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Seen in flakes & drops: local heterogeneity of marine snow, biogeochemistry, and plankton in Svalbard's glacial bays

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Abstract. Glacier retreat is one of the most spectacular effects of climate warming in the Svalbard Archipelago, and is having a substantial impact on physical, biogeochemical and ecological processes in marine ecosystems. Here we propose that marine snow acts as a direct agent linking water chemistry, mineral particles, and primary and secondary producers. Marine snow plays a key role in carbon export and also carries knowledge about the biophysical state of the pelagic ecosystems. We propose that structuring of marine snow, assessed via high-resolution imaging by the Underwater Vision Profiler (UVP6), may serve as an informative currency for inter-regional, inter-seasonal and fine-scale system comparisons. In this study, we investigated small-scale variability in nutrients, carbon, plankton and marine snow in fjord waters proximal to glaciers in Hornsund, Rechercherfjorden and Isfjorden. We observed strong seasonal differences in biogeochemical properties, shifts in plankton composition (protists and zooplankton) and marine snow morphology between late summers (2022, 2023) and spring 2023. Fine-scale observations show various interplays between marine snow populations with hydrography, turbidity, biogeochemistry, and composition of plankton communities. Alongside expected relations between marine snow composition and morphology with for example temperature and macronutrients, we also identified other potentially important correlations, including with manganese, iron, and total alkalinity. Given the high spatiotemporal variability in physical, biogeochemical conditions and associated particles and plankton, we conclude that seasons and local heterogeneity are the strongest drivers. These results provide new interdisciplinary insight into coupled physical-biogeochemical-ecological processes and improve our understanding of land-ocean interaction on marine production and carbon burial near glaciers at varying states of recession.

1 Introduction

No two fjords are the same, nor are the driving forces and main mechanisms that shape them. Likewise, the rates at which glaciated areas are retreating and how they influence marine ecosystems differ substantially across Arctic fjords. Consequently, the literature presents many contradictory findings about the role of glacier meltwaters on marine productivity in Arctic fjords

(Demidov et al., 2024; Halbach et al., 2019; Hop et al., 2023; Hopwood et al., 2020; Juul-Pedersen et al., 2015; Kanna et al., 2018; Lydersen et al., 2014; Meire et al., 2017; Oliver et al., 2023; van de Poll et al., 2021; Stuart-Lee et al., 2023; Vonnahme et al., 2025). There is considerable uncertainty also regarding the influence of glaciers at various recession stages, particularly when comparing marine-terminating and land-based glaciers (Demidov et al., 2024; Halbach et al., 2019; Hood et al., 2009; Hopwood et al., 2018; Szeligowska et al., 2021). Moreover, the majority of the fundamental studies have been performed in the Greenland fjords (Arendt et al., 2010; Bhatia et al., 2013; Hoshiba et al., 2024; Kanna et al., 2022a, b; Meire et al., 2017; Wiedmann et al., 2025), which differ from the ones in Svalbard. While Svalbard fjords also receive substantial freshwater, sediment, and nutrient inputs from glaciers, resulting in sharp physical and biogeochemical gradients, this input occurs in smaller and shallower basins. Furthermore, pronounced inter- and intra-catchment differences (Murray et al., 2015), result in various plankton communities and particles properties within fjords and even their individual bays (Dąbrowska et al., 2025; Piquet et al., 2014; Szeligowska et al., 2020; Trudnowska et al., 2020; Wiedmann et al., 2016). The Svalbard archipelago hosts numerous glacially carved fjords that differ markedly in sill depth, exposure to Atlantic Water, glacier type, and freshwater forcing. The uniqueness of each fjord, both in terms of topographic and hydrographic structure, together with the diverse influence of meltwaters from catchment of varying geologies, provides a natural laboratory for studying a range of biogeochemical coupling scenarios under different settings. The understanding of the ecosystem functioning of fjords has potentially far-reaching implications of because fjords can be efficient sinks for organic carbon (Cui et al., 2022; Koziorowska et al., 2016, 2018; Smith et al., 2015; Szymczycha et al., 2025), CO_2 (Akhoudas et al., 2025; Alekseeva et al., 2024; Ericson et al., 2019), and are important hotspots for marine productivity and feeding grounds for birds and mammals (Lydersen et al., 2014; Nishizawa et al., 2020).

Multiple region-specific case-studies are needed to broaden our knowledge about glacier retreat impact on marine ecosystems and carbon cycling, and high spatio-temporal resolution approaches are still lacking. Especially limited is our knowledge of processes occurring in short distances from the front of the glaciers (Borja et al., 2020; Hansen et al., 2025; Krawczyk et al., 2015; Mortensen et al., 2020). One of the main constraints for such studies derives from the life-threatening risk of sampling due to calving events. In this context, autonomous marine vehicles can play a role in collecting data in dangerous interface areas (Bruzzone et al., 2020; Pasculli et al., 2020; Rooijakkers et al., 2025). However, these modern approaches still do not fully eliminate the need for physical sampling. Moreover, fine-scale vertical resolution is also important, because many processes, including subsurface phytoplankton layers and particle plumes, may occur below the surface. The solution for this constraint is the growing fleet of *in situ* sensors, probes and cameras that often provide automatic measurements over fine scales, which can also be operated from autonomous vehicles, or small boats that have better capacity to reach glacier fronts with relatively small distances than large vessels.

Little information exists on the seasonal dynamics in fjords, even though different seasons preset sharp changes in biological productivity (Dąbrowska et al., 2021, 2025; Kubiszyn et al., 2017; Van De Poll et al., 2018). This seasonality has to be considered, especially given the traditional view that the main pulse of primary production occurs in spring, before the main melting phase. On the other hand, the glacier melting in the summer may contribute significantly to the extended time of the growing season (Arrigo et al., 2017; Oliver et al., 2018). Finally, truly interdisciplinary research is needed because quantifying the environmental impact of glacial discharge is very complex due to multiple concurrent, and sometimes confounding bio-physico-geochemical interactions. Thus far, much remains unknown about how glacially influenced fjords regulate the coupling between ocean biochemistry, primary production, marine life, and carbon export in the water column.

We propose that marine snow structuring may serve as an informative currency for inter-regional, inter-seasonal and fine-scale system comparisons, because the aggregates are direct agents linking water biogeochemistry, primary and secondary producers, mineral particles, and water constituents of other origins (Durkin, 2025; Durkin et al., 2016, 2021, 2022; Iversen and Ploug, 2010; Kiørboe, 2001; Omand et al., 2020; Turner, 2015). Hence, particles and aggregates at a specific depth may be composed of small cells of phytoplankton and individual mineral particles, as well as faecal pellets, or large marine aggregates formed from a mixture of organic and inorganic (e.g., lithogenic) particles. Information provided from marine snow spans from the knowledge of whether the waters are productive (high concentrations of flocks resembling fresh organic matter), whether the production was effectively utilized (prevalence of faecal pellets and low transfer due to remineralization), or exported towards the sea-bottom (high sedimentation). Morphology of marine snow informs us about the structure of the planktonic community, but also about the potential of their functional regulation of the export of particulate matter (Accardo et al., 2024; Soviadan et al., 2024; Trudnowska et al., 2021). Our limited knowledge about particle and aggregate transport and transformation (Markussen et al., 2020), which is caused by the heterogeneous and fragile nature of aggregates (Durkin, 2025; Guidi et al., 2008; Iversen and Ploug, 2010) can now be resolved by underwater imaging (Siegel et al., 2025; Soviadan et al., 2024; Trudnowska et al., 2021, 2023; Turner, 2015).

Here we present a study focused on the compositional differences in marine snow over depth profiles, across various horizontal gradients in distinct melting seasons, set against the comprehensive physical and biogeochemical background in several different sites of the west Spitsbergen shelf.

2 Materials & Methods

2.1 Field work

The study was performed during two peak summer melt periods (August of 2022 – Cruise I and August of 2023 – Cruise III), and in spring time, before the main melting (May 2023 – Cruise II) in several locations along the west Spitsbergen (Hornsund, Rechercherfjorden, and Isfjorden) (Fig. 1). The sampling was designed to analyse small-scale gradients in biogeochemical properties and their relations to particles and plankton over: i) distance from marine-/land- based glaciers (Hansbreen vs Gashammna, ii) two branches of Isfjorden (Trygghamna, Ymberbukta), iii) land based with and without a lagoon (Recherchbreen, Renardbreen), iv) along the fronts of meltwater inputs (Hansbreen, Esmarkbreen), and v) between seasons (May vs. August).

The research was carried out from the sailing boat S/Y *Azimuth* to perform sampling and measurements as close to the glacier fronts as possible and without the substantial impact on water structuring that the large ships may have. At each sampling station, the vertical profiles of CTD equipped with temperature-conductivity-depth-chlorophyll fluorescence-oxygen sensors (manufactured by RBR Ltd., Ottawa, Canada) and a rosette equipped with six Niskin bottles (3.5 l, Hydrobios, Germany) were proceeding the vertical casts of the UVP6 (Underwater Vision Profiler, Hydroptic, France) and zooplankton collection with WP2 net (180um mesh size). Sediment flux measurements were conducted using sediment traps (KC-Denmark 110 mm tubes), deployed 5 meters above the bottom.

Samples for chemical analyses were collected from several depths: 1, 5, 15, 25, 50 m, and bottom water. The full set of studied biogeochemical parameters included: total alkalinity (AT), dissolved inorganic and organic carbon (DIC and DOC), concentration of chlorophyll a (Chla), dissolved macronutrients (nitrate - NO_3, nitrite - NO_2, ammonium - NH_4, phosphate - PO_4 and dissolved silicate - SiO_2), micronutrients – labile particulate Iron and Manganese (FeD, FeA, MnA, MnD), suspended particulate matter (SPM), particulate organic carbon and total nitrogen (POC and PTN), and their stable isotopic compositions ($\delta^{13}C$ and $\delta^{15}N$). All the water samples were collected according to the commonly used techniques, described briefly below.

