville Glacier. These glaciers discharge meltwater and icebergs into the fjord through calving fronts that are several km wide (Sakakibara & Sugiyama 2018). Temperature, salinity, fluorescence, turbidity (Formazin turbidity units, FTU) and dissolved oxygen (DO) were measured with a CTD profiler (ASTD 102; JFE Advantech) at 6 stations. At these stations, water samples (500 ml) were collected in Niskin-X bottles (General Oceanics) from 0, 10, 20, 30, 40, 50, 70 and 100 m depth at all 6 stations except Stn 4, where samples were collected from 0–40 m (Fig. 1). The samples were fixed with 1% glutaraldehyde. For nutrient and chlorophyll *a* (chl *a*) measurements, seawater samples were collected from 5–8 depths (e.g. 0, 10, 20, 30, 40, 50, 70 and 100 m, depending on bottom depth). For chl *a* measurements, 100 ml of seawater from each sample was filtered on a GF/F filter. The filtered sample was immersed in *N,N*-dimethylformamide (Wako Pure Chemical Industries) under dark conditions for 24 h. Samples for nutrient and chl *a* (extracted in *N,N*-dimethylformamide) analyses were immediately placed in a freezer (–20°C), transported to Japan without melting and then stored in a cold laboratory (–20°C) until analysis. The nutrients (nitrate, nitrite, phosphate and silicic acid) in seawater were analyzed using an autoanalyzer (QuAatro; BL TEC) after sample filtration using syringe GF/F filters (Puradisc 13, Whatman). The measurement of all nutrients was quality controlled by using reference seawater materials (KANSO Technos). Chl *a* was measured with a fluorometer (10-AU; Turner Designs) using the nonacidification method of Welschmeyer (1994).

2.2. Microscopic analysis

In the laboratory, the 500 ml water samples were stored on a stone table for more than 1 d to allow the

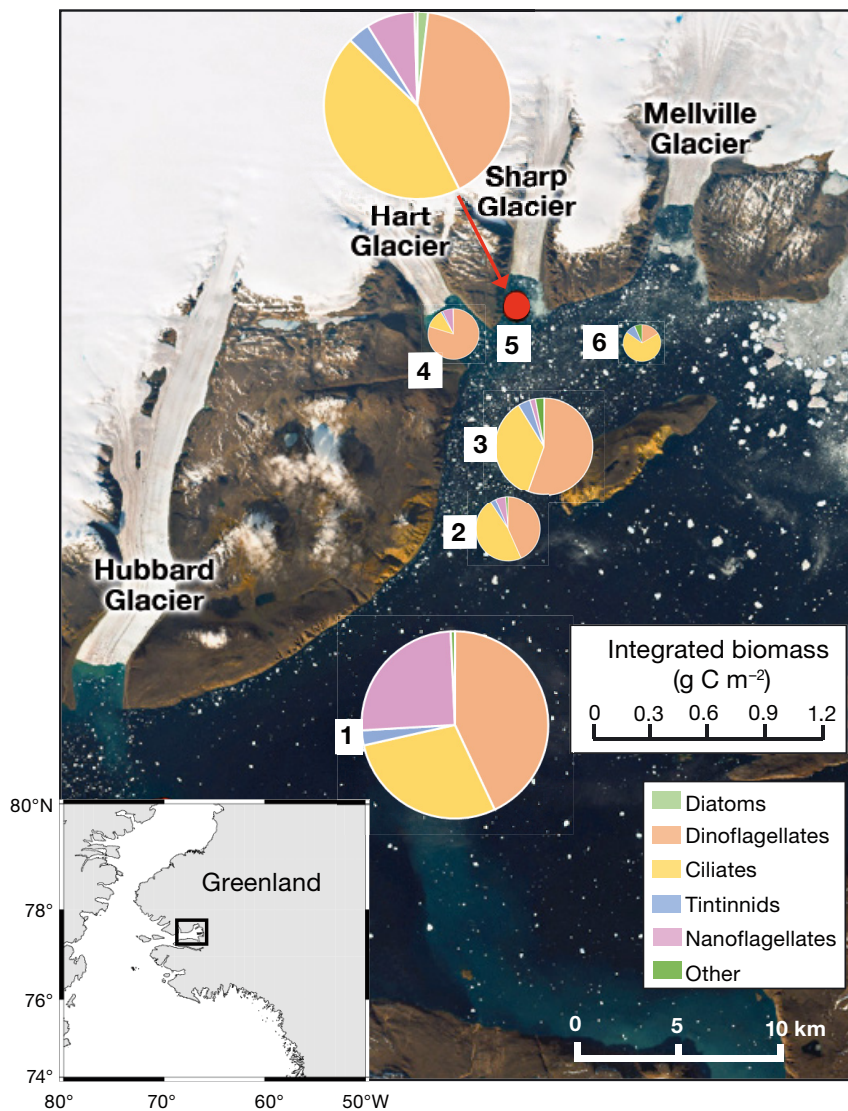


Fig. 1. Horizontal distributions of integrated carbon biomass (diameter of circles) and species compositions of the protist community in the water column (0–100 m for all stations except Stn 4 [0–40 m]) in Inglefield Bredning, northwestern Greenland, obtained during 13–17 August 2018. Numbers: station names. Background image is from Modified Copernicus Sentinel data (13 August 2018), processed with Sentinel flow (<https://github.com/juseg/sentinelflow>). Inset: study site location

