

1 **Macroalgal influence on particulate organic matter sources and early transformation in an**
2 **Arctic fjord**

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13 **Highlights**

- 14 • Macroalgal-dominated sites were observed with higher labile surface particulate organic
15 carbon and nitrogen signatures compared to adjacent waters.
- 16 • Biochemical and biomolecular composition indicated lateral transport from macroalgal-
17 beds with conservative reorganization.
- 18 • Brandal was identified as a model site for future biogeochemical studies related to
19 macroalgal expansion in Kongsfjorden.

24 **Abstract**

25 Accelerated Arctic warming is promoting the expansion of coastal macroalgal habitats; yet their
26 influence on pelagic organic carbon cycling remains unresolved. This study investigates the
27 influence of macroalgal beds on the biochemical composition of surface particulate organic matter
28 (POM) in Kongsfjorden, Svalbard, during late summer 2023. Surface waters were sampled at four
29 macroalgal-dominated sites (MDS) and from adjacent waters (Adj-W) located 500 m and 1500 m
30 away. A multi-proxy approach integrating elemental composition, stable isotopes, biopolymeric
31 fractions, monosaccharides, and amino acids was used to trace macroalgal contributions and their
32 lateral redistribution. Concentrations of particulate organic carbon, nitrogen, carbohydrates, and
33 proteins were consistently higher at MDS than in Adj-W, indicating localized enrichment of
34 biochemically labile organic matter within macroalgal habitats. Molecular analyses further
35 revealed elevated concentrations of macroalgal-associated sugars (glucose, galactose, fucose,
36 mannuronic acid) and labile amino acids (Asp, Glu, Gly, Ser, Ala) reinforcing macroalgal-derived
37 contributions to surface POM. While $\delta^{13}\text{C}_{\text{POC}}$ showed minimal spatial variation (-26.8 to -29.1%),
38 the biochemical and molecular signatures indicated a decreasing macroalgal contribution towards
39 Adj-W, along with internal reorganization, suggesting lateral transport of macroalgal-derived
40 POM with selective early-stage transformation. Overall, these findings indicate that Arctic
41 macroalgal beds act as dynamic coastal biogeochemical hotspots, redistributing and transforming
42 organic carbon beyond their habitat.

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44 **Keywords:** Arctic fjords; macroalgal-derived organic matter; coastal carbon cycling; lateral
45 transport

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48 **1. Introduction**

49 Accelerated warming of the Arctic has led to pronounced environmental changes, including a
50 reduction in sea ice extent and thickness, intensified glacier melt, widespread permafrost thawing,
51 and a shift toward more liquid precipitation (Dai et al., 2019; Rantanen et al., 2022). These changes
52 are altering marine primary production (Attard et al., 2024), coastal carbon sources (Mathew et al.,
53 2025), and nutrient dynamics within Arctic fjord systems (McGovern et al., 2020). Amid these
54 environmental transformations, macroalgae have demonstrated ecological resilience and
55 adaptability, enabling their expansion along Arctic coastlines (Assis et al., 2022). Recent estimates
56 from species distribution modeling indicate a substantial increase in subtidal (45%) and intertidal
57 (8%) brown macroalgal cover along the Arctic coastline over the past few decades (Krause-Jensen
58 et al., 2020). This rapid and ongoing macroalgal expansion contributes substantially to coastal
59 primary productivity and carbon dynamics in the Arctic (Attard et al., 2024; Krause-Jensen et al.,
60 2020). Macroalgal biomass and condition are strongly shaped by local environmental variability,
61 with runoff and site-specific forcing influencing kelp biochemistry and ecosystem functioning in
62 Arctic coastal systems (Castro de la Guardia et al., 2025; Niedzwiedz et al., 2025). Comparable
63 environment-driven changes in kelp biomass and distribution have been reported across the Arctic,
64 including Greenland and the Canadian Arctic, indicating pan-Arctic rather than site-specific
65 responses (Carlson et al., 2026; Filbee-Dexter and Wernberg, 2020; Krause-Jensen and Duarte,
66 2016). Kelp forest structure shifted markedly, with a reduced depth distribution, a declining
67 abundance of several kelp species, and an increasing dominance of *Alaria esculenta*, driven
68 primarily by rising turbidity and coastal darkening rather than temperature alone, thereby
69 reshaping kelp biomass, demography, and ecosystem functioning in Kongsfjorden (Düsedau et al.,
70 2024). Field experiments have also shown that macroalgal blades can lose approximately 3% of

71 their total area per day due to mechanical stress, physical abrasion against rocky substrates,
72 seasonal increases in tissue brittleness, and biological weakening by epiphytes. These processes
73 provide a substantial and continuous input of macroalgal-derived material to the coastal particulate
74 organic matter (POM) pool (Buchholz and Wiencke, 2016).