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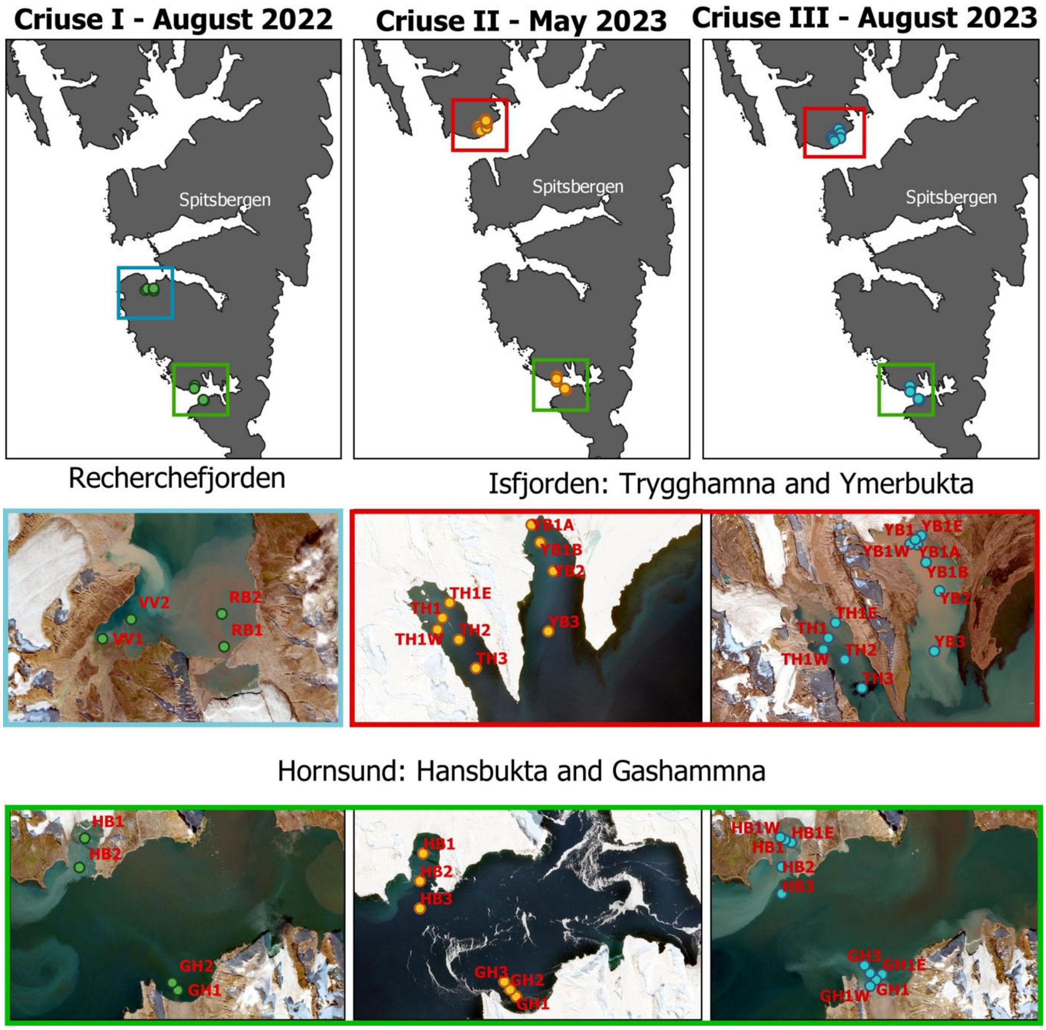

Figure 1. Maps of studied stations in various fjords (colours of the frames) during the three cruises (columns). Source: Sentinel3, processing: Qgis

2.2 Biogeochemical properties

Unfiltered water samples were collected in 250 mL glass bottles (avoiding gas exchange), preserved with 100 µL of saturated $HgCl_2$, and stored in the dark at 4 °C until analysis. DIC was determined using an automated DIC analyzer (Apollo SciTech

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Preprint. Discussion started: 20 May 2026

Inc.), equipped with a Li7815 CO_2 detector. AT was analyzed using an automated, open-cell potentiometric titration system (Dickson et al., 2007). Accuracy was verified using certified reference seawater (Scripps Institution of Oceanography, UC San Diego). Measurement precision was ±5 µmol kg^{-1} for DIC and ±4 µmol kg^{-1} for AT. Samples for DOC were filtered through pre-combusted glass fibre filters (pore size 0.4 µm) and acidified with 50 µL concentrated HCl. Then, samples were analyzed on the total organic carbon analyzer (TOC-L; Shimadzu Corp., Japan) equipped with an NDIR CO_2 detector. Precision of measurements was ±4 µmol/L (n = 5). Samples for particulate matter analyses were collected by filtering a known volume of water through pre-combusted, pre-weighed glass fibre filters (0.4 µm pore size) and stored at −20 °C until analysis. In the laboratory, filters were freeze-dried and weighed again to calculate SPM as the mass accumulated on the filter divided by the corresponding volume of water. Then filters were homogenized, weighed into silver capsules, acidified with 2M HCl to remove carbonates, and dried at 60°C for 24 h (the latter two steps were repeated four times). Analyses for POC and PTN concentrations and their stable isotopic composition ($\delta^{13}C$ and $\delta^{15}N$) were performed using an Elemental Analyzer Flash EA 1112 Series combined with the Isotopic Ratio Mass Spectrometer IRMS Delta V Advantage (Thermo Electron Corp., Germany). Quantitative measurements were calibrated against certified reference materials (Flußsediment) provided by HEKAtech GmbH (Germany) and yielded a precision better than 1.2% (n = 5). Isotopic measurements were corrected using IAEA standards—CO-8 and USGS40 for $\delta^{13}C$, and N-1 and USGS40 for $\delta^{15}N$.

2.3 Macronutrients

Samples for dissolved inorganic nutrient analysis (µmol L^{-1}) were collected using 60 mL syringes and immediately filtered through 0.45 µm cellulose acetate filters into 15 mL polypropylene tubes. All samples were stored frozen until laboratory analysis. Concentrations of dissolved nutrients, including nitrate (NO_3), nitrite (NO_2), ammonium (NH_4), phosphate (PO_4), and dissolved silicate (SiO_2), were determined using a SEAL AA500 AutoAnalyzer (SEAL Analytical) at the Institute of Oceanology, Polish Academy of Sciences, following standard colorimetric procedures (Saghravani et al., 2024). Method performance was verified through repeated analyses of certified reference materials (CRM RM-BU; National Metrology Institute of Japan, QC3179; Sigma Aldrich, and HAMIL; Environment Canada). Analytical accuracy exceeded 98.8% for all parameters, while precision, expressed as relative standard deviation, remained below 2%. Method detection limits were 0.006 µmol L^{-1} for NOx (NO_3 + NO_2), 0.003 µmol L^{-1} for NO_2, 0.045 µmol L^{-1} for NH_4, 0.012 µmol L^{-1} for PO_4, and 0.027 µmol L^{-1} for SiO_2. Nitrate (NO_3) concentrations were calculated by subtracting measured NO_2 from NOx.

2.4 Micronutrients: labile particulate Fe & Mn

Suspended particulate matter intended for selective sequential extraction was collected by filtering approximately 1 L of water sampled with a Niskin bottle through pre-weighed 25 mm polyethersulfone (PES) membrane filters (0.45 µm pore size). After filtration, filters were rinsed with ultrapure water (Milli-Q) to prevent sea-salt recrystallisation, air-dried, and stored in Petri dishes until analysis. The exact volume of filtered sample water was recorded for each sample.

Sediment-bound Fe and Mn were sequentially extracted using ascorbate solution (FeA, MnA) to dissolve highly reactive, poorly crystalline phases such as ferrihydrite and surface-bound Fe(II), together with associated poorly crystalline Mn oxides and phosphate, followed by a dithionite solution (FeD, MnD) targeting more crystalline and aged Fe-(oxy)hydroxides together with crystalline Mn oxides (Hawkings et al., 2018; Lenstra et al., 2021; Raiswell et al., 2010; Stachnik et al., 2025). Following each extraction step, samples were centrifuged and filtered (0.22 µm pore size, PES filters), diluted 1:10, and acidified prior to Fe and Mn determination by ICP-OES (Spectro Geneis). Limits of detection were 2 µg L^{-1} and 4 µg L^{-1} for Fe in the ascorbate and dithionite solutions, respectively, and 0.4 µg L^{-1} for Mn in both extraction steps. Procedural blanks were at or below detection limits.

2.5 Particles and Plankton

Sediment trap material was collected after 24 hours of deployment and filtered on Whatman GF/F 0.7 um filters (47 mm diameter, filters were previously dried in an oven at 200 °C for 2 hours and then weighed using a precision scale with an accuracy of 0.001 grams). After filtration, the filters were dried at 40 °C for 24 hours and then placed in a desiccator before being weighed again. The sediment weight is determined by calculating the difference in the dry weight of the filter before and after filtration. The daily sediment deposition is calculated by dividing the obtained sediment weight by the area of the tube and the duration of the deployment. The relative role between mineral and organic parts is determined as loss of ignition. Samples for chlorophyll *a* (Chl a) determination were filtered under low vacuum onto 25 mm Whatman GF/F filters (0.7 µm nominal pore size) and stored frozen (−20 °C) until analysis. Pigments were extracted in 96% ethanol for 24 h in darkness, and absorbance was measured using UV4-100 Unicam and Perkin Elmer Lambda 650 spectrophotometers. Chlorophyll concentrations were calculated following Strickland and Parsons (1972).

Samples for analyses of protistan plankton were collected from depths of 1–50 m. In 2022, samples were collected from discrete depth levels and analysed separately, yielding plankton composition and abundance expressed per m^3. In 2023, samples were collected from selected depths and integrated on board immediately after sampling, following the procedure described by (Dąbrowska et al., 2020) providing community structure expressed per m^2. To harmonise the results for the two-year analysis, plankton structure in 2022 was also presented per m^2 at the station level. Qualitative and quantitative analyses of planktonic protists were conducted using standard methods described previously (Dąbrowska et al., 2020; Kubiszyn et al., 2014, 2017), 200 mL subsamples were preserved in dark bottles with a mixture of acidic Lugol's solution and glutaraldehyde (1–2% final concentration), following recommendations for the preservation of fixation-sensitive taxa, including soft-bodied flagellates (Rousseau et al., 2007). Aliquots of 10–50 mL were transferred to sedimentation chambers and allowed to settle for 24 h prior to analysis. Protist cells were identified and enumerated using an inverted Nikon Eclipse TE-300 microscope equipped with phase-contrast and differential interference contrast optics. Microplankton (>20 µm) were counted over the entire chamber bottom at 100× magnification, whereas nanoplankton (3–20 µm) were enumerated at 400× magnification along three transverse transects. For the most abundant taxa, counting continued until at least 50 individuals had been recorded, with the number of examined fields adjusted as needed. Organisms were identified to the lowest possible taxonomic level and subsequently assigned to major taxonomic groups (class or phylum) according to the World Register of Marine Species (WoRMS).

The zooplankton were collected using a WP-2 net equipped with 180 µm mesh in three vertical tows, one from the sea bottom to 50 m depth, 50-10 m and the uppermost water layer (10–0 m). The zooplankton samples were preserved in 4% formaldehyde-in seawater solution, buffered with borax. The zooplankton identification and enumeration were performed under binoculars. Initially, the large (> 5 mm) zooplankters were picked out, counted, and identified to the lowest possible taxonomic level. Then the remaining part of the sample was examined for species composition and abundance in 2 ml subsamples. The number of subsamples was determined individually to count at least 300 individuals (Postel et al. 2000). Copepods were identified to species-specific copepodid stages, whereas nauplii were pooled together. Abundances of the whole zooplankton were expressed as a number of individuals per cubic metre (ind. m^{-3}) and then weighted per station as ind. m^{-2}.

2.6 Marine Snow

The concentrations and imaging of marine aggregates were assessed by the underwater imaging system - Underwater Vision Profiler (UVP) developed at the Laboratoire d'Océanographie de Villefranche-sur-Mer (LOV) and manufactured by Hydroptic (http://www.hydroptic.com/index.php/public/Page/product_item/UVP6-LP). In brief, UVP is the only intercalibrated camera-based device that counts particles in the size range between 80 and 2000 µm, and provides the images of objects larger than 700 µm within the illuminated volume of water (0,65 L (180 x 151 x 20 mm)(Picheral et al., 2021). Unfortunately, the water in August was too turbid at some stations and made UVP blind as it was overexposed to the particle density. Consequently, data from most turbid stations were discarded (mostly from Hansbreen).

