Response to RC2

RC2: 'Comment on egusphere-2026-4192', Anonymous Referee #2, 24 Oct 2026

General comments

This manuscript examines phytoplankton communities, dissolved carbohydrates, and TEP in the Fram Strait and Kara Sea, combining biogeochemical measurements with 18S rRNA sequencing. The dataset is valuable, and the methods and figures are generally clear and sound.

My main concern is that the manuscript does not convincingly establish what is new compared with previous Arctic work on carbohydrates and extracellular polymeric substances (EPS). Much of the discussion is descriptive, while the proposed links between phytoplankton taxa, carbohydrate signatures, TEP formation, and carbon cycling are stronger than the evidence allows. Several analyses and a more critical engagement with the literature would be needed to support the central conclusions.

Response: We thank the reviewer for evaluating our manuscript and for acknowledging the value of the dataset and the clarity of the methods and figures. We have considered all comments carefully. We believe that an additional analysis of chl-*a*–carbohydrate relationships and an assessment of regional and environmental effects will further strengthen the communication of our central conclusions. Preliminary analyses indicate that DCCHO composition varies primarily with phytoplankton community composition, and to a lesser extent with biomass or environmental conditions, and thereby support the central conclusion of our study.

However, we respectfully disagree with the reviewer's assessment that the novelty of our study is not established. We here combine taxonomically resolved phytoplankton community composition (18S rRNA gene amplicons) with the molecular composition of dissolved combined carbohydrates and TEP from three contrasting sites in the Arctic Ocean (i.e., Fram Strait, Kara Sea, and Kara Sea River Plume). To our knowledge, this is the first such dataset for pelagic Arctic waters. Our study not only presents novel observations but also provides analyses that directly link variability in seawater DCCHO to phytoplankton community composition. Previous findings on sea-ice algae cannot be directly extrapolated to phytoplankton communities in the water column (see our responses below) and therefore do not diminish the novelty of our study. We appreciate, however, the reviewer's suggestion to better emphasize the novel aspects of our study, sharpen the presentation of the research gap and highlight potential limitations more clearly. Our detailed responses to the reviewer's comments follow below.

Major comments 1. Scientific novelty and previous Arctic studies

The manuscript needs to make a much clearer case for its scientific contribution. Carbohydrate and EPS production, their relationships with algal biomass, and microbial processing have already been investigated in Arctic environments (e.g., Aslam et al., 2012a, 2012b, 2016, 2018), among other studies. Although those studies focus largely on sea ice, they provide important context. The authors should in a first place acknowledge these studies and then go beyond this literature: what do the present observations actually add, and which results mainly confirm what is already known? This is, in my view, the most important weakness of the manuscript.

Response: We agree that the sea-ice studies by Aslam et al. provide relevant context, and we will acknowledge the most relevant papers in the revised Introduction and Discussion. However, multiple studies proposed by the reviewer (Aslam et al. 2012a, 2012b, 2016, 2018) focus on sea ice systems and are mostly experimental and their findings do not necessarily apply to pelagic systems. For instance, in bottom sea ice, carbohydrate concentrations scale linearly with chl-*a* (Aslam et al., 2016), whereas in pelagic systems DCCHO and chl-*a* have been shown to be decoupled (Engel et al., 2012; Sperling et al., 2017), which is also confirmed by our own data (see our response to comment 2). In the water column, phytoplankton biomass alone therefore does not explain carbohydrate dynamics, and community composition may play a more important role. To our knowledge, the relationship between phytoplankton community composition and DCCHO composition has not yet been examined in the pelagic.

Knowledge of taxon-specific carbohydrate release by pelagic phytoplankton comes almost exclusively from culture experiments (e.g., Aluwihare & Repeta, 1999; Urbani et al., 2005; Becker et al., 2014). Previous field comparisons of *Phaeocystis*- and diatom-dominated blooms addressed particulate organic matter (Jo et al., 2021; Misic et al., 2024) or bacterial communities (Skouroliakou et al., 2024). Field studies of dissolved carbohydrates either did not resolve the phytoplankton community or focused on single bloom events (Engel et al., 2012; Vidal-Melgosa et al., 2021).