75 Macroalgal beds contribute a significant amount of macroalgal-derived organic carbon,
76 approximately 60% as particulate organic carbon (POC), and approximately 30% as dissolved
77 organic carbon (DOC) (Kennedy and Blain, 2025; Pessarrodona et al., 2022) to the surrounding
78 environment, and play a crucial role in supporting secondary production via detrital food web and
79 coastal Arctic carbon cycling (Pedersen et al., 2021; Renaud et al., 2015; Simpkins et al., 2025).
80 Macroalgal POM appears in multiple forms, including whole thalli and tissue fragments, and is
81 often buoyant due to structural features such as pneumatocysts, allowing particles to stay
82 suspended in surface waters (Carlson et al., 2026; Kennedy and Blain, 2025). This buoyancy
83 promotes extensive lateral transport across coastal and fjord systems, effectively linking benthic
84 macroalgal production with pelagic environments and shaping the spatial distribution of organic
85 carbon (Carlson et al., 2026; van der Mheen et al., 2024). A substantial fraction of the carbon
86 produced in macroalgal beds is exported to surrounding environments, with only about 2%
87 remaining and settling at the site of production (Kennedy and Blain, 2025; Krause-Jensen and
88 Duarte, 2016; Pessarrodona et al., 2022). Macroalgal POM undergoes microbial-mediated
89 transformation and degradation during transit and thereby affects biogeochemical processes in
90 macroalgal beds as well as adjacent waters (Adj-W) (Duarte et al., 2013; Krause-Jensen and
91 Duarte, 2016; Ortega et al., 2019). Biochemical compositional and lipid biomarker studies have
92 shown hints of macroalgal contribution to POM (Singh et al., 2024b) and sediments (Roy et al.,
93 2025) in Kongsfjorden. Similarly, studies from saline lake systems demonstrate that microbial

94 transformations of organic matter require high-resolution molecular proxies to distinguish carbon
95 sources (Jiang et al., 2022; Yang et al., 2020). However, the spatial variability and magnitude of
96 macroalgal-derived organic carbon contributions to POM along coastal gradients remain poorly
97 understood.

98 To better resolve the sources and transformation pathways, and to understand how the
99 expansion of macroalgal forests will influence Arctic coastal biogeochemistry, a systematic
100 biochemical characterization of POM in and around macroalgal-dominated sites is necessary.
101 Thus, the present study investigated the biochemical composition of POM from the surface waters
102 of Kongsfjorden (Svalbard) at four macroalgal-dominated sites (MDS), and their respective
103 adjacent waters (Adj-W) located 500 m and 1500 m from the MDS sites. Here, we addressed three
104 key questions: (i) To what extent do the biochemical characteristics of surface POM at MDS reflect
105 inputs from macroalgal-derived organic matter? (ii) How does the biochemical composition of
106 POM changes from MDS to Adj-W, and (iii) What do these changes reveal about the lateral
107 transport and early alteration of macroalgal-derived organic matter?

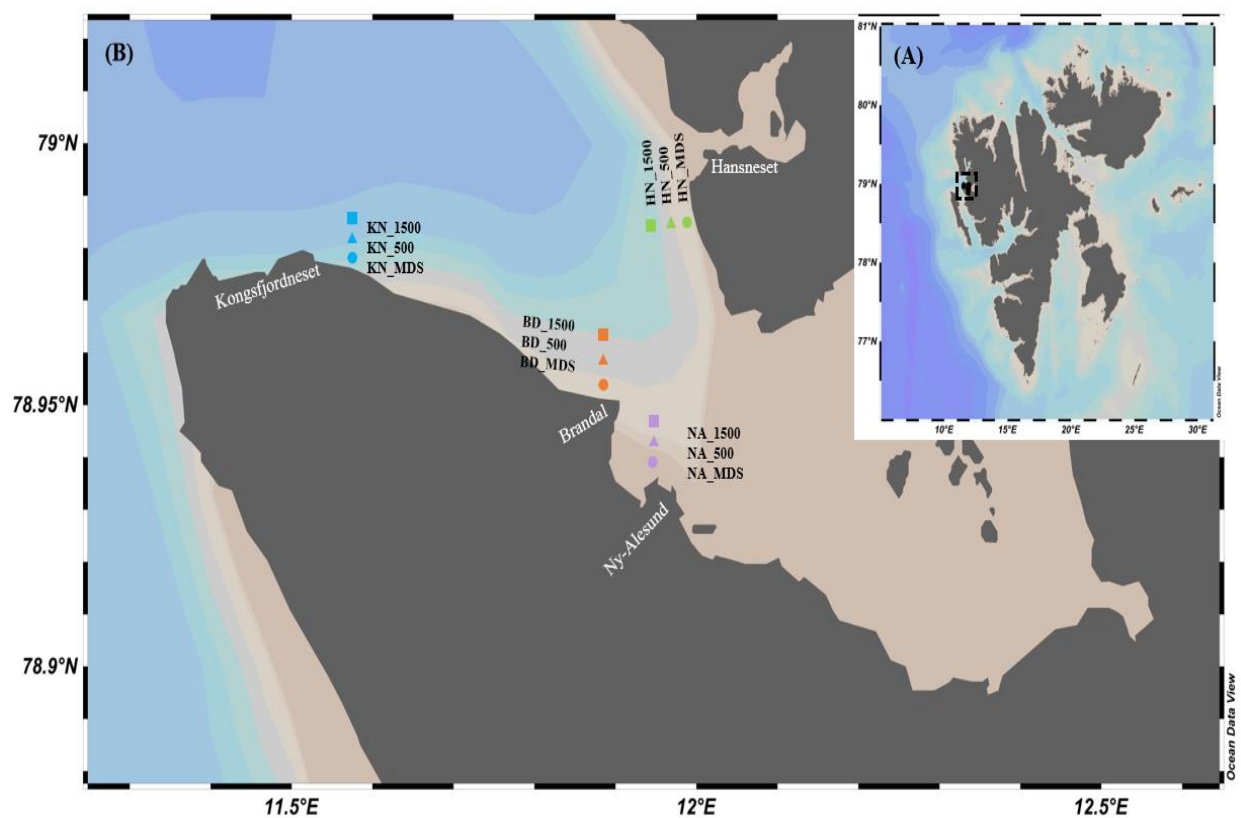
108

109 **Material and Methods**

110 **2.1 Sampling site and locations**

111 Surface water samples were collected during late summer 2023 (September–October) from four
112 MDS distributed along and across the Kongsfjorden coast using the workboat Teisten, with a
113 Niskin sampler deployed at 3 m depth, as well as from adjacent locations (Adj-W) located 500 m
114 and 1500 m away from each MDS site (Figs. 1A and 1B). The seawater was pre-filtered using a
115 200 μm mesh to remove larger particles. Seawater samples (3 L) were filtered using pre-combusted
116 (4 hours at 450 $^{\circ}\text{C}$) 0.7 μm pore size glass fiber filters (GF/F) to collect particulate matter.