First, all the vignettes taken by the UVP were uploaded to the Ecotaxa web application (https://ecotaxa.obs-vlfr.fr/), where their categorization was predicted automatically based on deep learning algorithms. Later, the results of this automated initial step were manually verified. Overall, 350 419 vignettes representing detritus were used for further analyses. The categorization into morphotypes was based on Principal Component Analysis (PCA, libraries "FactoMineR" and "factoextra" in Rstudio, of 24 morphological traits of which the coordinates within first four dimensions were clustered by the k-means method (Trudnowska et al., 2021, 2023). Consequently, four morphotypes named after their most prominent trait in their distinguishing were defined: *Large, Elongated, Light,* and *Dark* (Fig. 2). *Large* morphotype was definitely the largest, but also elongated and symmetrical in shape, quite dark and very heterogeneous. *Elongated* morphotype was first of all distinguished by the shape, they were also symmetrical but much smaller and darker than *Large* ones (Fig. 2). *Light* particles were small, rather circular and heterogeneous. *Dark* morphotype characterized the smallest particles, with the highest opacity and most solid and homogenous structure. Size is represented by the area, shape by elongation, vertical symmetry by 'symmetriev', lightness by the mean grey value, heterogeneity by the slope of the spectrum of grey level histogram, and structure assessed as skewness of the histogram of grey level values. Diversity of marine snow communities was calculated by package "vegan" in R based

215 on 100 categories made by an extra k-means clustering. The concentrations of marine snow were calculated over 5-m depth intervals for which the imaged volume of water was provided.

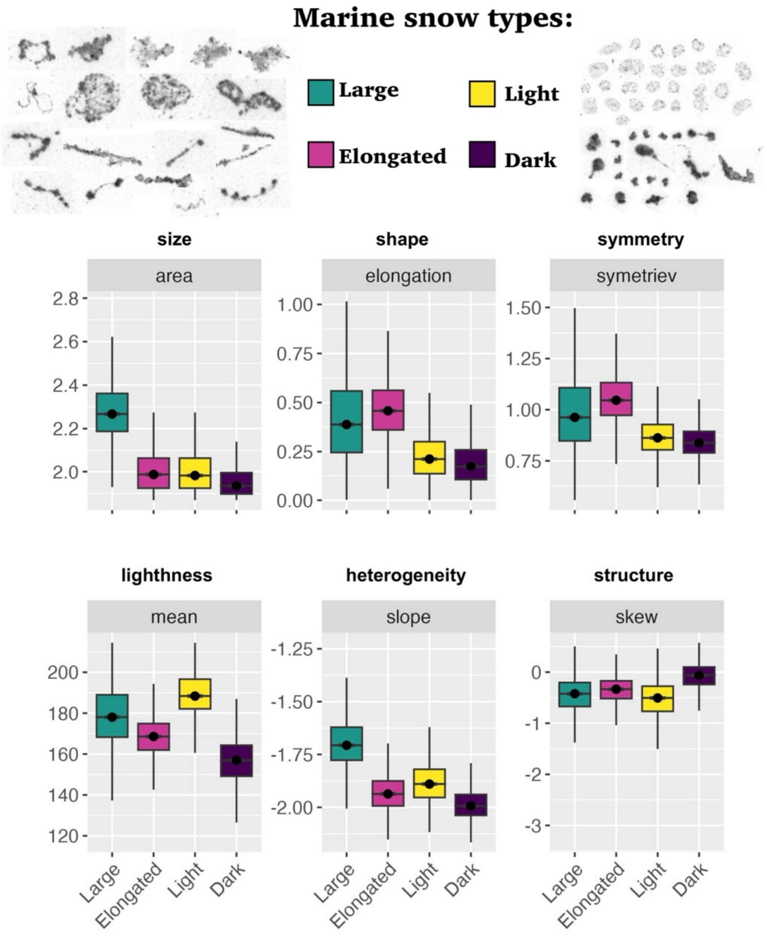

Figure 2. Morphotypes of marine snow: examples of the distinguished categories and most important morphological traits presented in boxplots of the mean and quartiles. Units are from image processing by Ecotaxa portal (e.g. size in log-transformed pixel values), the plots are to present the relative roles of selected 6 traits in characterising the distinguished morphotypes. 220

2.7 Statistical analyses

Permanova was used to analyse the importance of factors, such as season (defined by cruise), region (fjords and bays), and distance from the glacier/river source (stations coded as 1-2-3 along the studied gradients). The multivariate scaling was

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Preprint. Discussion started: 20 May 2026

performed on the holistic database consisting of 56 parameters, including hydrography (temperature, salinity, oxygen saturation, SPM, chlorophyll a), macronutrients (NH4, NO_3, NO_2, PO_4, SiO_2), sediment-bound micronutrients (FeD, FeA, MnA, MnD), biochemistry (AT, POC, DOC, DIC, PTN, $\delta^{13}C$ and $\delta^{15}N$), marine snow (concentrations of 4 morphotypes, total abundance of particles, their morphological traits: lighthness, size, shape, symmetry, heterogeneity, structure), protists (11 taxonomical categories), and zooplankton (10 taxonomical categories) at 40 stations that had a complete set of measurements. Furthermore, partial Redundancy Analysis (RDA) was calculated to test both the effects of all factors individually on marine snow, zooplankton, and protists, and to test effects of each group of factors separately. In these models, we removed the seasonal variation, by controlling the effect of cruise. Additionally, because too many predictors relative to samples and response variables were available, the number of environmental variables was reduced by removing the redundant factors that were highly co-correlated with others. After the forward selection, the step model was run on only significant predictors for which bar plots were made to present the percent of variance explained by factors selected as the most significant.

3 Results

3.1 Seasonal differences

There were striking differences in marine snow compositions between August and May (Fig. 3A). In both August campaigns, a dominating morphotype of marine snow were *Dark* aggregates, followed by the *Elongated* forms, while *Light* forms dominated in May, with substantial amounts of *Large* flocks (Fig. 3A). Compositions of marine snow slightly differed between years in August, with higher concentrations of *Elongated* morphotypes and presence of *Large f*orms in 2022 compared to 2023, which resulted in overall higher marine snow diversity in 2022 than in 2023. The sediment flux assessed by sediment traps was higher in August than in May (Fig. 3B) and more of mineral than organic origin (lower loss of ignition), however with high variance in both parameters across stations (Fig. 3B).

Zooplankton abundance was typically dominated by *Oithona* spp. and *Pseudocalanus* spp. in both years in August, whereas in May it was drastically dominated by naupliar stages of barnacles (Cyrripedia nauplii) and of copepods (Fig. 3C). *Calanus* spp. copepods were found in relatively high concentrations in August 2023. Appendicularians were abundant both in August 2022 and May 2023. The abundance of protists was drastically higher in August 2022, dominated by nanoflagellated taxa, mainly *Raphidiophyceae*, *Prymnesiophyceae*, and *Cryptophyta* (Fig. 3D). In contrast, in August 2023, the protist community was dominated almost exclusively by cryptophytes, a typical component of summer plankton communities in Svalbard. The lowest concentrations of protists were found in May, when the community composition was relatively diverse. Cryptophyta was the single protist dominant in August 2023.

Physico-biogeochemical properties differed between cruises, with the widest range of observed values in August 2023 (Fig. 3E). The most significant factors shaping the PCA scaling of all the parameters considered together were DIC, AT, temperature, SPM, and salinity along the first axis explaining 20% of variability; whereas the variability in PTN and POC was expressed along the second axis explaining 11% of variability (Fig. 3E).

In both years August was characterised by higher temperature, SPM, SiO_2, FeD, MnD, and lower salinity, AT, PO_4, DIC, POC, and PTN in comparison to May (Fig. 4). Differences between August 2022 and 2023 were observed in terms of the very low oxygen saturation, the highest chlorophyll concentrations, the lowest $\delta^{13}C$, high DOC, and much elevated levels of FeA and MnD, respectively. August 2023 was characterised by the lowest chlorophyll concentrations, DOC, NO_3, high concentrations of SiO_2 and the highest MnA.

May was cold, saline, highly oxygenated, with rather low chlorophyll concentrations, SPM and micronutrients, but elevated $\delta^{13}C$ and nitrates (NO_2, NO_3), and the highest AT, DIC, PO_4, POC, PTN (Fig. 4).

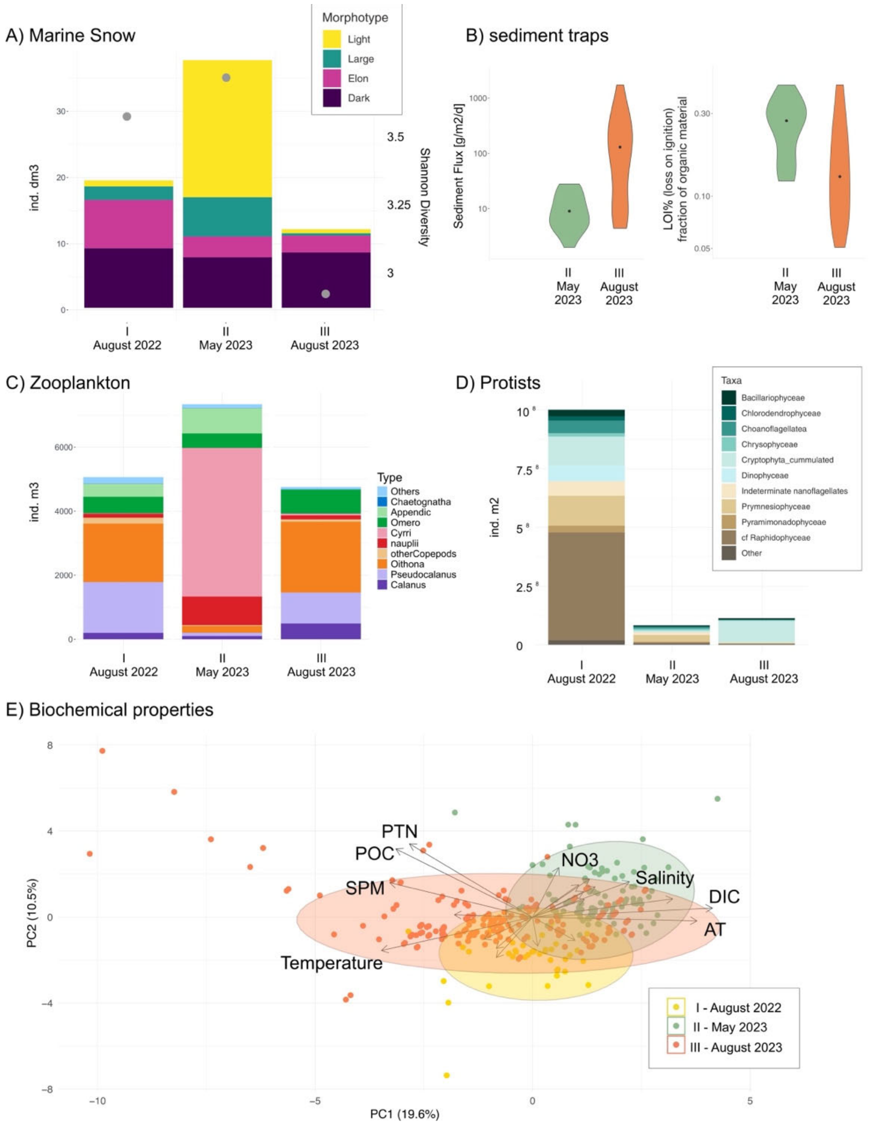

Figure 3. Seasonal (across three cruises) differences across marine snow morphocategories assessed by the underwater imaging (A), sediment traps (B), zooplankton (C), protists (D), and physico-biogeochemical properties (E), with a few most significant factors shaping the variability (AT – total alkalinity, DIC – dissolved inorganic carbon, NO_3 - nitrates, PTN - particulate total nitrogen, POC - particulate organic carbon, SPM - suspended particulate matter).