microprotist cells to settle to the bottom of each bottle. Then, the samples were concentrated to 20 ml using a siphon. Subsamples (0.25–1 ml) were mounted on glass microscope slides with lines, and the diatoms, dinoflagellates and ciliates were counted and identified to species/genus levels under an inverted microscope at 40–400 \times magnification. Nanoflagellates, i.e. flagellates with cell sizes of 5–10 μm , were also counted, but their cell densities might have been underestimated due to their small size. All of the nanoflagellates were classified as autotrophic/mixotrophic/

heterotrophic because we did not use epifluorescence microscopy to check whether or not the cells had chloroplasts. We enumerated 8–2272 protist cells (including nanoflagellates) per sample. As we concentrated each sample from a volume of 500 ml to a volume of 20 ml, the limit of detection was 160 cells l^{-1} for each 0.25 ml subsample and 40 cells l^{-1} for each 1 ml subsample.

Species identifications were made to the lowest possible level (e.g. species or genus) (see Box 1). For species identification, we referred to Hasle & Syvertsen (1997) for diatoms, Fukuyo et al. (1997) and Evagelopoulos (2002) for dinoflagellates and Maeda (1997) and Taniuchi (1997) for ciliates. Silicoflagellates and cysts of each taxon were omitted from the analyses due to their low densities. Our preservative (glutaraldehyde) is an adequate fixative for diatoms and dinoflagellates but not for ciliates. Because ciliates are better preserved with acidic Lugol's solution (Stoecker et al. 1994) than with glutaraldehyde, our preservative may have led to biased estimates of community structure and biomass (through the loss of unloricated ciliates).

Using the cell sizes (length and width) measured during the counting process, protist biovolumes were calculated following the method reported by Sun & Liu (2003). Then, carbon biomasses were estimated using the carbon–volume relationship proposed by Menden-Deuer & Lassard (2000). Finally, biomasses

($\mu\text{g C l}^{-1}$) were calculated from the carbon biomass per cell and from the abundances (cells l^{-1}).

2.3. Data analysis

To evaluate environmental factors controlling changes in the protist community, we applied structural equation modeling (SEM) analysis (Stomp et al. 2011). For SEM analysis, the environmental parameters (temperature, salinity, turbidity, silicate

and chl *a*) and biomass of each protist taxon were normalized (average: 0; SD: 1), and regressions among all parameters were calculated. For the path analysis, we set the parameters for 3 categories (1: temperature, salinity, turbidity and silicate; 2: chl *a*, diatoms and nanoflagellates; 3: dinoflagellates, oligotrich ciliates and tintinnids). Subsequently, parameters with nonsignificant relationships ($p > 0.05$) were removed from the final model (cf. Matsuno et al. 2016). SEM analysis was performed using add-in software for MS Excel (<https://www.ohmsha.co.jp/book/9784274069253/>).

3. RESULTS

3.1. Environmental conditions

Surface water temperatures ranged from 0.67–4.3°C (Fig. 2). The temperatures between 0 and 20 m depth were lower at Stns 4 and 5 than at the other stations. Salinities in the surface layer ranged from 27.5–30.2 and, similar to temperature, were lower at stations near the glacier (i.e. Stns 4 and 5) than at those in the down-fjord region (Fig. 2). Turbidity levels showed marked differences among the stations. Near glaciers, high turbidities were observed below 50 m at Stns 5 and 6 and at approximately 10 m at Stns 4 and 5. The fluorescence and chl *a* levels showed similar patterns. High chl *a* concentrations were observed near 10 m at the near-glacier stations and relatively high values were observed near 75 m at Stns 2, 3 and 6. The nitrite+nitrate and phosphate levels showed ranges of 0.03–14.1 and 0.18–1.05 $\mu\text{mol kg}^{-1}$, respectively, and high concentrations of both were observed below 60 m at the near-glacier stations (Stns 5 and 6). The distribution patterns of silicate were similar to the nitrite+nitrate patterns. Comparing the temperature and turbidity at the subsurface layer (10 m depth), water at Stns 3 and 4 was significantly colder and more turbid (mean 1.2°C and 0.82 FTU) than those at the other sta-

tions (mean 3.0°C and 0.22 FTU) (U -test, $p < 0.01$ and $p < 0.05$) (Fig. 3). Low chl *a* concentrations and high nutrient levels were found in the deeper layer (>60 m depth), whereas in the surface layer, chl *a* concentrations were highly variable and nutrient concentrations were low (Fig. A1 in the Appendix). The relationship between chl *a* and nitrite+nitrate was significantly negative (Spearman's correlation analysis, $p < 0.05$).