117 Immediately after filtration, the GF/F filters were stored at -80 °C until analysis. An aliquot of 100
118 mL seawater sample for dissolved nutrients analysis was collected in high-density polyethylene
119 bottles from each sampling location and stored at -80 °C until analysis.



120
121 **Figure 1.** Study area and sampling locations in Svalbard (A) and the detailed map of sampling
122 stations in Kongsfjorden (B) across nearshore macroalgal beds (MDS), mid-fjord (500 m), and
123 offshore (1500 m) sites at BD, NA, KN, and HN.

124

125 **2.2 Physicochemical characteristics of seawater**

126 The vertical profiles of temperature, salinity, and turbidity at each sampling location were recorded
127 using an SBE 911 plus instrument (Seabird Electronics Inc., USA). The concentrations of
128 dissolved nutrients (nitrate, nitrite, silicate, and phosphate) were determined using a Seal AA3
129 analytical auto-analyzer with a standard deviation of $\pm 1\%$ and an R^2 value of >0.99 (Grasshoff et

130 al., 2009). Chlorophyll *a* was extracted following (Singh et al., 2024a) with minor modifications.
131 Briefly, GF/F filters were extracted in 90% acetone under low-light conditions by keeping them
132 overnight at $-20\text{ }^{\circ}\text{C}$. The pigment extracts were centrifuged ($10,000\times g$, $4\text{ }^{\circ}\text{C}$, 10 min), filtered (0.2
133 μm PVDF), and analyzed using an Agilent 1200 HPLC with a ZORBAX 300 Extend-C8 column
134 (1.1 mL min^{-1} , $40\text{ }^{\circ}\text{C}$). Pigments were separated using a reverse-phase methanol–ammonium
135 acetate gradient and identified by comparing retention times and absorption spectra (250–850 nm)
136 against a DHI chlorophyll-*a* standard.

137

138 **2.3 Elemental and isotopic analyses of POM**

139 Filters containing particulate matter were dried at $45\text{ }^{\circ}\text{C}$ for 24 h, after which carbonates were
140 removed by exposing the filters to fumes of 35% HCl for 6 h in a desiccator. The treated filters
141 were then weighed and tightly packed into tin capsules for elemental and isotopic analyses (Jain
142 et al., 2019; Singh et al., 2024b). Particulate nitrogen (PN), particulate organic carbon (POC), $\delta^{13}\text{C}$ -
143 POC, and $\delta^{15}\text{N}$ -PN were measured at the Marine Stable Isotope Laboratory, National Centre for
144 Polar and Ocean Research, Goa, India, using an elemental analyzer coupled to an isotope ratio
145 mass spectrometer (EA-IRMS; Isoprime Vario Isotope Cube) operated in continuous-flow mode.
146 External analytical precision for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ was $\pm 0.10\text{‰}$ and $\pm 0.14\text{‰}$ (1σ), respectively,
147 determined by repeated analysis of caffeine (IAEA-600) and ammonium sulphate (IAEA-N1)
148 standards. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values are reported relative to VPDB and Air- N_2 , respectively, with
149 ammonium sulfate (IAEA-N1) used for normalization to Air- N_2 . External precision for %C and
150 %N was $\pm 0.96\%$ and $\pm 0.95\%$ (1σ), respectively, based on repeated measurements of
151 sulfanilamide.

152

153 **2.4 Biochemical analysis of POM**

154 The dried, pre-weighed filters with POM were cut into smaller pieces using clean stainless-steel
155 scissors and then used for further analysis. The total particulate carbohydrates (P-CHO),
156 particulate proteins (P-PRT), and particulate lipids (P-LIP) were analyzed using the phenol-
157 sulfuric acid (Dubois et al., 1956), Lowry (Upreti et al., 1988), and Phosphovanillin (Folch et al.,
158 1957) methods, respectively, and as described earlier in (Singh et al., 2024b). Biopolymeric carbon
159 (BPC) was determined as depicted by (Danovaro et al., 2001), using the sum of the carbon
160 equivalents of P-CHO, P-PRT, and P-LIP (conversion factors of 0.4, 0.49 and 0.75, respectively).

161

162 **2.5 Monosaccharide composition analysis of POM**

163 For monosaccharide analysis, POM samples were acid-hydrolyzed and then analyzed using High-
164 Performance Anion Exchange Chromatography coupled with a Pulsed Amperometric Detector
165 (HPAEC-PAD) as described earlier by (Singh et al., 2024a). In brief, GF/F filters with POM were
166 treated with 1 mL of 12 M H₂SO₄ at 25 °C for 2 h, diluted to 1.2 M with Milli-Q water, purged
167 with N₂, sealed, and incubated at 100 °C for 4 h. After cooling, the internal standard (myo-inositol)
168 was added, and the samples were neutralized with pre-combusted CaCO₃, centrifuged (6000 rpm,
169 10 min), and filtered (0.22 µm PTFE). The samples were analyzed using HPAEC-PAD (Metrohm
170 940 Professional IC Vario) equipped with an Au working electrode and Ag/AgCl reference
171 electrode, on a Metrosep Carb 2 (250/4.0) coupled with a guard column at 30 °C. Sugars were
172 separated using gradient elution (0.6 mL min⁻¹) with solvent A (1 mM NaOH, 1 mM sodium
173 acetate) and solvent B (150 mM NaOH, 100 mM sodium acetate) over 120 min. Neutral sugars,
174 amino sugars, and mannitol were resolved isocratically with solvent A, while acidic sugars were

175 separated using a solvent B gradient. Identification and quantification of monosaccharides were
176 achieved using calibration with a mixture of sugar standards (Sigma-Aldrich, USA).