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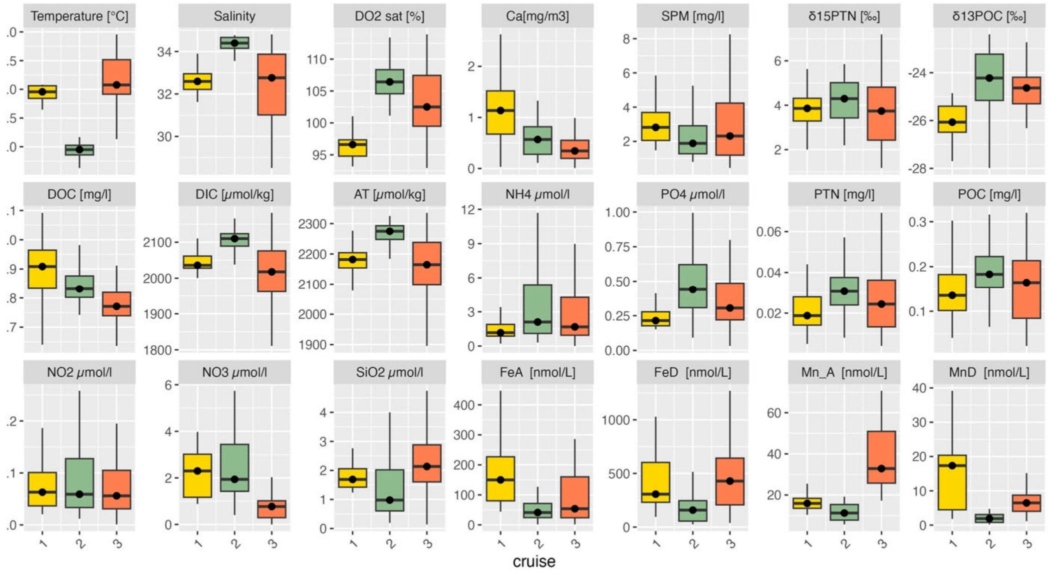

Figure 4. Box plots presenting medians and quartiles of physico-biogeochemical properties (hydrography, oxygen saturation (DO2 sat), chlorophyll a (Ca), suspended particulate matter (SPM), particulate organic carbon and total nitrogen (POC and PTN), and their stable isotopic compositions (δ^{13}C and δ^{15}N), dissolved inorganic and organic carbon (DIC and DOC), total alkalinity (AT), nitrates (NO_3), nitrites (NO_2), ammonium (NH_4), phosphates (PO_4), dissolved silicates (SiO_2), and labile micronutrients (FeD, FeA, MnA, MnD) across three cruises (1-August 2022, 2- May 2023, 3-August 2023).

3.2 Examples of the coupling between composition of marine snow, phytoplankton, zooplankton, and biogeochemical properties

3.2.1 Land- vs. marine-terminating glaciers: Hornsund, May 2023

At the study site under the influence of the river (GH) in Hornsund we observed an increase in marine snow concentrations along the distance from the source towards offshore (Fig. 5). The concentrations increased also with depth there, regardless of the morphotype. Temperature was low at each station (<0°C), slightly higher at GH3, where the lowest salinity was observed (Fig. S1). Chlorophyll slightly increased with the distance from the shore, and its maximum was observed at 10-20 m layer. The most distant station (GH3) had peaks of DOC, POC, NH_4, NO_3, SiO_2, and δ^{13}C while the elevated values of SPM, NO_2, δ^{15}N, FeD and MnD occurred in the surface waters of the most coastal station (GH1) (Fig. 5, S2). The abundance of protists slightly increased with a distance from the river outflow, with subtle compositional changes (Fig. 5). Because the GH1 station was shallow, the concentrations of zooplankton were mostly made of the benthic larvae. The expected trend of higher abundance towards more offshore waters was true for other zooplankton taxa (*Oithona*, *Pseudocalanus*)(Fig. 5).

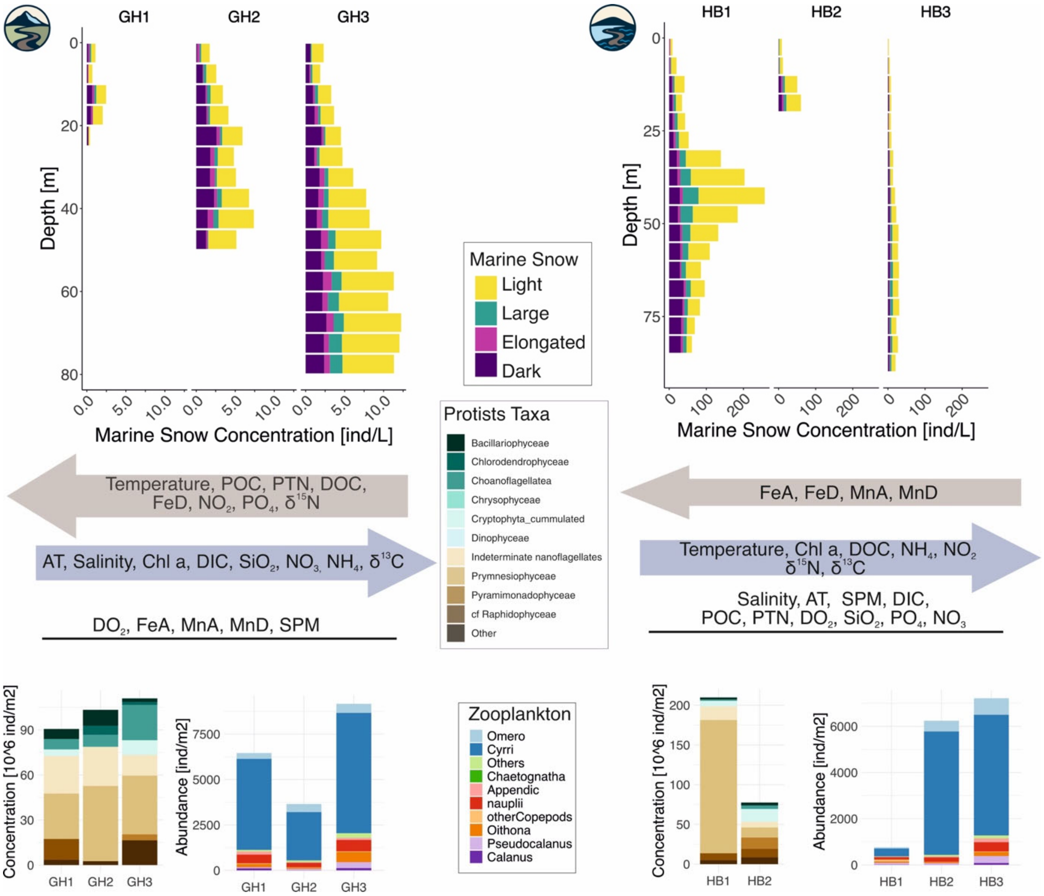

Figure 5. Example of the effect of the distance to the source between land-based (GH) and marine terminating glaciers (HB) in Hornsund in May 2023. Marine snow composition and concentrations over depth profiles at stations (upper bar plots). Biogeochemical properties: the increasing/decreasing trends simplified as arrows, list of parameters above the solid black line when there was no clear trend with distance. Lower bar plots: abundance and compositions of plankton over studied stations, with protists on the left side and zooplankton on the right side.

The opposite situation was observed near marine-terminating Hansbreen where the extremely high concentrations of marine snow were found close to the glacier front (HB1), while the concentrations were lower further out of the bay (Fig. 5). Marine snow concentrated within the mid part of the water column (approx. 30-40m), below the thermocline. Chlorophyll fluorescence was high across all the stations and concentrated above (10-15m) thermocline (Fig. S1). The near glacier HB1 station had

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higher concentrations of micronutrients, and in deeper layers high also elevated values of DIC, AT, and PO_4 (Fig. S2), whereas DOC, POC, $\delta^{15}N$, $\delta^{13}C$, NH_4, NO_2, NO_3 showed peak values towards fjord basin (HB3) (Fig. 5, Fig. S2). Higher variability in biogeochemical parameters was observed along the studied gradient in Hornsund, with overall slightly higher values of SPM, $\delta^{13}C$, NO_2, and micronutrients (Fe, Mn), whereas $\delta^{15}N$, DIC, and PO_4 and were slightly higher the at river-based plume (Fig. S3).

3.2.2 Land- vs. marine-terminating glacier: Isfjorden, May 2023

At the study site under the influence of the river in Tryghamna (TH, Isfjorden) the highest amount of marine snow found was close to the river outflow, especially below the thermohaline (15 m) and where the peak chlorophyll fluorescence occurred (Fig. 6A & Fig. S4). The chlorophyll concentrations decreased with distance, showing a kind of bi-modal vertical distribution pattern further offshore, with slightly elevated values at 15 m and then below 70 m (Fig. 6A). Temperatures lower than 0°C was observed at each station but with varying depths, starting from ~15 m at innermost TH1, at 30m at middle TH2, and at 50 m at outermost TH3 (Fig. S4). Chlorophyll fluorescence was low throughout all the profiles. Surface waters were close to the oxygen saturation level of the atmosphere, but deeper waters were oversaturated, indicating the influence of primary production at depth. Only micronutrients and PO_4 were higher near the river source, while few biogeochemical parameters showed a slight increase from the river towards the main basin (e.g. SPM, POC, PTN, $\delta^{15}N$), and most other did not show any horizontal gradients (Fig. 6A). The middle station TH2 was characterized by the highest DOC and POC (Fig. S5) and contained the highest concentrations of protists, dominated by Prymnesiphycea, but also high contribution of Chlorodenrynophycea (Fig. 5A). Zooplankton clearly increased from the most coastal station towards the main basin. As typically for May, zooplankton abundance was highly dominated by benthic larvae of Cirripedia, but nauplii stage of copepods as well as Appendicularians were also observed (Fig. 6A).