3.2. Spatial distributions of protists

In this study, we identified 33 protist taxa. These included 6 diatom taxa (5 different genera and 1 species), 6 dinoflagellate taxa (5 different genera and 2 different species), 7 oligotrich ciliate taxa (6 different genera and 1 species), 7 tintinnid ciliate taxa (5 different genera and 6 different species), one silicoflagellate taxa, cyst/resting spore for each

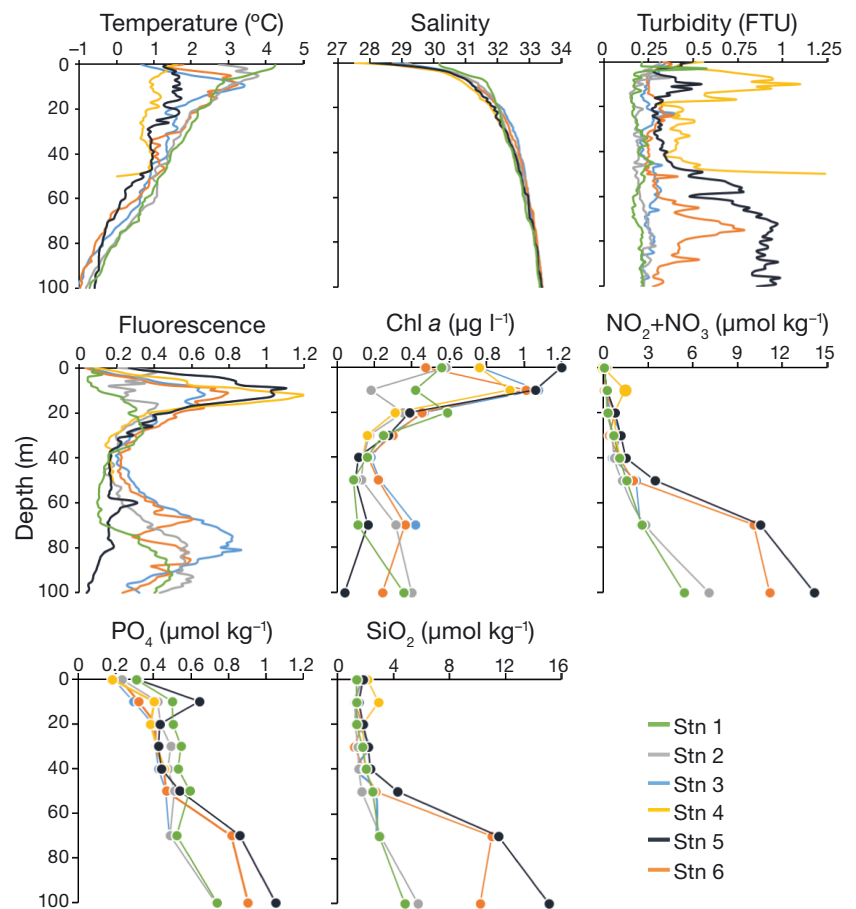


Fig. 2. Vertical profiles of environmental parameters in Inglefield Bredning, northwestern Greenland, obtained during 13–17 August 2018. Dots in the plots of chlorophyll *a* and nutrients are data obtained from water samples

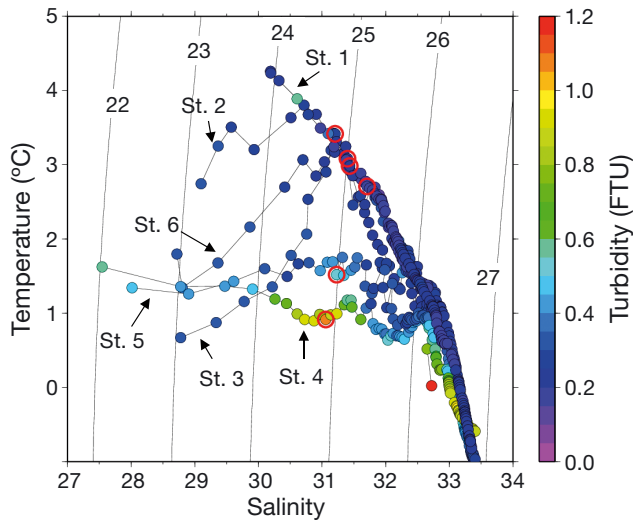


Fig. 3. Temperature–salinity diagram with turbidity in Inglefield Bredning, northwestern Greenland, during 13–17 August 2018. Red circles: value at 10 m depth. FTU: Formazin turbidity units