177

178 **2.6 Amino acid composition analysis of POM**

179 For amino acid analysis, POM samples were acid-hydrolyzed using HCl and then analyzed using
180 High-Performance Liquid Chromatography coupled with a Diode Array Detector (HPLC-DAD)
181 using the method outlined by (Kim et al., 2024). GF/F filters with POM were cut into small pieces,
182 placed in Pyrex tubes with 10 mL of 6 M HCl, purged with N₂, sealed, and hydrolyzed at 110 °C
183 for 22 h. After cooling, nor-leucine was added as an internal standard. The hydrolysate was
184 centrifuged, freeze-dried, reconstituted in 1 mL of Milli-Q water, vortexed, and filtered (0.22 µm).
185 Amino acids were derivatized by sequentially mixing 2.5 µL borate buffer with 1 µL sample (0.5
186 min), followed by addition of 1 µL OPA reagent, mixing, and dilution with 15.5 µL of Milli-Q
187 water in the HPLC (Agilent 1200) autosampler prior to injection. HPLC separation of the
188 derivatized amino acids was carried out using a Zorbax AAA column (5 µm, 4.6 × 150 mm), a 20
189 µL injection volume, and a flow rate of 2 mL min⁻¹. Detection was performed using a DAD
190 (Agilent) at 338 nm (reference 390 nm). The separation was carried out using gradient elution with
191 mobile phase A (40 mM phosphate buffer, pH 8.2) and mobile phase B (acetonitrile:
192 methanol:water, 45:45:10). Identification and quantification were performed using external
193 calibration with a 17 amino acid standard mixture (Fig. S1: 10, 100, 250, 1000 pmol, Agilent,
194 USA).

195

196 **2.7 Statistical analysis**

197 Statistical analysis were performed using R (version 4.6.0). Prior to analysis of variance (ANOVA)
198 the assumptions of normality and homogeneity of variance were assessed using the Shapiro-Wilk
199 and Levene's tests (Table S1). Pearson correlation analysis was performed at a significance level
200 of 0.05 to examine the relationship between the variables. Principal component analysis (PCA)
201 was employed using the vegan and factoextra packages to visualize the biogeochemical gradient,
202 and all plots were generated using ggplot2.

203

204 **3. Results**

205 **3.1 Salinity, temperature, nutrients, and chl-a**

206 Surface seawater salinity exhibited spatial variation, with the lowest salinity (27.4 ± 0.0 PSU)
207 recorded at NA_1500 station, a site most influenced by glacier meltwater, and the highest salinity
208 (31.6 ± 0.1 PSU) observed at KN_MDS, the outermost site under the influence of oceanic
209 circulation (Table 1). Surface seawater temperature was lowest (4.2 ± 0.0 °C) at NA_500 and
210 highest at KN_MDS (5.5 ± 0.0 °C). The lowest turbidity (2.1 ± 0.1 NTU) was recorded at both
211 BD_MDS and HN_MDS, while maximum turbidity (7.4 ± 0.0 NTU) was observed at KN_MDS.

212 Nitrate varied from 0.05 μM (BD_MDS) to 0.80 μM (NA_1500) and showed an increasing
213 trend from MDS to Adj-W for NA, BD, and HN (Table 1). The overall average nitrate
214 concentration was lower in MDS (0.39 ± 0.23 μM) than in Adj-W (0.56 ± 0.13 μM). Comparing
215 different stations, the average nitrate concentration of all NA stations were high (0.66 ± 0.12 μM),
216 followed by KN (0.53 ± 0.10 μM), HN (0.51 ± 0.08 μM), and lowest at BD stations (0.30 ± 0.22 μM).
217 Nitrite concentration showed a similar pattern, with an increasing trend from MDS to Adj-W sites.
218 However, phosphate concentrations showed minor differences (0.01 to 0.02 μM) among MDS and
219 Adj-W sites.

220 Chlorophyll *a* (Chl *a*) concentrations ranged from 0.04 $\mu\text{g L}^{-1}$ to 0.18 $\mu\text{g L}^{-1}$ across all
 221 stations (Table 1) with no clear trend observed in other photosynthetic pigments (Table S2).
 222 Similar to nitrate, Chl *a* showed an increasing trend from MDS to Adj-W sites at the NA, BD, and
 223 HN stations, while KN exhibited relatively low concentrations at both MDS and Adj-W sites.
 224 Overall, the average Chl *a* concentration was lower at MDS (0.07 $\mu\text{g L}^{-1}$) compared to Adj-W
 225 (0.08 $\mu\text{g L}^{-1}$). Among stations, BD stations recorded the highest average Chl *a* concentrations
 226 (0.11 $\mu\text{g L}^{-1}$), followed by HN and NA with 0.07 $\mu\text{g L}^{-1}$, whereas KN (0.04 $\mu\text{g L}^{-1}$) stations
 227 exhibited the lowest average concentrations.

228
 229 **Table 1.** Sampling stations and measured physicochemical parameters (temperature, salinity,
 230 nutrients, and chlorophyll *a*) across sampling stations.