To our knowledge, our study is the first to combine 18S rRNA-based community composition, DCCHO composition and TEP concentrations in a comprehensive field dataset across contrasting Arctic phytoplankton communities. Our data show that DCCHO concentrations differ between regions, which cannot be explained by water masses or depth alone, and our additional analyses indicate that DCCHO composition is related primarily to phytoplankton community composition rather than biomass or environmental conditions (see our response to comment 2). Furthermore, we compare two important Arctic phytoplankton groups, *Phaeocystis* and diatoms, under natural conditions, at a time when their relative importance is changing, as shown by the recent first observation of *Phaeocystis* colonies in the Kara Sea (Sergeeva et al., 2025). In doing so, we test whether taxon-specific carbohydrate signatures known from cultures are recognisable in natural pelagic communities, which cannot be inferred from sea-ice or culture studies alone.

We acknowledge that sea-ice melt can contribute organic matter to the pelagic system, especially at the ice edge. Our data indicate, however, that the DOM signatures we observed were dominated by pelagic phytoplankton production. The 18S community was dominated by pelagic taxa such as *Phaeocystis pouchetii, Chaetoceros* spp. and *Thalassiosira* spp., whereas typical sea-ice algae such as *Melosira arctica* and *Fragilariopsis cylindrus* contributed less than 1% of the reads in all regions.

In the revised Introduction, we will condense the general background on DOM release and carbon cycling (lines 36–59) and the hydrographic description of the Fram Strait and Kara Sea (lines 69–82). This will make more room to expand the description of the current state of knowledge, including the sea-ice studies discussed above. Furthermore, we will sharpen the research gap: a field-based assessment linking taxonomically resolved phytoplankton community composition to the molecular composition of dissolved carbohydrates and to TEP across three contrasting pelagic regions in the Arctic Ocean.

The Discussion already compares our findings with taxon-specific culture studies, for example the enrichment of rhamnose and arabinose in *Phaeocystis*-derived carbohydrates (lines 575–578) and glucose-rich carbohydrate release by *Thalassiosira* (lines 594–597). In the revision, each section will state more explicitly where our results confirm these findings and where they extend them to natural

pelagic communities, and a separate section will address the limitations of our observational approach (see also our responses to comments 3 and 4).

2. Phytoplankton biomass and dissolved carbohydrates

The relationships between chl-α and dissolved carbohydrate concentrations are not sufficiently examined. The multivariate analyses (Figs. 3B and 7) are useful, but direct correlations with total DCCHO and individual monosaccharides would help determine whether observed patterns reflect phytoplankton biomass, changes in carbohydrate composition, or other environmental controls. These analyses appear feasible with the existing dataset.

Response: We thank the reviewer for this suggestion and agree that direct correlations would complement the multivariate analyses already presented (Figs. 3B and 7). We have now calculated these correlations for total DCCHO as well as for individual monosaccharides. To address the reviewer's question more comprehensively, we additionally performed a variance partitioning analysis to quantify the relative contributions of biomass, community composition, environmental variables and region to carbohydrate composition. Preliminary analyses indicate that DCCHO composition reflects phytoplankton community composition more strongly than biomass or environmental conditions, and that region does not explain any variation beyond these factors. A summary is given below.

Biomass and total DCCHO. Within regions, chl-*a* was not significantly related to total DCCHO concentrations (Fram Strait: r_s = 0.31, p = 0.056, n = 38; Kara Sea: r_s = 0.17, p = 0.43, n = 24). This is consistent with the decoupling of DCCHO and chl-*a* reported for pelagic systems (Engel et al., 2012; Sperling et al., 2017) and contrasts with the close coupling observed in bottom sea ice (Aslam et al., 2016).

Biomass and individual monosaccharides. Chl-*a* was, however, significantly correlated with specific monosaccharides (Spearman, Benjamini–Hochberg corrected), and these differed between regions. In the Fram Strait, chl-*a* correlated positively with arabinose, rhamnose and glucuronic acid, both in concentration and mol%, and negatively with amino sugars. In the Kara Sea, chl-*a* correlated positively with the relative contribution of glucose (Fig. R1, see our response to Reviewer 1).