taxon and nanoflagellates from different categories based on cell size and shape (Box 1). Total protist abundances and biomasses ranged from 408–273 019 cells l^{-1} and 0.09–72.84 $\mu g C l^{-1}$, respectively (Table S1 in the Supplement at www.int-res.com/articles/suppl/m642p055_supp.xlsx). Diatom densities ranged from 0–526 cells l^{-1} (representing 0–14% of total protist density), and the biomass

exhibited a range of 0–0.74 $\mu g C l^{-1}$ (0–11% of total protist biomass). Dinoflagellates ranged in density from 0–21 270 (0–35% of total protist density) and their biomass ranged from 0–39.30 $\mu g C l^{-1}$ (0–96% of total protist biomass). The density of oligotrich ciliates ranged from 0–4563 cells l^{-1} (0–56% of total protist density) and the oligotrich ciliate biomass ranged from 0–23.57 $\mu g C l^{-1}$ (0–97% of total protist biomass). Tintinnids ranged in density from 0–601 cells l^{-1} (0–30% of total protist density) and their biomass ranged from 0–7.15 $\mu g C l^{-1}$ (0–92% of total protist biomass). Nanoflagellate densities ranged from 106–248 505 cells l^{-1} (10–98% of total protist density), and their biomass ranged from 0.0007–14.04 $\mu g C l^{-1}$ (0.009–58% of total protist biomass). At each station, within the total protist biomass over the whole water column, dinoflagellates and oligotrich ciliates were the dominant taxa, with mean compositions of 46.4 and 39.5%, respectively (Fig. 1, Table S2). The highest total biomasses were observed near the glacier (Stn 5) and at Stn 1. The different taxa of the protist community exhibited varying spatial patterns. Oligotrich ciliates were abundant in the surface layer at most stations (Fig. 4). Large (>60 μm equivalent spherical diameter, ESD) dinoflagellates (e.g. *Protoperidinium* spp.) were found in the surface layer and/or at 30–70 m at all of the near-glacier stations except Stn 6 (e.g. Stns 3, 4 and 5).

Box 1. Species of protists observed in Inglefield Bredning, northwestern Greenland, during 13–17 August 2018

Diatoms	Tintinnids
<i>Cocconeis</i> spp.	<i>Codonella galea</i>
<i>Cylindrotheca closterium</i>	<i>Favera azorica</i>
<i>Navicula</i> spp.	<i>Parafavera denticulata</i>
<i>Odontella</i> spp.	<i>Parafavera hada</i>
Pennate diatoms	<i>Parafavera hadai</i>
<i>Thalassiosira</i> spp.	<i>Parafavera jorgenseni</i>
Dinoflagellates	<i>Ptychocylis obtusa</i>
<i>Amphidinium</i> spp.	<i>Tintinnopsis</i> spp.
<i>Dinophysis</i> spp.	
<i>Gymnodinium</i> spp.	Silicoflagellates
<i>Gyrodinium</i> spp.	<i>Dictyoca</i> spp.
<i>Protoperidinium depressum</i>	
<i>Protoperidinium divergens</i>	Other
Ciliates	Ciliate cysts
<i>Laboera strobila</i>	Diatom resting spores
<i>Leegardiera</i> spp.	Dinoflagellate cysts
<i>Lohmanniella</i> spp.	Nanoflagellates (slender, 5–10 μm)
<i>Mesodinium</i> spp.	Nanoflagellates (spherical, <5 μm)
Scuticociliates	Nanoflagellates (spherical, 5–10 μm)
<i>Strobilidium</i> spp.	
<i>Strombidium</i> spp.	

3.3. SEM analysis

SEM analysis revealed a negative correlation between chl *a* and salinity (path coefficient, $pc = -0.66$), i.e. chl *a* levels increased as salinity decreased (Fig. 5). The diatom biomass showed positive correlations with turbidity and with the biomass of oligotrich ciliates ($pc = 0.48$ and 0.39 , respectively). Nanoflagellates were positively correlated with temperature, nitrite+nitrate, dinoflagellates and oligotrich ciliates; the correlations with temperature and dinoflagellates were particularly high ($pc = 0.92$ and 0.76 , respectively) (Fig. 5). Oligotrich ciliates showed positive correlations with diatoms ($pc = 0.39$) and nanoflagellates ($pc = 0.37$), whereas they were negatively correlated with temperature ($pc = -0.48$), salinity ($pc = -0.85$) and turbidity ($pc = -0.37$).