Station	Station depth [m]	Temperature [°C]	Salinity [PSU]	Turbidity [NTU]	Nitrate (μM)	Phosphate (μM)	Nitrite (μM)	Chlorophyll <i>a</i> [$\mu\text{g L}^{-1}$]
NA_MDS	3.5	5.0±0.1	31.3±0.0	3.5±0.4	0.58	0.18	0.09	0.09
NA_500	122	4.2±0.0	30.1±1.3	5.0±0.1	0.61	0.17	0.11	0.04
NA_1500	300	5.2±0.1	27.4±0.0	2.9±0.4	0.80	0.20	0.11	0.08
BD_MDS	6.7	5.1±0.0	29.9±0.0	2.1±0.1	0.05	0.13	0.01	0.09
BD_500	146	4.7±0.3	30.3±0.1	2.9±0.1	0.39	0.15	0.04	0.18
BD_1500	362	5.4±0.0	30.9±0.6	4.4±0.3	0.45	0.15	0.06	0.05
KN_MDS	3.4	5.5±0.0	31.6±0.1	7.4±0.0	0.49	0.14	0.06	0.05
KN_500	216	5.0±0.5	29.5±0.1	3.1±0.4	0.65	0.16	0.08	0.06
KN_1500	240	4.5±0.0	29.8±0.0	2.9±0.1	0.45	0.14	0.07	0.05
HN_MDS	4.5	4.5±0.2	28.7±1.8	2.1±0.1	0.43	0.14	0.04	0.06
HN_500	76	4.3±0.0	29.8±0.0	3.8±1.7	0.58	0.13	0.05	0.06
HN_1500	315	4.3±0.0	29.8±0.3	3.8±0.5	0.52	0.13	0.07	0.09

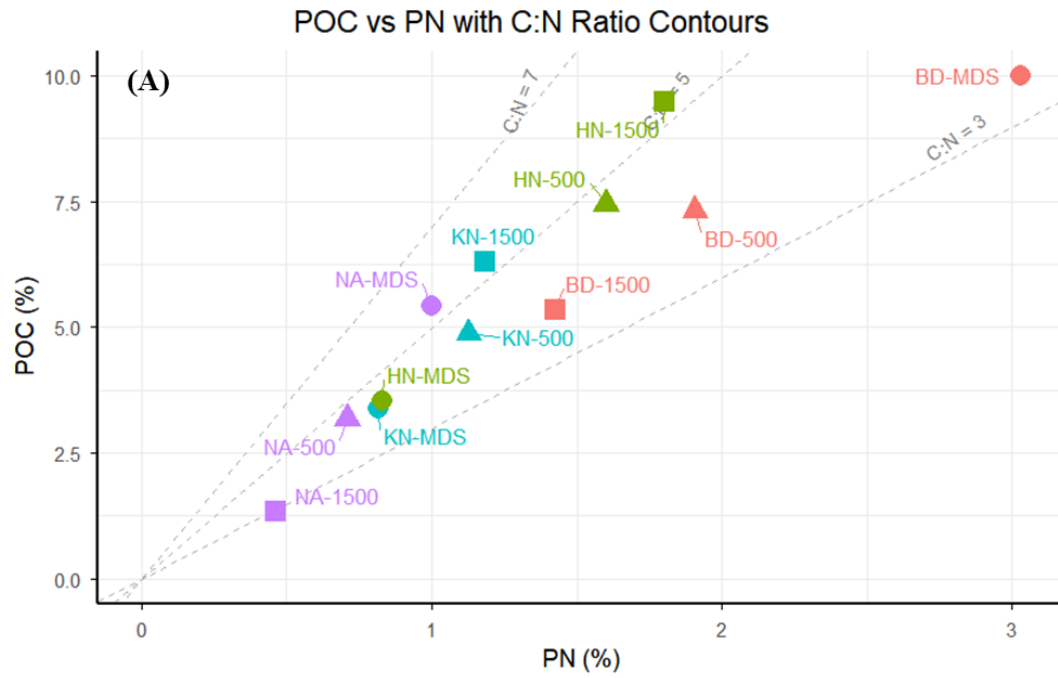
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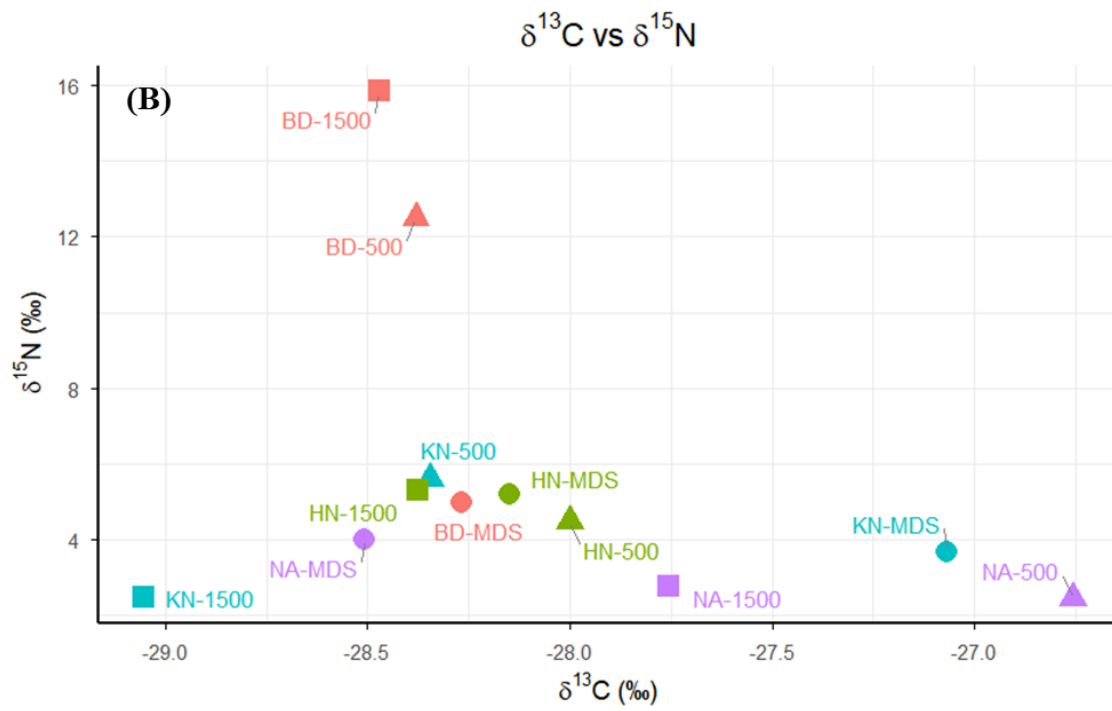
233 3.2 Elemental and stable isotopic composition