The concentrations of marine snow were much higher in the neighbouring branch of Isfjorden (Ymberbukta) where there is a marine-terminating glacier (Fig. 6B). Marine snow noncentrations were especially high towards the sea floor at two innermost stations and significantly decreased at the last YB3 station in the main basin of the fjord. Compositionally, marine snow was more dominated by the *Light* forms than in Tryghamna, where numerous *Dark* morphotypes were also found (Fig. 6B). Waters were very cold (mostly < 0°C), with no stratification observed at the last station (YB3), and a temperature gradient at 25 m inside associated with decreased oxygen below the thermocline, opposed to oversaturated Tryghamna (Fig. S4). A horizontal gradient in biogeochemical parameters was most visible for increased amounts of all micro- and macro-nutrients near glacier front (Fig. 6B, Fig. S5), which resulted in higher amounts of phytoplankton there, dominated by Chrysophycae and flagellates (Fig. 6B). The outermost station was characterized by the highest temperature, salinity, oxygen, DIC and $\delta^{15}N$, accompanied by the quite diversified protists community, including the Raphidophycea. Zooplankton was less dominated by larvaes of barnacles than in Tryghamna but rather by younger stages of copepods and Appendicularians. The amount of secondary production (nauplii of copepods) was the highest at the glacier front (Fig 6B).

Overall, no clear differences between those two basins were observed in terms of biogeochemical parameters, but occasionally higher values of NH_4, MnD, and NO_2 were observed in a fjord with the influence of marine-terminating glacier (YB), while higher PO_4, POC and PTN, levels were found in a fjord with the influence of the river (TH) (Fig. S6).

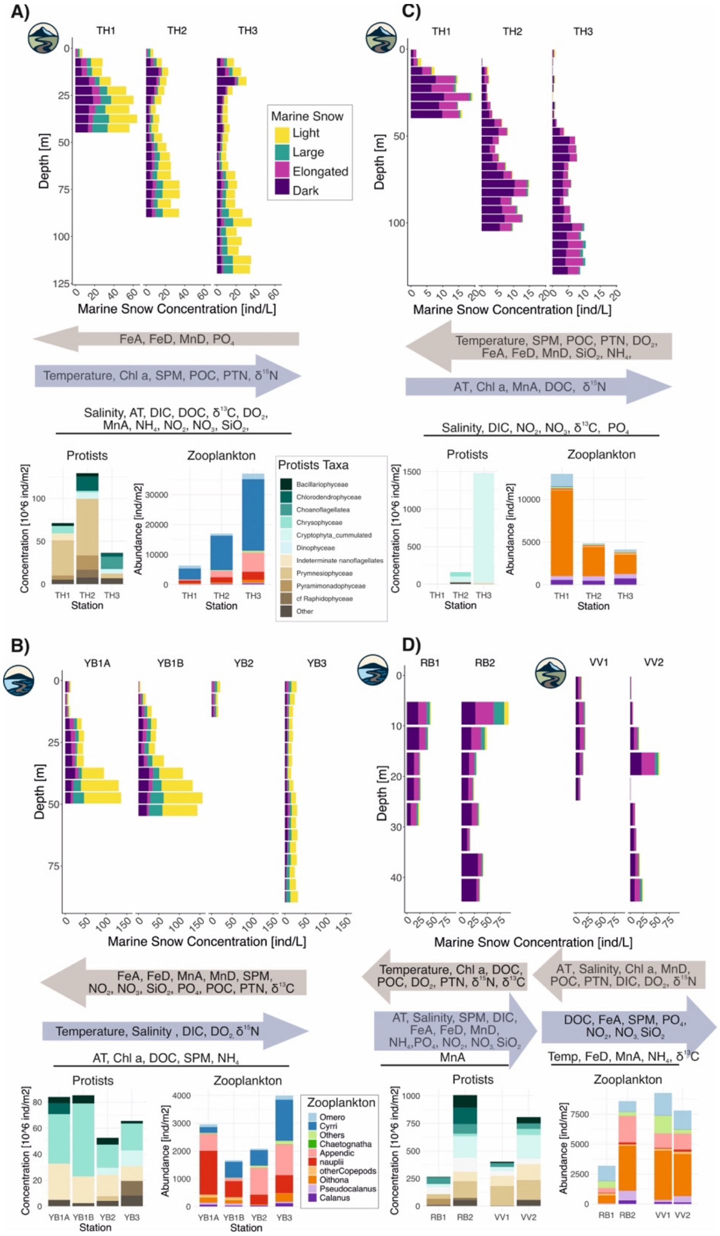

Figure 6. Examples of the comparisons between land-based (A) and marine terminating (B) glaciers in Isfjorden in May 2023, between seasons in Tryghamna (TH; Isfjorden: May (A) vs. August 2023 (C), and between lagoon (RB) and land-

based glaciers (VV) in Recherchefjorden in August 2022 (D). Marine snow composition and concentrations over depth profiles at stations (upper bar plots), biogeochemical properties: the increasing/decreasing trends simplified as arrows, while no clear trend with distance – list of parameters above the solid black line. Abundance and compositions of plankton at studied stations: lower bar plots, protists on left side, zooplankton on right sides of sub-panels.

3.2.3 Seasonal difference of land-based glacier impacts on Isfjorden

The concentrations of marine snow were much lower in August than in May, and represented by very different morphotypes – totally dominated by *Dark* and *Elongated* forms in August, and the absence of *Light* and *Large* morphotypes that dominated in May (Fig. 6AC). Vertical pattern, with the accumulation of aggregates below the thermal stratification was very similar, with the difference that during August surface concentrations were extremely low (Fig. 6C). Hydrography also differed, waters got much warmer (up to 10 °C) and less saline (<30) near the surface in August. Thermal stratification was accompanied by the salinity gradient at a depth of ~15 m, similar to spring (Fig. S7). Although chlorophyll concentrations were three times higher in August, this was not reflected in O2 saturation, which was comparable in both seasons, with deeper waters supersaturated with O2 and a decrease in O2 concentrations towards the surface related to the influence of water-atmosphere gas exchange (Figs. S5 & S7). Horizontal gradients also differed between the seasons, because many more parameters than micronutrients and phosphates, as observed in spring, showed elevated values near the river outflow (e.g. SPM, POC, PTN, SiO_2, NH_4) in August (Fig. 6C). Protists composition and concentrations were also vastly different between the seasons – with the observation of exceptionally high (4.14 x 10^9 cells m-3) abundance of Cryptophytes in August at TH3. Zooplankton also shifted the compositional structure – towards the dominance of the *Oithona* spp. in late summer (Fig. 6C). The late summer situation was characterized by higher SPM, SiO_2, FeD, and MnD, while the spring was characterized by higher $\delta^{13}C$, DIC, AT, NO_3, NH_4, PO_4, PTN, POC (Fig. S8).

3.2.4 Lagoon-based vs. land-terminating glaciers: Rechercherfjorden, August 2022

Marine snow was slightly more abundant in front of the glacier-fed lagoon than in front of the river (Fig. 6D), and compositionally it was similar to other stations studied in August (Fig. 6C). The two further stations (RB2 & VV2) had similar hydrography with warm (>5°C) and less saline (<33) waters in the upper layer, but stratification was approximately 5 m deeper at RB2 than at VV2 stations, and below this the concentrations of nutrients increased (Fig. S9). Chlorophyll profiles differed between the innermost stations. A homogenous vertical structure was observed near the river and elevated values were observed near the surface next to the lagoon. A significant increase with depth was observed at RB2 station of most of the biogeochemical parameters (e.g., AT, DIC, SPM, NH_4, PO_4, NO_2, NO_3, SiO_2, FeD)(Fig. S9). On average, the stations closer to the land (RB1, VV1) had elevated Chl a, POC, DO_2, PTN, $\delta^{15}N$, and the one closer to the lagoon had higher DOC and $\delta^{13}C$, whereas the station closer to the river source had slightly higher AT, DIC, and MnD compared to the more distant station (Fig. 6D). The lower concentrations of protists were observed at both of those coastal stations, and they slightly different compositions (e.g., more Prymnesiophycea and other nanoflagellates near the river (VV1 station at Fig 6D)). Zooplankton abundance and composition was very similar across the Recherchefjorden, with the only exception at the station in front of the lagoon, which was much more depleted in larger copepods (*Pseudocalanus* spp., *Calanus* spp.) and Appendicularians. Comparisons of those two pairs showed that the stations nereast the river had slightly elevated DOC, DIC, AT, PO_4, NO_2, NO_3, SiO_2 compared to the lagoon facing stations which had higher SPM, $\delta^{13}C$, and FeD (Fig. S10).

3.2.5 Along glacier fronts gradients

The distribution of marine snow had a very consistent pattern along the front of the Hansbreen with the concentrations of aggregates peaking at each station at very similar water layers (35-45 m) (Fig. 7A). Most of the biogeochemical parameters did not differ along the glacier terminus, but the central part of the glacier (HB1) was the main source of macronutrients, DIC and increased total alkalinity, with the highest abundance of protists, represented by Prymnesiophycea. However, the central station contained slightly lower concentrations of zooplankton, POC, PTN and NH_4 than the side stations. A distinct protist community was observed at the western station (HB1W), where zooplankton abundance was the highest (Fig. 7A).

In Trygghamna, the central TH1 station, which is much deeper than the side stations, had the highest concentrations of marine snow, concentrated below 20 m depth, regardless of the season (Figs. 7A&B). The shallower side stations had lower concentrations of marine snow with mixed vertical patterns. For example, the peak abundance near the surface at TH1W station in August comprised different morphotype composition than the ones at the central and eastern stations (Fig. 7B). In both seasons the central station had slightly higher salinity, DIC, NO_2 and $\delta^{13}C$ and lower temperature, SPM, FeD, MnA and $\delta^{15}N$. Also, in both seasons the concentrations of protists increased from western to eastern part. The concentration increase in May was also associated with compositional differences among the stations, with more taxa observed at the eastern side (TH1E). In August, due to the high load of suspended particulate material, only microplankton could be identified with confidence and it was dominated by tintinnids, particularly *Tintinnopsis turbo* and *T. beroidea*, while other abundant taxa included the oligotrich ciliates *Strombidium* spp. and *Lohmanniella oviformis*, as well as the dinoflagellate *Lebouridinium glaucum*. Zooplankton showed opposed patterns between the seasons, with the lowest abundances at the central station in May, and the highest in August., but compositionally showed consistent patterns across those small spatial scales (Fig. 7B&C).