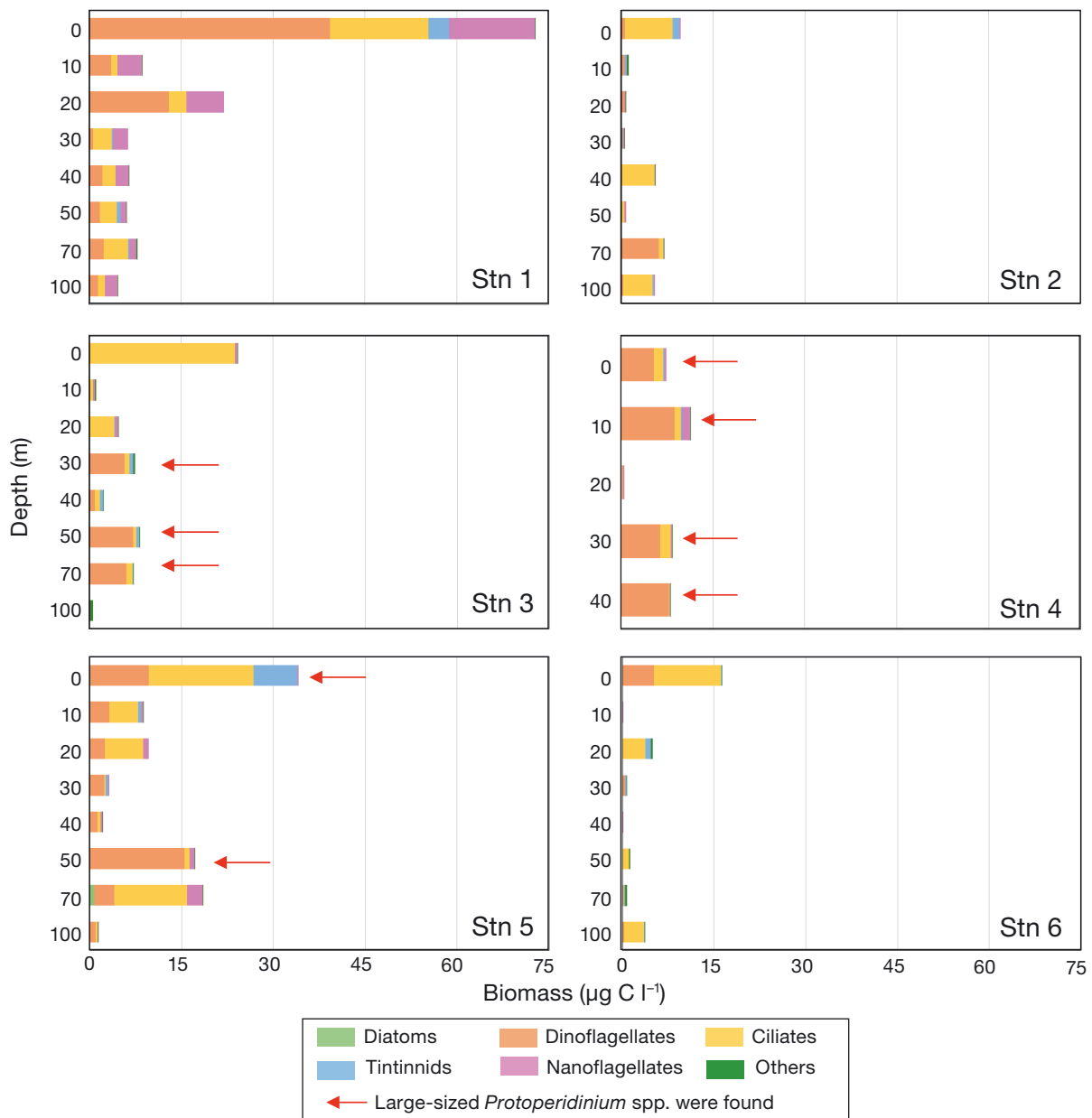


Fig. 4. Vertical distributions of the protist community in Inglefield Bredning, northwestern Greenland, during 13–17 August 2018

4. DISCUSSION

4.1. Protist biomass in the fjords around Greenland

Heterotrophic protists, which mainly include HNFs, ciliates and HDFs, consume a broad range of prey ranging from bacteria to diatoms (Gast 1985, Paranjape 1987, Sherr et al. 2003, Calbet et al. 2011). These heterotrophic protists, in turn, are important prey items for mesozooplankton (Levinsen et al. 2000, Levinsen & Nielsen 2002) and thus play significant

roles in the pelagic food webs of the Arctic Ocean (and many other ocean systems) (Sherr et al. 1997, Rysgaard et al. 1999, Seuthe et al. 2011).