234 POC and PN concentrations varied over a wide range from 0.17 mg L⁻¹ (KN_500) to 0.45 mg L⁻¹
235 (BD_MDS) and from 0.04 mg L⁻¹ (KN_500 and KN_1500) to 0.14 mg L⁻¹ (BD_MDS),
236 respectively (Fig. 2A). BD_MDS recorded the highest POC concentration (0.45 mg L⁻¹), followed
237 by NA_MDS and HN_MDS (0.32 mg L⁻¹), with the lowest POC at KN_MDS (0.21 mg L⁻¹).
238 Overall average POC and PN concentrations were higher at MDS (0.32±0.10 and 0.08±0.04 mg
239 L⁻¹, respectively) than at Adj-W (0.26±0.08 and 0.06±0.02 mg L⁻¹), respectively. Across stations,
240 mean POC was highest at BD (0.37±0.10 mg L⁻¹), followed by HN (0.32±0.01 mg L⁻¹) and NA
241 (0.24±0.07 mg L⁻¹), and lowest at KN (0.19±0.02 mg L⁻¹) (Fig. 2B). A similar pattern was
242 observed for PN, with the highest values at BD (0.10 ± 0.03 mg L⁻¹), followed by HN (0.07±0.01
243 mg L⁻¹), NA (0.06±0.00 mg L⁻¹), and KN (0.04±0.01 mg L⁻¹). The POC/PN ratio ranged from 2.9
244 (NA_1500) to 5.4 (NA_MDS). The POC/PN ratio showed an increasing trend from MDS to Adj-
245 W for all stations, except NA (Fig. 2C). The NA station showed a decreasing trend in POC/PN
246 ratio from MDS (5.4) to Adj-W (2.9) with the highest change of 2.5.

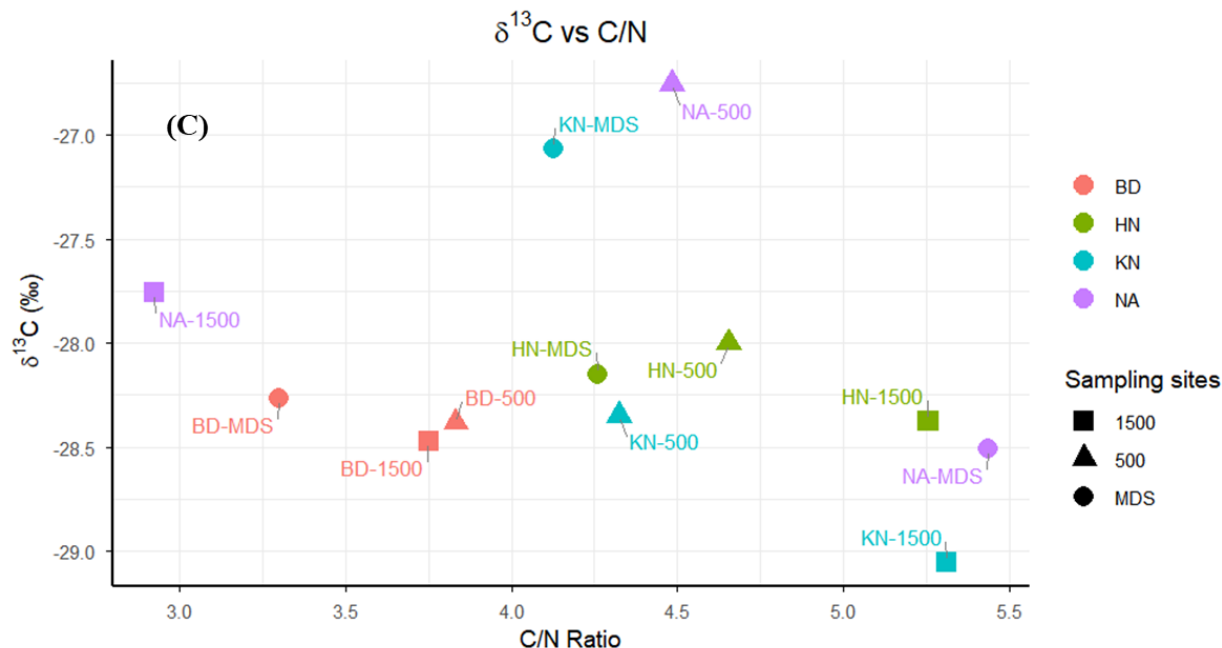
247 The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of POM varied from -26.8‰ (NA_500) to -29.1‰ (KN_1500)
248 and from 2.5 (KN_1500) to 15.9 (BD_1500), respectively. Mean $\delta^{13}\text{C}$ values of all MDS stations
249 (-28.0±0.64‰) were similar to those of Adj-W stations (-28.1±0.67‰). However, individually
250 KN showed a prominent decreasing trend in $\delta^{13}\text{C}$ (-27.1‰ to -29.1‰) and NA showed an increase
251 of -28.5‰ to -27.5‰ from MDS to Adj-W, while HN and BD values were confined to a narrow
252 range (-28.0‰ to -28.5‰). For $\delta^{15}\text{N}$, the overall average at MDS sites was lower (4.5 ± 0.73‰)
253 than at Adj-W (6.4 ± 5.02‰). $\delta^{15}\text{N}$ value variations were minor (2.5‰ to 5.6‰) for the KN, HN,
254 and NA stations, while the observed values for BD_500 (12.5‰) and BD_1500 (15.9‰) were
255 quite high (Fig. 2B).