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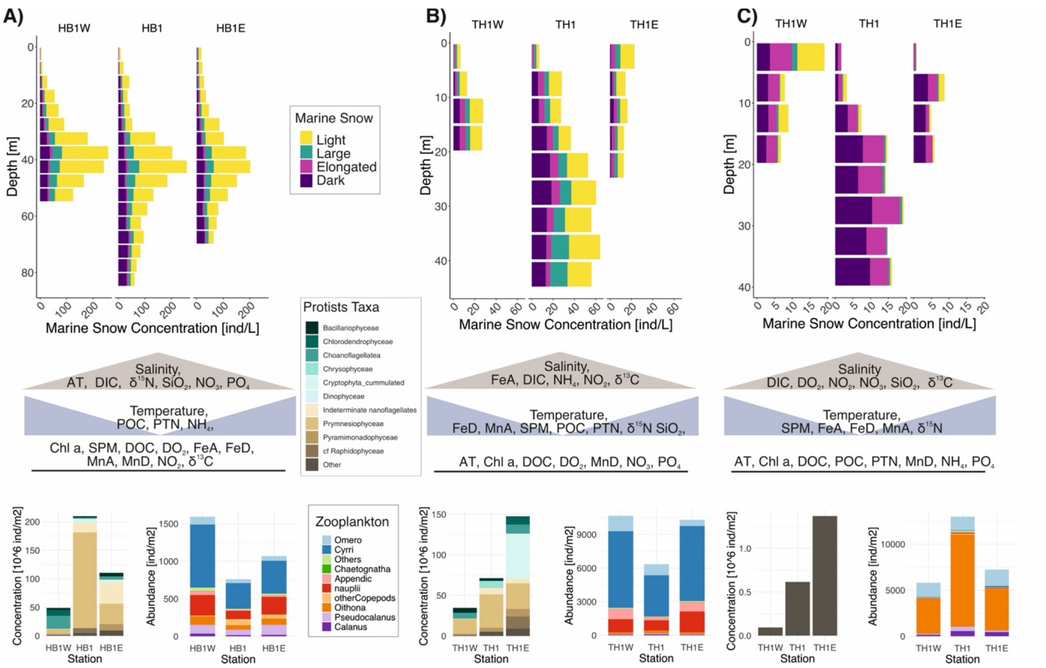

Figure 7. Examples of the stations spread along the marine terminating glacier in Hornsund in May (A), and in front of the rivers outflow in Trygghamna in May (B) vs. August (C). Marine snow composition and concentrations over depth profiles at stations (upper bar plots), biogeochemical properties: the increasing/decreasing trends simplified as the shapes of triangles, while a list of parameters with no clear trend above the solid black line. Abundance and compositions of plankton at studied stations: lower bar plots, protists on the left sides, zooplankton on the right sides of sub-panels.

3.3 Multidimensional scaling

By exploring the large variation of small-scale variability and the examples how each fjord and even each bay presents specific environmental conditions hosting various marine snow and plankton compositions and shaping various distribution patterns, no clear statistical relations were expected. Moreover, the multivariate scaling of the bulk dataset showed mostly the very strong seasonal effect (Fig. 8). Spatio-temporal structure explained most of the biogeochemical variability assessed (77% of variance in Permanova analysis). This holistic scaling of all the parameters showed that temporal effect of sampling campaign (cruise) was most significant factor (Permanova: 29%, p=0.001), followed by the spatial effect of fjord (12%, p=0.001) and distance to the meltwater source (5%, p=0.001), while glacier type (marine- vs. land- terminating) had the smallest effect (4%, p=0.003).

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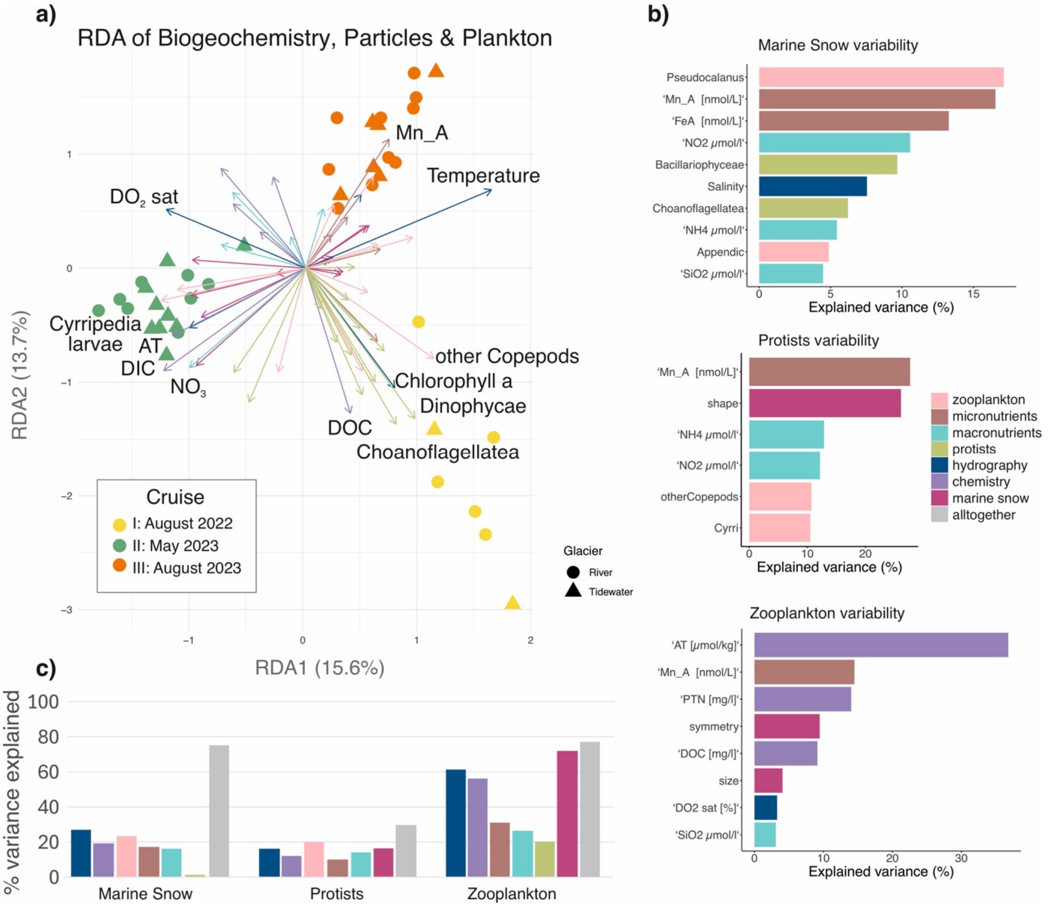

Figure 8. Results of Multivariate Redundancy Analyses (RDAs), a) scaling of 56 parameters, including hydrography (temperature, salinity, oxygen saturation, SPM, chlorophyll a), macronutrients (NH4, NO_3, NO_2, PO_4, SiO2), labile micronutrients (FeD, FeA, MnA, MnD), biochemistry (AT, POC, DOC, DIC, PTN, δ13C and δ15N), marine snow (concentrations of 4 morphotypes, total abundance of particles, their morphological traits: lightness, size, shape, symmetry, heterogeneity, structure)), protists (11 taxonomical categories), and zooplankton (10 taxonomical categories) at 40 stations that had a complete set of measurements. Arrows are color-coded according to the type of the factor and 12 most impactful parameters are labelled; b) bar plots present individual most significant factors in partial RDA which was calculated separately for marine snow, protists, and zooplankton. In these models, seasonal variation was removed, by controlling the effect of Cruise. c) bar plots present the portion of variance explained in RDAs models performed separately for marine snow, protists, and zooplankton and separately for the groups of factors.

After removing seasonal effect in forward selection of partial RDA, marine snow variability was significantly correlated with *Pseudocalanus*, micronutrients (Mn, Fe), nitrates, and diatoms as the main individual predictors selected for best relations with marine snow morphology and abundance (Fig. 8B). This model, including all types of explanatory factors, was very strong, explaining 75% of the total variation. When separate models were run for sets of parameters, their individual powers were much lower with the least correlation with protists (1%) and the highest with hydrography (27%) (Fig. 8C). The significance levels of the RDA models were low for protists, either for the full set of parameters (9%), in which MnA, shale of marine snow, some macronutrients and zooplankton were best correlated, or when groups of factors were tested individually (10-22%)(Fig. 8C). When analysing community composition of zooplankton, partial RDA selected AT, MnA, PTN, shape of marine snow (symmetry & size), and DOC as factors best correlated (Fig. 8B). The model, considering all the parameters, explained 77% of the total variation in zooplankton community composition, and separately also marine snow, hydrography and chemistry were also strong predictors (56-72%).

4 Discussion

How the melting of glaciers impacts coastal Arctic marine biogeochemistry with both desirable and undesirable components and/or dilutes the seawater is a broad and widely studied topic that has yielded numerous, yet variable, conclusions over the regions and years (Demidov et al., 2024; Halbach et al., 2019; Hop et al., 2023; Hopwood et al., 2020; Juul-Pedersen et al., 2015; Kanna et al., 2018; Lydersen et al., 2014; Meire et al., 2017; Oliver et al., 2023; van de Poll et al., 2021; Stuart-Lee et al., 2023; Vonnahme et al., 2025). This study addresses an important knowledge gap by zooming in this complex paradigm. Depending on glacier type, fjord topography, and season, markedly different processes, states and consequences are observed. Therefore, rather than forming a single uniform pattern, the observations resemble a mosaic of local situations, each shaped by a different combination of a suite of parameters and ecosystem components assessed by fine-scale, high-resolution, and highly interdisciplinary investigation over various spatio-temporal scales.

4.1. Marine Snow – vehicles of matter and knowledge

The few studies that analysed the composition of marine snow populations based on their morphotypes advocate that those aggregates are not only the vehicles of matter but also carry knowledge about the biophysical state of the pelagic ecosystems functioning (Accardo et al., 2024; Durkin et al., 2021; Song et al., 2025; Soviadan et al., 2024; Trudnowska et al., 2021, 2023). Here we also highlight their role as agents linking biogeochemistry with plankton activity.

The composition of marine snow populations clearly reflected seasonality, with very different dominating morphotype in spring (*Light*) compared to late summer (*Dark* & *Elongated*). The *Dark* morphotype has been shown to dominate in the summer during peak glacier melting conditions (Trudnowska et al., 2023), Zielińska et al. under rev). This morphotype is considered to contribute most to vertical export of carbon (Trudnowska et al., 2021), with sinking rates even faster if ballasted by mineral particles (Iversen and Ploug, 2010; Iversen and Robert, 2015; van der Jagt et al., 2018; Many et al., 2019; Passow and De La

Rocha, 2006; Ploug et al., 2008). Lithogenic minerals may not only make those particles heavier but also may slow the degradation of POC, and serve as adsorption surfaces for DOC (Hedges et al., 2001; Lamborg et al., 2008). The average amount of *Dark* morphotype was very similar among the three cruises so the differences in marine snow community compositions were shaped by the occurrence of other morphotypes.

Light flocks that dominated in May may represent the fresh aggregates of decaying phytoplankton but they could also have been formed by glacial flour flocculation during meltwater mixing with saline waters ((Trudnowska et al., 2023); Zielińska et al. under rev), indicating that marine snow may serve as an early signal of the transition to the meltwater and associated sediment production period. Despite being larger in size, *Light* flakes have been suggested to be less efficiently exported than small dark dense and heavy particles because of their light structure (Soviadan et al., 2024; Trudnowska et al., 2021).

The two August sampling periods differed in terms of structuring of marine snow, with much lower diversity in August 2023 than in 2022, mostly caused by the lack of *Large* forms. This suggests that formation of *Large* morphotype needs specific conditions. Particles may get aggregated by physical forcing as for example brownian motion, laminar or turbulent shear (Burd and Jackson, 2009; Jackson, 1995; Jackson and Burd, 2015; Takeuchi et al., 2019), but also by biologically mediated mechanisms as for example some phytoplankton species may attach to and thus stabilize flocs. Coagulation occurs when both particle concentrations and stickiness are high. Stickiness is typically caused by gel-like transparent exopolymer particles (TEP) that are the outcome of sugar-rich phytoplankton exudates (Amadei Martínez et al., 2025; Engel et al., 2002; Ingri et al., 2004; Jackson, 1995). Recently it has been found that two types of TEP exist: a more reactive and labile fraction - “fresh TEP” and a less reactive, refractory fraction “mineral- associated TEP” and that their roles may differ between the seasons (Fettweis et al., 2022). Maybe the influence of other TEP types may explain a drastic difference in marine snow appearance between the seasons.