Relative contributions of biomass, community composition, environment and region. Variance partitioning based on redundancy analysis (adjusted R^2) for the Fram Strait and the Kara Sea (n = 61) showed that chl-*a*, community composition, environmental variables and region together explained 43% of the variation in DCCHO composition (p = 0.001; Fig. R2). Community composition explained the largest unique fraction (10%, p = 0.001), whereas chl-*a* (2%, p = 0.051) and environmental variables (4%, p = 0.045) contributed smaller unique fractions, and region explained no unique variation (p = 0.63). Although chl-*a* and region alone explained 12% and 23% of the variation, respectively, these fractions were largely shared with community composition. These results indicate that carbohydrate composition reflects primarily phytoplankton community composition, and only to a minor extent biomass or environmental conditions. In the revised manuscript, these analyses will be presented in a new figure and discussed in a reorganised Discussion.

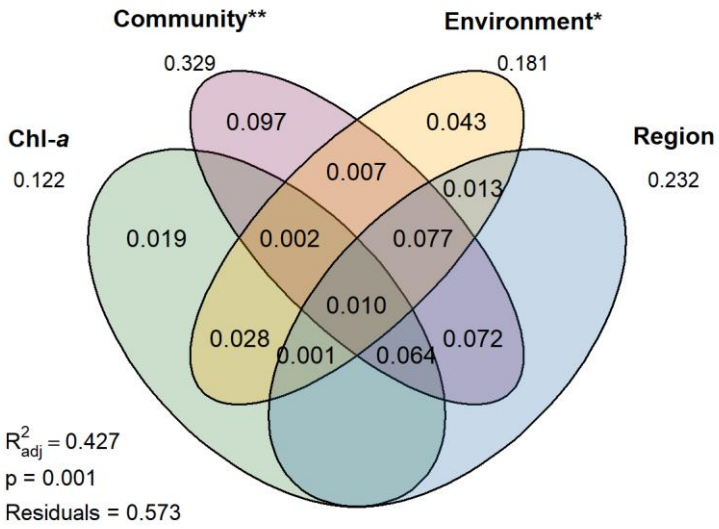


Figure R2: Variance partitioning of DCCHO composition (mol%) among phytoplankton biomass (chl-*a*), phytoplankton community composition (Community), environmental conditions including temperature, salinity and nutrients (Environment) and region. Values next to the labels give the variation explained by each set alone; values within the ellipses give unique or joint contributions. All fractions are based on adjusted R^2 values. Negative fractions are not shown. Asterisks indicate significant unique fractions (* $p < 0.05$, ** $p < 0.01$). Adjusted R^2, significance of the full model and the residuals are depicted at the bottom left.

In addition, the use of neutral sugar yields to define bloom conditions raises questions about the independence of the subsequent comparisons of carbohydrate concentrations between bloom and non-bloom samples.

Response: Regarding the use of neutral sugar yields to define bloom conditions, please see our detailed response to Reviewer 1 (Specific comment 1), where we describe how the bloom classification is replaced by a correlation analysis.

3. Taxonomic attribution, TEP formation, and carbon cycling

The proposed associations between carbohydrate signatures, Phaeocystis pouchetii, Thalassiosira spp., and TEP formation are interesting, but remain largely correlative. Taxonomic effects are difficult to distinguish from environmental variability and microbial processing, particularly since the Fram Strait and Kara Sea were sampled in different seasons and under different hydrographic conditions.

Moreover, the observed associations do not necessarily demonstrate a direct role of specific carbohydrates or phytoplankton communities in TEP formation. Similarly, the proposed implications for carbon export versus microbial recycling are not directly supported by the available data.

The authors should better acknowledge these limitations, compare their findings with previous taxon-specific studies, and distinguish observed relationships from proposed mechanisms. Where possible, the influence of regional and environmental factors should also be assessed.

Response: The relationships reported in our study are based on field observations and are therefore correlative. As, to our knowledge, the first dataset that exploits the combination of 18S rRNA sequencing with molecular carbohydrate analysis in the field, our study aims to test whether taxon-specific carbohydrate signatures known from culture experiments can be recognised in natural pelagic communities, and to identify associations between phytoplankton taxa, carbohydrate composition and TEP under natural conditions. The original manuscript already presents the results in this way: the title uses the wording “associated with” carbohydrate signatures and TEP, and the abstract states that our findings “indicate an association” and that shifts in phytoplankton biodiversity “may” alter carbon processing pathways. Where the wording in the Discussion and Conclusion goes beyond this, we will revise it, clearly separating observed relationships from hypotheses about mechanisms, including TEP formation and carbon fate.