256



257



258

259 **Figure 2.** Relationship between Particulate Organic Carbon (POC %) and Particulate Nitrogen
 260 (PN %) relative to C/N ratio contours (A), dual isotope plot of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures (B) and
 261 $\delta^{13}\text{C}$ versus C/N ratio in particulate organic matter (C)

262

263 3.3 Biochemical and biomolecular composition of POM

264 3.3.1 Concentrations of carbohydrates, proteins, and lipids

265 Particulate carbohydrate (PCHO) and proteins (PPRT) concentrations showed a decreasing trend
 266 from MDS (PCHO: 55.7 to 109.7 $\mu\text{g L}^{-1}$; PRT: 56.7 to 145.5 $\mu\text{g L}^{-1}$) to Adj-W (PCHO: 46.2 to
 267 84.6 $\mu\text{g L}^{-1}$; PPRT: 32.1 to 94.4 $\mu\text{g L}^{-1}$) for all stations (Table 2). Unlike PCHO and PPRT,
 268 particulate lipids (PLIP) concentrations showed an increasing trend from MDS to Adj-W for NA
 269 (59.6 $\mu\text{g L}^{-1}$ to 106.7 $\mu\text{g L}^{-1}$) and KN (51.6 $\mu\text{g L}^{-1}$ to 70.9 $\mu\text{g L}^{-1}$), and a decreasing trend for BD
 270 (122.7 $\mu\text{g L}^{-1}$ to 83.3 $\mu\text{g L}^{-1}$). For HN stations, HN_500 (118.1 $\mu\text{g L}^{-1}$) showed the highest PLIP
 271 concentrations, followed by HN_MDS (77.8 $\mu\text{g L}^{-1}$) and HN_1500 (47.5 $\mu\text{g L}^{-1}$). Among stations,

272 BD stations showed the highest average PCHO (90.7 $\mu\text{g L}^{-1}$), PPRT (105.4 $\mu\text{g L}^{-1}$), and PLIP
 273 (105.4 $\mu\text{g L}^{-1}$) concentrations.

274

275 **Table 2.** Concentrations of particulate biochemical components, including carbohydrates (P-
 276 CHO), proteins (P-PRT), and lipids (P-LIP), alongside their biopolymeric carbon equivalents
 277 (BPC-CHO, BPC-PRT, BPC-LIP) and total biopolymeric carbon (BPC) across the sampling
 278 stations.

Station	P-CHO ($\mu\text{g L}^{-1}$)	P-PRT ($\mu\text{g L}^{-1}$)	P-LIP ($\mu\text{g L}^{-1}$)	BPC-CHO ($\mu\text{g L}^{-1}$)	BPC-PRT ($\mu\text{g L}^{-1}$)	BPC-LIP ($\mu\text{g L}^{-1}$)	BPC (%)	BPC/POC (%)	Labile (%)
NA_MDS	67.7	61.1	59.6	27.1	29.9	44.7	31.7	31.7	17.8
NA_500	54.9	45.5	67.7	22.0	22.3	50.8	45.1	45.1	21.0
NA_1500	46.2	32.1	106.7	18.5	15.7	80.0	60.0	60.0	18.0
BD_MDS	109.7	145.5	122.7	43.9	71.3	92.0	46.3	46.3	25.7
BD_500	84.6	94.4	110.3	33.8	46.3	82.7	40.0	40.0	19.7
BD_1500	77.8	64.2	83.3	31.1	31.5	62.4	47.7	47.7	23.9
KN_MDS	55.7	56.7	51.6	22.3	27.8	38.7	42.2	42.2	23.8
KN_500	46.8	42.6	51.9	18.7	20.9	38.9	46.9	46.9	23.7
KN_1500	53.4	39.1	70.9	21.4	19.2	53.1	50.1	50.1	21.7
HN_MDS	78.6	97.0	77.8	31.4	47.5	58.3	43.4	43.4	25.0
HN_500	75.3	86.2	118.1	30.1	42.2	88.6	49.5	49.5	22.2
HN_1500	73.7	81.8	47.5	29.5	40.1	35.6	33.5	33.5	22.2

279 BPC_CHO: Biopolymeric carbon equivalent carbohydrate; BPC_PRT: Carbon equivalent
 280 biopolymeric protein; BPC_LIP: Carbon equivalent biopolymeric lipid