The *Elongated* morphotype has typically been found to correlate with chlorophyll *a* (Accardo et al., 2024)(Zielińska et al. under rev) and has been found during the early phases of the bloom (Soviadan et al., 2024; Trudnowska et al., 2021). Thus, they are assumed to present aggregated chains of phytoplankton rather than faecal pellets of the zooplankton (Soviadan et al., 2024; Trudnowska et al., 2021, 2023). The highest importance of the *Elongated* forms found in August 2022 coincided with still highly abundant protists, including diatoms. The termination of a diatom bloom is frequently viewed as a single event of rapid diatom aggregation, triggered when nutrient limitation causes bloom senescence, and subsequent sedimentation of carbon-rich, fast-sinking diatom aggregates (Alldredge and Gotschalk, 1988; Romanelli et al., 2024; Smetacek, 1985). However, the clear determination of their origin is challenging, especially in the view of numerous specific forms of this morphotype (Fig. 9). It definitely needs further investigation to understand the mechanisms creating such beads of matter on a string. Also, contrary to open ocean studies in which *Elongated* forms were observed almost only in surface waters, and suggested not to be efficiently transported towards sea-bottom in this form (Accardo et al., 2024; Soviadan et al., 2024; Trudnowska et al., 2021), in this study they were common also at deeper layers of the Arctic fjords, which has also been reported in other study (Trudnowska et al., 2023).

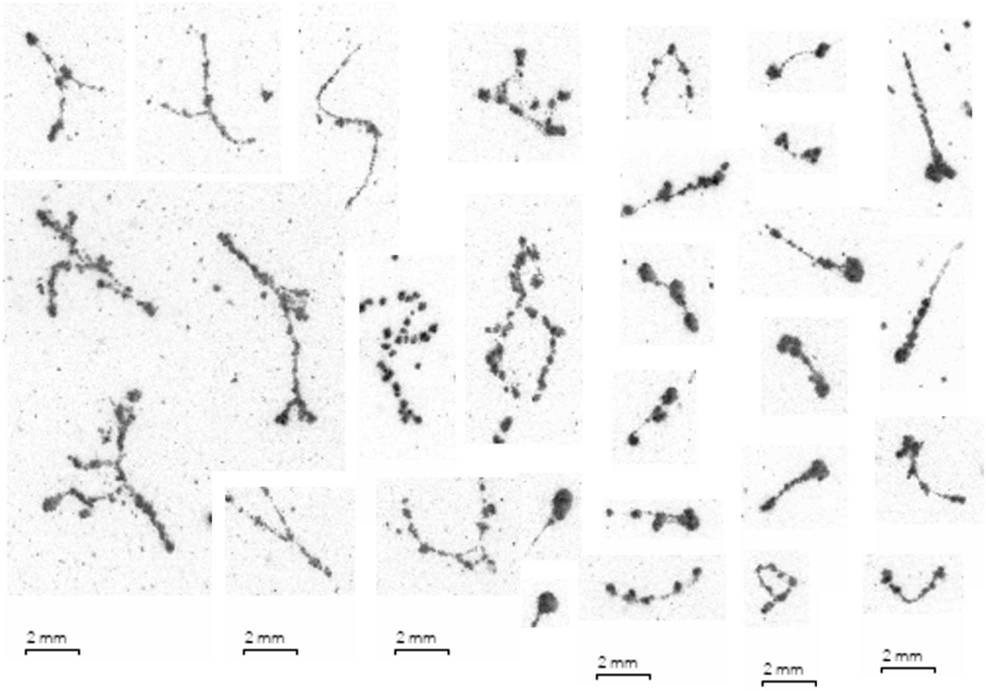

Figure 9. Examples of marine snow with beats of matter attached to the *Elongated* forms.

4.2. Seasonal context

While the summer season is the most crucial in terms of the impact of glacier melting, the pre-melting but already productive phase in spring is also important to get a broader perspective of glacier influence on coastal ecosystems. At the same time, including different seasons introduces substantial variability into the dataset, as spring and summer can be regarded as distinct physico-biogeochemical regimes (Dąbrowska et al., 2025; Gattuso et al., 2023; Gluchowska et al., 2025; McGovern et al., 2020; Moskalik et al., 2018; Retelletti Brogi et al., 2019). The May observations most likely represent the pre-bloom conditions, based on the low phytoplankton concentrations, species composition, and low micronutrient and silicates levels (Fig. 3; Figs. S1, S2, S4, S5). Moreover, it was a time of still cold, highly oxygenated and saline water conditions, with high availability of macronutrients. Meanwhile, this season was massively loaded with *Light* forms of marine snow. Zooplankton was overwhelmingly dominated by the meroplankton, namely the Cirripedia - larvae of barnacles, which is typical for spring (Stübner et al., 2016; Weydmann-Zwolicka et al., 2021), but also with high abundances of nauplii of copepods indicating a synchronized recruitment pulse (Gluchowska et al., 2025), which must have been triggered by the phytoplankton activity.

Therefore, low protist concentrations may also reflect strong grazing pressure, one of the main controls on Arctic primary production alongside light and nutrient availability (Arrigo and van Dijken, 2015; Rysgaard et al., 1999).

Late summer cruises investigated generally warmer, fresher, more turbid, less oxygenated, and nutrient depleted conditions (Fig. 3). Protists, including phytoplankton, showed high variability throughout the study, with the greatest variability observed in August 2022, when numerous groups were present, including Bacillariophyceae, Prymnesiophyceae, and abundant Raphidophyceae (cf. *Heterosigma*). The raphidophyte component likely included Heterosigma-like cells, recognised by their numerous peripheral golden-brown discoid chloroplasts and the blackberry-like appearance typical of this genus after fixation. The observed morphotype closely matched the taxon illustrated by Dąbrowska et al. (2025) from Isfjorden and described by those authors as resembling Heterosigma. This interpretation is also consistent with the typical mid-summer bloom period of Heterosigma in cold-temperate coastal waters and with previous records from Svalbard.

Typically, protist communities become more heterogeneous towards the later part of the growing season, reflecting the natural succession of plankton groups (Assmy et al., 2023; Dąbrowska et al., 2021, 2025). In our case, Cryptophytes dominated at most stations in August 2023, which may reflect the advantage of small, motile cells under late-summer conditions, when nutrient concentrations are often reduced following seasonal drawdown. Their small size provides a favourable surface-to-volume ratio for nutrient uptake at low concentrations, while flagellar motility may facilitate exploitation of microscale gradients and shifts between microhabitats (*inter alia*, Kubiszyn et al., 2014, 2017). It shows that by August, escalating turbidity from meltwaters may severely constrain photic conditions, suppressing protistan biomass despite sustained nutrient availability (Dąbrowska et al., 2025). However, while micronutrients, silicates and phosphates were relatively high during that time, NO_3 was the lowest among the cruises, and its availability is expected to limit primary production across much of the Arctic (Popova et al., 2010; Tremblay et al., 2015). Differences between August 2022 and 2023 may have been caused by different timing of the spring bloom in both years because the beginning of the growth season determines which group dominates during the succession of the protist's community towards the end of the summer. Marine snow was also more diversified and more abundant in August 2022, especially due to increased concentrations of the *Elongated* forms. Zooplankton composition was very similar between August 2022 and 2023, dominated by the smaller copepods (*Oithona* spp., *Pseudocalanus* spp.), which is typical for late summer (Balazy et al., 2021; Gluchowska et al., 2025; Svensen et al., 2011). Those copepods are efficient exploiters of the dominating at that time ciliates and heterotrophic protists, but also of marine snow. Thus, this study, as others, present the transition of plankton communities from spring bloom exploitation by newly reproduced forms to autumnal reliance on regenerated production by holoplankton typical for late communities.

4.3. Case studies comparing marine-, land-, and lagoon- based glaciers

Types of glaciers and their melting impact vary from one fjord to another, influencing productivity and carbon fluxes in different ways. Long-term observations from Svalbard fjords demonstrate that glacier-influenced zones exhibit strong spatial variability in primary production, driven by meltwater-induced changes in light conditions, stratification, and nutrient availability (Dragańska-Deja et al., 2024). Moreover, by recessing onto the land, their roles will most probably be further modified (Demidov et al., 2024; Halbach et al., 2019; Hood et al., 2009; Hopwood et al., 2020; Ljungberg et al., 2026; Szeligowska et al., 2021). Typically, it is expected that marine-terminating glaciers are a better source of nutrients than rivers which rather dilute the rich oceanic waters but the results of this study show that rivers may also contribute to the elevated nutrient supply, e.g. in the case of phosphates (Figs. S3 & S6). This observation agrees with studies showing that macronutrient concentrations in Arctic rivers can be sometimes even higher than in glacier discharge (Holmes et al., 2012; Hopwood et al., 2020). With glaciers retreating onto land, the glacial meltwater will flow longer distances over land before getting into the fjord, which indeed may result in nutrient enhancement. In this way silicates and nitrates may additionally originate from bedrock weathering (Wan et al., 2021), while phosphates may originate from seabirds' guano contributing to the land-sea connection in nutrient loading (Dąbrowska et al., 2025; Zwolicki et al., 2013).

On the contrary, marine-terminating glaciers are often associated with upwelling of nutrient-rich deep waters (Meire et al., 2017; Oliver et al., 2023; van de Poll et al., 2021; Schmidt et al., 2025; Vonnahme et al., 2020). This may explain our observations of high concentrations of marine aggregates below the thermohaline and below the chlorophyll peak, which points toward the up-welling source of their supply rather than source from primary production, especially that some of them resembled benthic algae (Fig. 9). A similar situation, in which elevated chlorophyll *a* was associated with macroalgal debris, was reported by Kubiszyn et al. (2017).

Based on the measurements performed in May, we observed that the abundances of marine aggregates were indeed much higher in front of the marine-terminating glaciers than in front of the river outflows (Figs. 5&6). This was especially evident in Hornsund fjord in form of much higher concentrations of both marine snow and protists observed in front of Hansbreen compared to the Gåshamna. While zooplankton was almost absent near glacier front in May, station HB1 was a refugium for copepods (*Pseudocalanus* pp. and *Calanus* spp.) during both cruises in August (Fig. S11), confirming that glacier bays of Hornsund may serve as hotspots for secondary production (Trudnowska et al., 2014). The same was also the case in another marine-terminating system – YB in Isfjorden, where numerous nauplii of copepods were found at the innermost location. The interplay between the nutrients, protists and oxygen saturation indicate that there must have also been primary production ongoing in Ymberbukta (Figs. S4 & S5).

The common aspect between both river-influenced systems (TH and GH) was that marine snow concentrations increased with depth in both basins, and that they had higher contributions of *Dark* morphotypes than their marine-terminating counterparts. It is difficult to resolve why both neighbouring bays in Isfjorden contained totally different species compositions of protists and zooplankton, whether various advection might have played a role, or their various environmental settings due to glacier- vs river- impact could have shaped diverse plankton communities. For example, in Greenland fjords the advection of Atlantic waters was associated with increases in microplankton diversity (Vonnahme et al., 2025), which might be the case between Hansbukta and Gåshamna as located on opposite sides of Hornsund, they are under a different influence of an estuarine circulation potentially bringing different plankton communities.