In Arctic waters, protist communities are dominated by athecate dinoflagellates and oligotrich ciliates, whereas thecate dinoflagellates and tintinnids show low abundances (Levinsen & Nielsen 2002). Similar patterns have been observed in Disko Bay (Nielsen & Hansen 1995, Levinsen et al. 1999, 2000) and Young Sound (Rysgaard et al. 1999) in Greenland. Despite the fact that oligotrich ciliates can be underestimated by suboptimal preservation, our

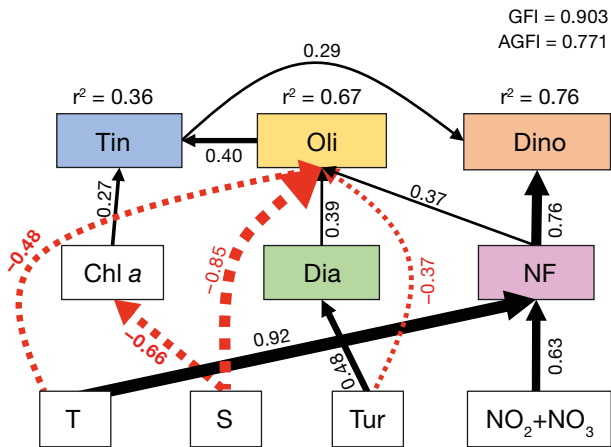


Fig. 5. Structural equation modeling of protist biomasses and environmental factors. Numbers along pathways: standardized path coefficients; arrows with solid and dashed lines: positive and negative effects, respectively (arrow thickness varies with path coefficient values). The overall fit of the model was evaluated using a goodness-of-fit index (GFI) and adjunct goodness-of-fit index (AGFI). Tin: tintinnids; Oli: oligotrich ciliates; Dino: dinoflagellates; Dia: diatoms; NF: nanoflagellates; T: temperature; S: salinity; Tur: turbidity; NO₂+NO₃: nitrite+nitrate

findings regarding protist community structures and biomass are similar to those of previous studies.

We summarize the mean biomass of each heterotrophic species for our site and other well-studied sites around Greenland in Table 1. Our biomass values are higher than those for Young Sound (northeast Greenland) and lower than those for Disko Bay (west Greenland). Two geophysical factors influence protist biomass: glacier type (marine- vs. land-terminating) and sea-ice coverage. Inglefield Bredning is characterized by the intrusion of marine-terminating glaciers. Upwelling subglacial discharges from those

glaciers affect the water properties (e.g. temperature, salinity and turbidity) and caused the relatively high chl a concentrations at Stns 4 and 5. Regarding sea-ice coverage, the fjord is covered by sea ice until late summer (typically July) (Sugiyama et al. 2015). Accordingly, the protist biomass in the present study was intermediate between that of the highly productive Disko Bay (short sea-ice cover duration and marine-terminating glaciers) and less productive Young Sound (long sea-ice cover duration and land-terminating glaciers) during summer.

4.2. Relationships between environmental parameters and the protist community

Temperature and salinity distributions revealed a cold and fresh surface water layer near the glaciers. Oligotrich ciliates dominated in this layer, and SEM analysis revealed strongly negative correlations between these ciliates and both temperature and salinity. These findings suggest that fresh surface water is a suitable habitat for oligotrich ciliates. Higher temperatures are known to enhance the growth of ciliates in polar regions (Hansen & Jensen 2000), and Matsuno et al. (2014) reported a positive relationship of ciliates with temperature in the western Arctic Ocean during autumn. Thus, the relationship between ciliates and temperature in this study was opposite to that reported in previous studies. This result means that environmental parameters (especially temperature) are not critical factors that affect ciliates in this study region during summer.

Ciliate dominance in the region is possibly controlled by available carbon sources. Ciliates ingest bacteria, phytoflagellates and small diatoms (Gast

Table 1. Biomass standing stock of ciliates, dinoflagellates and nanoflagellates (NF) around Greenland. MTG: marine-terminating glacier; LTG: land-terminating glacier. Mean biomass shown as integrated biomass for each taxon

Area	Glacier type	Depth (m)	Period	Integrated biomass (mgC m ⁻²)			Reference
				Ciliates	Dinoflagellates	NF	
W Greenland (Disko Bay)	MTG	0–30	July	330	393	246 ^a	Nielsen & Hansen (1995)
			August	270	500		Levinsen & Nielsen (2002)
		0–200	July–September	286	486		Levinsen et al. (1999)
			August	620	910		Levinsen et al. (2000)
SW Greenland	MTG	0–200	June	243	386	134 ^b	Pedersen et al. (2005)
NE Greenland (Young Sound)	LTG	0–35	June	98	40	48 ^b	Nielsen et al. (2007)
			August	20–143	20–70		Rysgaard et al. (1999)
NW Greenland (Inglefield Bredning)	MTG	0–100	August	241	294	74 ^c	This study