Specifically, we will revise the statements on carbon export in the Conclusion (lines 616–619), the inference from glucose enrichment to structurally simpler polysaccharides and enhanced microbial recycling (lines 599–603, 610), and the causal wording in the graphical abstract caption and the heading of Section 4.3.

Limitations and regional and environmental factors. In the original manuscript, the different sampling seasons and hydrographic conditions of the Fram Strait and the Kara Sea were primarily used to describe the environmental setting of the two regions. In the revision, we will also discuss potential limitations in a dedicated section, stating that taxonomic effects cannot be fully separated from regional, environmental and microbial influences. The influence of environmental factors on phytoplankton community composition is already assessed by redundancy analysis, which identified salinity, nitrite and phosphate as significant drivers (Section 3.5, Fig. 7A). To further assess their influence on carbohydrate composition itself, we performed a variance partitioning analysis (see our response to comment 2), quantifying the contributions of phytoplankton community composition and environmental variables, including nutrients.

Comparison with taxon-specific studies. The manuscript already compares our findings with previous taxon-specific studies, including the enrichment of rhamnose and arabinose in *Phaeocystis*-derived carbohydrates (Biersmith & Benner, 1998; Aluwihare & Repeta, 1999; Alderkamp et al., 2007; lines 575–578), glucose-rich carbohydrate release by *Thalassiosira* sp. (Urbani et al., 2005; lines 594–597), interspecific variability in TEP production by *Thalassiosira* sp. (Burns et al., 2019; line 591), TEP production by Phaeocystis (Mari et al., 2005; line 582) and uronic acid contributions during high-TEP blooms (Engel et al., 2012; Sperling et al., 2017; lines 583–585).
We will extend this comparison with field observations of *Phaeocystis*-associated TEP in the Fram Strait (Engel et al., 2017), the carbohydrate composition of *Phaeocystis globosa* colony mucus in the North Sea (Janse et al., 1996), TEP production of *Phaeocystis globosa* under nutrient limitation (Li et al. 2023) and the carbohydrate composition of sea-ice diatoms (Aslam et al., 2012b, Aslam et al., 2016).

4. Structure and focus

The manuscript is extremely long and very very descriptive than necessary, with repetitions in several occasions of regional, hydrographic, and bloom-related patterns. A shorter, more focused discussion

organized around the research questions would make the scientific message easier to follow. Some secondary hydrographic details may in my opinion be moved to the Supplement. A combined Results and Discussion section might also help.

Response: We acknowledge the length of the manuscript, which reflects a trade-off between completeness and focus that we initially resolved in favour of completeness, given the novelty and scope of the dataset. As the dataset includes, to our knowledge, the first TEP measurements in the Kara Sea and the first spatially extensive characterisation of DCCHO composition across the Kara Sea shelf, including neutral, amino and acidic sugars, extending previous neutral sugar data from the Ob and Yenisei estuaries (Amon & Benner, 2003; Kaiser et al., 2017), we aimed to document the hydrographic context, community composition and biogeochemical properties of this data-scarce region comprehensively. We agree, however, that a sharper focus will make the scientific message clearer, and in the revision, we will shift this balance towards focus. Specifically, we will:

- move secondary hydrographic details, water-mass-specific information and detailed descriptions of the 18S community composition to the Supplement,
- remove the categorical bloom classification and use region as the primary grouping throughout the manuscript,
- restructure the Results to improve readability and reduce repetitions of regional and hydrographic patterns (see also our response to Reviewer 1).

The Discussion will be reorganised around the two research aims already stated in the Introduction: i) to assess regional differences in DOM quantity and quality across contrasting hydrographic regimes, and ii) to examine the potential influence of phytoplankton community composition on the composition of dissolved combined carbohydrates and on TEP concentrations. Section 4.1 on regional and seasonal bloom dynamics will be removed, the detailed discussion of DOM sources in the river plume (Section 4.2) will be condensed, and a final section will address limitations and implications.

We carefully considered combining the Results and Discussion sections but prefer to keep them separate. The reviewer asks both for a less descriptive presentation and for a clearer distinction between observed relationships and proposed mechanisms (comment 3). We believe that separate sections serve both aims best: the Results present the observations once and concisely, so that the Discussion can focus on interpretation without repeating them, and readers can evaluate the field data independently of our interpretation.

Minor comments

-The title would benefit from a more engaging and elegant formulation that better highlights the study's scientific contribution. As currently phrased, the title lacks appeal and largely repeats findings that are already well established in the literature.