Another interesting glacier recession state is a formation of a proglacial lake or lagoon (Ljungberg et al., 2026; Lukashanets et al., 2026; Wiedmann et al., 2025), which may serve as a catchment step delaying the delivery of terrestrial material to coastal waters, or even as the environmental strainer Based on our very limited, in this context, dataset from only one region it is difficult to decide whether the in Recherchefjorden acts as such a biogeochemical filter. However, because the difference with the neighbouring river-impacted stations was smaller than in other studied systems, it is likely that the lagoon somehow contributed to modifying, storing, and transforming meltwater constituents before they reached fjord.

4.4. Small-scales at outflows

Meltwater enters fjords through multiple pathways. It can be supplied as surface runoff, released as subglacial discharge, or produced through submarine melting. Each pathway affects fjord stratification and mixing in distinct ways (Hansen et al., 2025; Kanna et al., 2022b; Rooijakkers et al., 2025). The meltwater plumes provide not only fresh water supply but also elevated concentrations of some inorganic components which together affect seawater alkalinity (Fransson et al., 2015; Koziorowska-Makuch et al., 2023; Yde et al., 2014), silica (Meire et al., 2016) and iron (Kanna et al., 2020; Statham et al., 2008; Stimpfle et al., 2026) that either are immediately assimilated in front of the terminus, or are transported and diluted in more distant waters. In our case, the best 'indicators' of the influence of meltwaters were micronutrients, clearly showing that both marine- and land- based glaciers are the important but very local sources of them, which was also observed in Greenland (Kanna et al., 2020). Moreover, in most cases $\delta^{13}C$ was a good indicator in demonstrating the increase of the marine- origin of particulate organic matter over the studied horizontal gradients.

Unfortunately, very little direct observations at glacier fronts are available (Hansen et al., 2025). In Hansbukta, the plume of marine snow was spread over all three stations along the glacier terminus (Fig. 7A), whereas in Tryghamna the outflow seemed to be more streamlined through the middle deepest station, with less pronounced presence at the shallow side stations, regardless of the season (Figs. 7B&C). Therefore, our results show that the input may vary horizontally at the terminus depending on topography and water circulation patterns. Because the concentrations of marine snow and multiple biogeochemical parameters rather drastically decreased within a short distance from the source, this indicates that influence of river mouth/glacier front can be very local, as was also suggested before (Sejr et al., 2022; Szeligowska et al., 2021; Trudnowska et al., 2020; Zajaczkowski and Włodarska-Kowalczuk, 2007).

Moreover, the particles at the surface differed from the ones near sea bottom, indicating that the surface outflow is presumably creating a different microhabitat compared to the one at depth. In general, the vertical patterns differed among the stations, regardless of the glacier type and a distance from the outflow. At most of the stations, the concentrations of marine snow were observed to greater with increasing depth compared to surface which may be caused by upwelling, horizontal advection or become created by midwater physico-biogeochemical dynamics. Such vertical differentiation is consistent with observations that particle composition, size distribution, and mineral origin vary significantly within the water column of glacial fjords, affecting both light conditions and particle dynamics (Dragańska-Deja, 2024). Since sedimentation of phytoplankton-derived material is the primary food source for benthic organisms, pulsed flux out of surface waters could also potentially have an important impact on benthic animals reliant on this particle rain (Goldthwait and Alldredge, 2006; Trudnowska et al., 2026).

4.5 Holistic view

In Svalbard fjord systems, observed trends toward fresher, more turbid surface waters have been suggested to cause alterations in biogeochemical processes and ecosystem dynamics (Konik et al., 2021). Our study adds a number of other relations and factors important in shaping particles and plankton community structures. The striking result of the multivariate scaling of the factors and their relations was the high significance of ascorbate manganese in each model (Fig. 8). First of all, it can be interpreted by the fact that in general manganese was a parameter that had a strong seasonal signal, which correlated well with other seasonally-driven components. Moreover, manganese occurred mostly in the form of poorly crystalline oxides and phosphates (MnA), which could be potentially bioavailable.

Other important factors shaping the variance in the bulk dataset were also temperature scaling positively with stations from August 2023, AT, oxygen, nitrates, DIC and Cirripedia larvae scaling positively with stations sampled in May and some groups of protists and copepods with August 2022, showing that each sampling campaign was governed by different eco-biogeochemical-physical settings.

The relation between marine snow and *Pseudocalanus* has already been observed in waters of Svalbard (van der Jagt et al., 2020). Also other studies show that zooplankton, especially small copepods, can be an important determinant of marine aggregates size and transformations (Møller, 2005; Möller et al., 2012; Ohman and Browman, 2019; Svensen et al., 2024). Appendicularians, by producing and discarding mucus-like houses every few hours, and even more often in waters full of particles as their filtration systems quickly get clogged, can greatly contribute to the formation of marine snow (Deja, 2025; Gimenez et al., 2023; Goldthwait and Alldredge, 2006; Koski et al., 2007; Lombard and Kiørboe, 2010; Steinberg et al., 1994), which might have also been the case in some locations.

Significant relations between marine snow and iron, nitrites, silicates, ammonium, salinity and the presence of diatoms were also anticipated. Iron is mostly removed from the system by flocculation which may explain its highly significant interactions with marine snow (Boyd and Trull, 2007; Lund-Hansen et al., 2010; Markussen et al., 2016; Meslard et al., 2018; Schroth et al., 2014; Zhang et al., 2015). Thus, with increasing melting, higher iron supply may have a significant impact on particle flux, especially that aggregation of organic matter in high chlorophyll water was shown to scavenge dissolved iron, making it unavailable to phytoplankton (Stimpfle et al., 2026). However, with observed high local variations it is difficult to assess if the effect may extend with distance, or rather stay capsulated only near the source. While aggregation phenomena typically require biogenic organic matter and generally occur further offshore, the flocculation process is strongly controlled by the SPM and turbulence, as well as the salinity gradient. Fresh water is enhancing flocculation processes through the shifts in the ionic strength, and estuaries often show rapid flocculation where river water meets seawater (Kanna et al., 2022b; Markussen et al., 2016; Meslard et al., 2018; Ming and Gao, 2022). The flocculation process has largely been described in temperate estuaries where it controls the dynamics of fine particles, but the role of flocculation/aggregation phenomena in glacial environments is poorly documented. Most studies of marine snow seek for correlations between marine aggregates and chlorophyll *a* (Jackson and Checkley, 2011; Soviadan, 2024)Zielińska et al. under rev) which agrees with relations with productive waters in this study (nutrients and diatoms). Ammonium is typically found released from organic particles by remineralization (Karthäuser et al., 2021; Zehr and Kudela, 2011) which shows their contribution in controlling fjords nutrient budgets.

The statistical model for protists showed the expected association between their community structure with nutrients and the specific shape of marine snow. Zooplankton relations with AT can be explained by its high correlation with salinity. Whereas the relation with DOC and PTN may suggest that succession of zooplankton may be related to the state of the biogeochemical situation described by those parameters. Because ammonium and urea are major excretion products of zooplankton (Hernández-León et al., 2008), the correlation between NH_4 suggests active zooplankton grazing. It may contribute to the correlation between marine snow size and symmetry as interactions based on flocs of matter encapsuled in marine snow in the form of the zooplankton faecal pellets.

Overall, despite various statistically significant interactions found, we hold the previous conclusion that the influence of glacial meltwater on biological dynamics emerges from nonlinear interactions among multiple physical, biogeochemical, and ecological processes operating across various spatial and temporal scales (Hopwood et al., 2018).

4.6 Limitations

Even though this study applies a methodologically comprehensive and highly interdisciplinary approach across several glacial bays and over various stages of the seasonal cycle, it faces several limitations. As typically in field-based studies, more stations and higher temporal coverage could have strengthened the conclusions. We are fully aware that the results represent only snap-shots of conditions in a highly dynamic environment, therefore, our observations should be interpreted primarily within a narrow spatio-temporal context rather than broadly extrapolated to other systems or time periods.

We are also aware that advection was likely an important factor shaping the physical and biogeochemical conditions of the studied areas (Hunt et al., 2016; Pavlov et al., 2013; Strzelewicz et al., 2022; Vonnahme et al., 2025). For example, the presence of oceanic groups such as Phaeocystis or Choanoflagellatea along with fresh nutrient supply may be a good indicator of the recent advection. However, because it was not measured directly, its role can only be inferred indirectly and remains speculative based on biogeochemical properties or the occurrence of plankton taxa.

Furthermore, it would be of great additional value if future studies could also collect samples from the sources (directly from the river/glacier), before being diluted in the bays.

Nevertheless, these studies brilliantly demonstrate the high complexity of systems in the vicinity of meltwater inflows and glacier outlets, and that its complexity deserves integrated monitoring (Giudice et al., 2026).

4.7 Conclusions

1. Spring and summer present distinct environmental regimes, differing markedly in interactions between meltwater impact, biogeochemistry and productivity.

2. Except for the seasonal effect, no other common pattern emerged across glaciers and fjords – most biogeochemical and plankton-related parameters showed strong spatial variability, not clearly associated with glacier type.
3. Local heterogeneity is so prominent that even branches of the same fjord system may function as distinct environments controlled by different biogeochemical regimes and inhabited by contrasting plankton communities.
4. Marine aggregates act not only as carriers of organic and mineral matter, but also as valuable indicators of environmental conditions and ecological interactions in the water column.
5. Marine snow formation and characteristics are strongly linked to plankton composition and seawater biogeochemistry, while their morphological traits scales with plankton taxonomic structure.
6. This study highlights both expected relationships, such as those involving temperature and nutrients, and less obvious ones, including the role of manganese, in shaping interactions between seawater properties and suspended matter in glacier-influenced coastal waters.
7. Glacier-influenced coastal zones remain challenging to study because of strong physical dynamics, high spatial heterogeneity, and technical sampling constraints.
8. The interdisciplinary approach applied here represents a further step towards a holistic understanding of ecological connectivity and water-column functioning in glaciated fjords.

Code and data availability

https://essd.copernicus.org/articles/16/4511/2024/essd-16-4511-2024.pdf
https://dataportal.igf.edu.pl/dataset/spm_and_sedflux_hornsund

https://geonetwork.iopan.pl/geonetwork/srv/eng/catalog.search#/metadata/6b7f30f4-26b6-4033-977d-e91c9b1f9c5c

Author contributions

Conceptualization: ET, KKo, KKu, BSZ, ŁK, MM; Data curation: ET, KKo, AD, RB, BSZ, KDD, ŁK, JH, MeK, MaK, MM; Formal analysis: ET, KKo, AD, ŁK, JH, KDD, MK; Funding acquisition: ET, KKu, MM; Investigation: ET, KKo, KDD, ŁK, MeK, MaK, MM; Methodology: ET, KKo, AD, BSZ, KDD, ŁK, JH, MM; Project administration: KKu, MM; Visualization: ET, KDD, Writing (original draft preparation): ET, Writing (review and editing): all.

Competing interests

The authors declare that they have no conflict of interest.

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