^aAutotrophic/mixotrophic; ^bheterotrophic; ^cautotrophic/mixotrophic/heterotrophic

1985, Paranjape 1987, Sherr et al. 2003). In this study, diatoms and nanoflagellates had positive relationships with ciliates, and prey abundances were higher under warmer, higher-nutrient conditions, which indicates that hydrographic conditions influence prey concentrations. Levinsen et al. (2000) suggested that the threshold concentration at which the growth rate equals zero for ciliates and HDFs is $18 \mu\text{g C l}^{-1}$. Assuming that all of the oligotrich ciliates, tintinnids and dinoflagellates in this study were heterotrophic organisms, the average contribution of ciliates to the carbon biomass of the heterotrophic organisms in this study was 53.5%. The threshold concentration for ciliates is estimated to be $9.63 \mu\text{g C l}^{-1}$ ($= 18 \times 0.535$). In this study, the maximum biomass of potential prey (i.e. diatoms and nanoflagellates) for ciliates was $14.07 \mu\text{g C l}^{-1}$ at 0 m at Stn 1, and average biomass throughout the study region was $0.936 \mu\text{g C l}^{-1}$. Since the average prey concentration was much lower than the threshold concentration needed for ciliate growth, ciliate growth would have been limited by the low prey concentrations (Levinsen et al. 2000).

We did not examine bacterial abundances in this study. Bacterial production has been reported to be high ($0.13 \mu\text{g C l}^{-1} \text{ d}^{-1}$) in the surface layer of Young Sound (northeastern Greenland) during summer despite low dissolved organic carbon concentrations from river inflows (Paulsen et al. 2017). High bacterial productivity may contribute to the dominance of ciliates in the surface layer, supporting the HNF linkage between bacteria and ciliates (Nielsen & Hansen 1995). Seasonally, maximum ciliate biomasses were seen in surface water after diatom blooms and under decreased grazing pressure from copepods following the migration of large copepods (e.g. *Calanus* spp.) to the deeper layers (Levinsen et al. 1999). Despite no information on grazing pressure by copepods in this study, ciliate abundances are believed to be controlled by bottom-up effects, not only by sufficient food concentrations (diatoms and nanoflagellates) but also by HNF thriving via high bacterial production.

4.3. Effects of glacial meltwater discharge on protists

HDFs dominate the microzooplankton biomass in the Arctic Ocean during summer (Andersen 1988, Nielsen & Hansen 1995, Sherr et al. 1997). Levinsen et al. (1999) reported that HDFs represented, on average, 70% of the integrated microzooplankton biomass when diatoms formed subsurface blooms. After the diatoms declined, large HDFs became less

abundant. In the present study, diatom abundances were low throughout the study region, suggesting that HDF abundances were likely low due to food limitations (Levinsen et al. 1999). SEM analysis revealed that dinoflagellates had a significant positive relationship with nanoflagellates but not with diatoms. This result suggests that the HDF population was maintained by grazing nanoflagellates after the diatom blooms (Levinsen & Nielsen 2002). According to Jakobsen & Hansen (1997), the ability of HDFs to cope with starvation is greater than that of planktonic ciliates, because under starvation conditions, dinoflagellates can extend their minimum generation time to beyond that of ciliates. Thus, HDFs can survive due to their flexible grazing strategy (changing prey types in response to availability) and their marked ability to tolerate starvation in fjords during the summer.

Freshwater discharges from the bottom of marine-terminating glaciers induce strong upwelling near the glacier fronts, which transports nutrient-rich deep-layer water into the euphotic layer (Bendtsen et al. 2015, Meire et al. 2017, Kanna et al. 2018). In this study, upwelling water was represented by a highly turbid and low-temperature subsurface layer observed near the glaciers. Due to the nutrient input into the euphotic layer, chl *a* concentrations and primary production increased within the relatively thin subsurface layer (Calbet et al. 2011, Meire et al. 2017). As with previous studies, chl *a* concentrations in the subsurface layer (10 m) were slightly higher at the near-glacier stations (i.e. Stns 4 and 5) than at the other stations (0.99 vs. 0.67 ; *U*-test, $p = 0.39$). The nutrient concentrations were uniformly distributed among the stations, but relatively high concentrations were found at Stns 4 and 5 (0.85 vs. 0.14 ; *U*-test, $p = 0.13$). These observations suggest that the relatively high chl *a* levels were maintained by nutrients upwelling near the glacier. Previous studies have indicated that the euphotic depth is very important for chl *a* distribution. During summer in Disko Bay, the euphotic zone is situated at around 30 m (Levinsen et al. 1999). Although we did not measure vertical profiles of light intensity in the water column, high chl *a* concentrations were found in the highly turbid layer. This observation suggests that high turbidity did not prevent primary production by phytoplankton, at least in the subsurface layer. We did not measure primary production, however, and do not have field data from other seasons. Nevertheless, our study results suggest that nutrient concentrations in the upwelling water near the glacier play a critical role in primary production in Inglefield Bredning during summer.