Response: We thank the reviewer for the suggestion. As the revised manuscript no longer relies on a categorical bloom classification, we will adapt the title once the revision is complete to better reflect the main findings of our study. The revised title will likely be along the lines of "Arctic phytoplankton community composition is associated with distinct dissolved carbohydrate signatures"

- The discussion of marine carbohydrates several sections rely on older references older references, particularly from the 1980s, 1990s, and 2000s. While these pioneering studies remain relevant, the

authors should incorporate more recent literature on carbohydrate production, composition, and dynamics to better reflect current knowledge and place their findings in a broader scientific context.

Response: We respectfully note that the manuscript already cites a substantial body of recent literature on carbohydrate production, composition and microbial processing (e.g., Engel et al., 2012; Kaiser et al., 2017; Sperling et al., 2017; Unfried et al., 2018; Burns et al., 2019; Becker et al., 2020; Sichert et al., 2020; Kieft et al., 2021; Vidal-Melgosa et al., 2021; von Jackowski et al., 2022; Amon et al., 2024; Barthelmeß et al., 2025). Older studies are cited where they are the original source of concepts and methods that remain standard in the field, such as the overflow hypothesis, neutral sugar yields as indicators of the diagenetic state of DOM, and the spectrophotometric TEP assay.

As part of the revision of the Introduction and Discussion (see our response to major comment 1), we will add studies on carbohydrate and EPS dynamics in sea ice (Aslam et al., 2012b, 2016) and further recent work, including field comparisons of diatom- and *Phaeocystis*-dominated blooms (Jo et al., 2021; Misic et al., 2024; Skouroliakou et al., 2024), studies on *Phaeocystis* and TEP (Engel et al., 2017; Li et al., 2023) and recent Arctic field studies of dissolved carbohydrates (Panagiotopoulos et al., 2025).

Overall assessment and recommendation

The manuscript presents a valuable Arctic field dataset, but its scientific novelty remains insufficiently demonstrated. Previous studies have already examined carbohydrate and EPS production, composition, and microbial processing in Arctic sea-ice environments. While the present study addresses pelagic communities, the authors need to put in front the novelty of their work and its added value. The limited examination of chl-*α* and carbohydrate relationships, the overlap between taxonomic and regional or seasonal differences, and the largely correlative links proposed between carbohydrates, TEP, and carbon cycling merit in my opinion a better analysis.

For these reasons, I recommend rejection of the manuscript in its present form. However, if the Editor-in-Chief considers that a substantially improved manuscript could be produced by addressing the concerns raised in my review, I would have no objection for a new submission being considered.

Response: We thank the reviewer for the evaluation of our manuscript and for acknowledging the value of our Arctic field dataset. We believe that the revisions outlined above will address the concerns raised. Specifically, we will (i) better emphasize the novelty of our study relative to previous Arctic work on carbohydrates, including the studies by Aslam et al.; (ii) add direct analyses of the relationships between chl-*α* and dissolved carbohydrates; (iii) remove the bloom classification; (iv) assess the influence of regional and environmental factors on carbohydrate composition and distinguish more clearly between observed relationships and proposed mechanisms; and (v) shorten and restructure the manuscript. We believe that these revisions will help to communicate the main messages of our manuscript more clearly and that a revised version will address the reviewer's concerns.

References

Aslam et al. (2012a). Dissolved extracellular polymeric substance (dEPS) dynamics and bacterial growth during sea ice formation in an ice tank study. Polar Biology 35, 661–676. DOI: 10.1007/s00300-011-1112-0.

Aslam et al. (2012b). Production and characterization of the intra- and extracellular carbohydrates and polymeric substances (EPS) of three sea-ice diatom species, and evidence for a cryoprotective role for EPS. Journal of Phycology 48, 1494–1509. DOI: 10.1111/jpy.12004.

Aslam et al. (2016). Patterns and drivers of carbohydrate budgets in ice algal assemblages from first year Arctic sea ice. Limnology and Oceanography 61, 919–937. DOI: 10.1002/lno.10260.

Aslam et al. (2018). Identifying metabolic pathways for production of extracellular polymeric substances by the diatom Fragilariopsis cylindrus inhabiting sea ice. ISME Journal 12, 1237–1251. DOI: 10.1038/s41396-017-0039-z.