Nanoflagellates are important components of the food web in fjords because they are grazed upon by larger heterotrophic species, as mentioned above. They are abundant in the summer fjords, particularly where plumes occur in front of glaciers (e.g. Middelbo et al. 2018). In Young Sound, phytoplankton smaller than 10 μm were dominant near the glacier throughout the year (Middelbo et al. 2018, 2019, Holding et al. 2019). Near the glacier, strong stratification due to fresh surface water prevents upwelling of nutrients to the surface layer. Thus, small phytoplankton dominate in a low-nutrient surface layer (Daufresne et al. 2009, Li et al. 2009, Gardner et al. 2011). Compared to micro-sized autotrophs (e.g. diatoms), the small cells of nanoflagellates (<10 μm) and even smaller picophytoplankton (<2 μm) are adapted to low-light intensities and are capable of generating efficient primary production (Taguchi 1976, Raven 1998, Holding et al. 2019). SEM analysis revealed that the nanoflagellates had positive relationships with temperature and nitrite+nitrate. Since the trophic type of the nanoflagellates were not identified in this study, 2 mechanisms could provide feasible explanations for these observations. High-temperature conditions potentially increase the growth rate of HNFs (Choi & Peters 1992). Because of that, the strong relationship between temperature and nanoflagellates revealed in the SEM means that the HNFs potentially increase in high temperatures. The nitrite+nitrate levels potentially stimulate primary production by autotrophic nanoflagellates (Middelbo et al. 2018, 2019, Holding et al. 2019).

On the other hand, large-sized *Protoperidium* spp. were found only at stations near glaciers where nutrients were supplied by upwelling water. Large *Protoperidium* spp. (mean size: 104 μm ESD) can graze on small dinoflagellates (e.g. *Gymnodinium* spp.; 31 μm ESD) and small ciliates (e.g. *Strombidium* spp.; 41 μm ESD) (Levinsen & Nielsen 2002); the small dinoflagellates and ciliates graze on nanoflagellates (Jakobsen & Hansen 1997). Based on these facts, we speculate that the nanoflagellates (we assume autotrophic and mixotrophic nanoflagellates here) used the upwelling nitrite+nitrate, and that the resulting production was transported to the large *Protoperidium* spp. via the small dinoflagellates and ciliates. As the HNFs have a strong link to bacteria and small dinoflagellates and ciliates (Nielsen & Hansen 1995), bacterial production was supported by the labile carbon supplied by meltwater from glaciers (Paulsen et al. 2017, 2019). Therefore, both auto- and heterotrophic nanoflagellates could be increased by the upwelling nutrients and high bacterial production, resulting in the abun-

dance of large HDFs only near glaciers. We conclude that the upwelling subglacial discharge not only affects chl *a* concentrations, but can also stimulate nanoflagellate production, ultimately and here increasing production via HDFs and ciliates.

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Appendix.

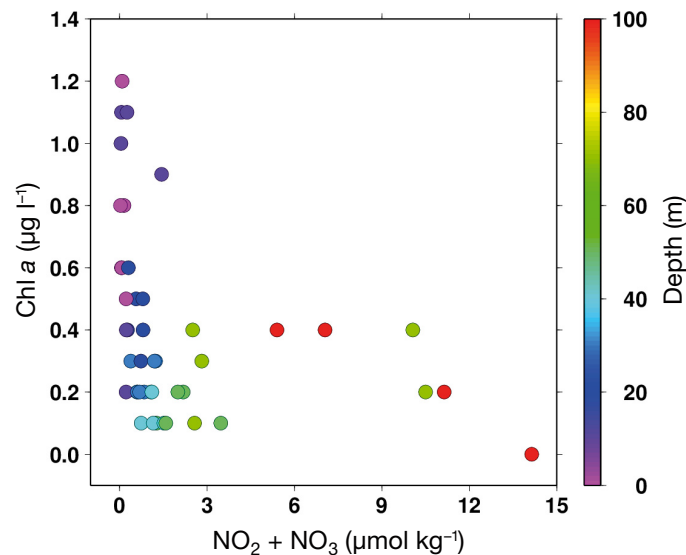


Fig. A1. Comparison between chlorophyll *a* and nutrients with depth in Inglefield Bredning, northwestern Greenland, during 13–17 August 2018. Colors indicate sampling depth of the water samples