281

282 *3.3.2 Biopolymeric vs. Non-Biopolymeric Carbon in POM*

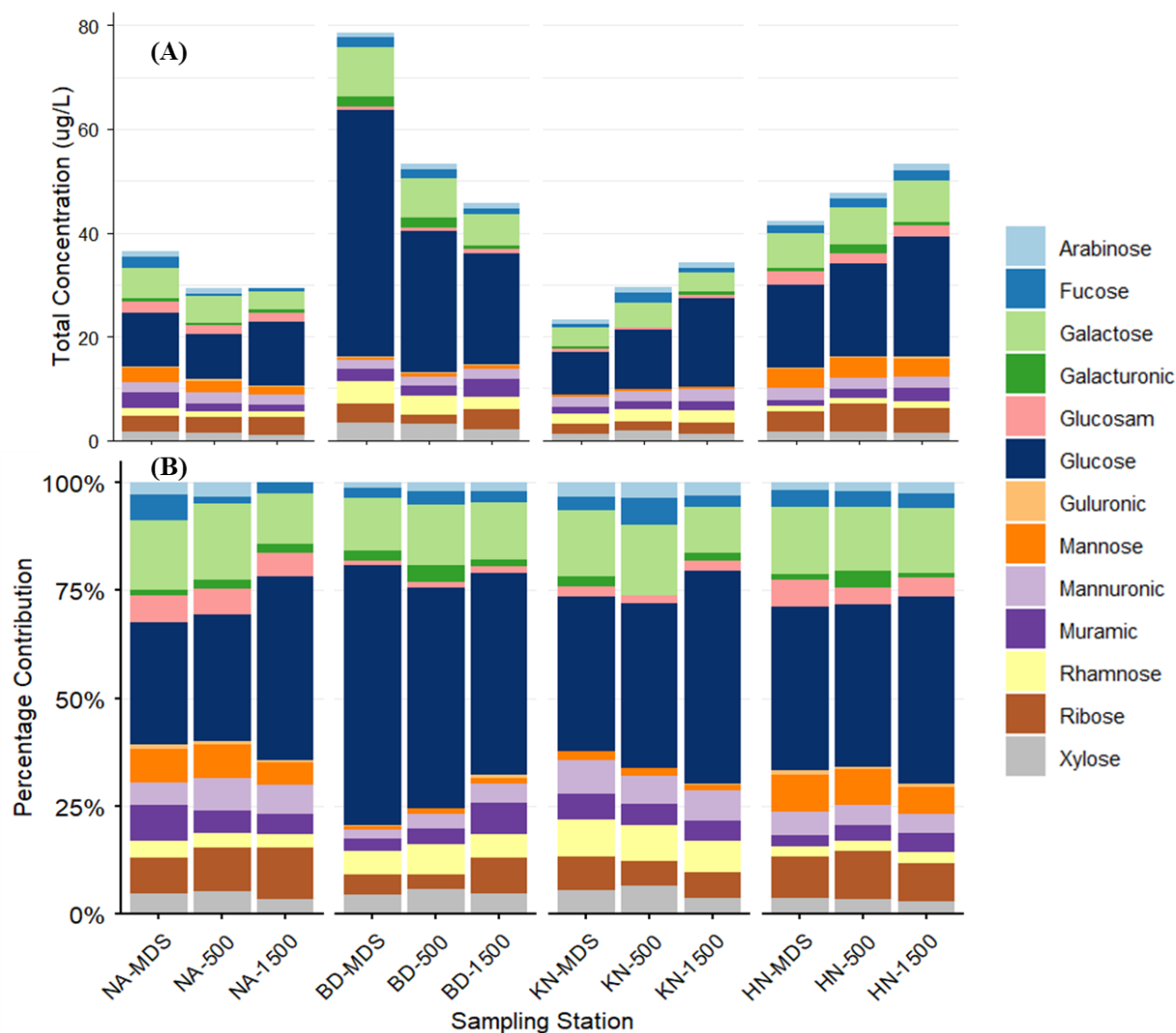
283 A consistent increase in BPC (%) from MDS to Adj-W was observed at NA and KN (Table 2 and
284 Table S3). In contrast, BD exhibited lower BPC at BD_500 compared to both BD_MDS and
285 BD_1500 (Table 2). For HN, BPC% was highest at HN_500 compared to HN_MDS and
286 HN_1500. Overall, BPC_CHO and BPC_PPRT, representing labile components of POC, showed
287 a consistent difference of 2-6% between MDS and Adj-W at individual sampling stations. The
288 most significant variation occurred at BD sites, with BD_500 showing 19.6% of labile component
289 contributions, followed by BD_1500 (23.9%) and BD_MDS (25.7%).

290

291 *3.3.3 Monosaccharide composition of POM*

292 Total monosaccharide concentrations at NA and BD declined from MDS to Adj-W (Fig. 3A and
293 Table S3). In contrast, KN and HN exhibited increasing monosaccharide concentrations from
294 MDS to Adj-W. Glucose (8.6 - 47.5 $\mu\text{g L}^{-1}$) and galactose (3.4 - 9.6 $\mu\text{g L}^{-1}$) dominated the
295 monosaccharide pool and followed trends similar to total monosaccharides from MDS to Adj-W
296 across stations. Station-wise, average monosaccharide concentrations were highest at BD (59.2 μg
297 L^{-1}), followed by HN (47.9 $\mu\text{g L}^{-1}$), NA (32.0 $\mu\text{g L}^{-1}$), and KN (29.0 $\mu\text{g L}^{-1}$).

298 The mol% monosaccharide concentrations showed a consistent pattern across MDS and
299 Adj-W for each station, with minor differences (Fig. 3B). However, BD and KN stations showed
300 different compositions compared to NA and HN stations, mainly due to the contributions of
301 glucosamine and rhamnose. Glucose, the dominant monosaccharide, exhibited a decreasing mol%
302 trend from MDS to Adj-W at the BD station, whereas it showed an increasing mol% trend offshore
303 at the other stations.



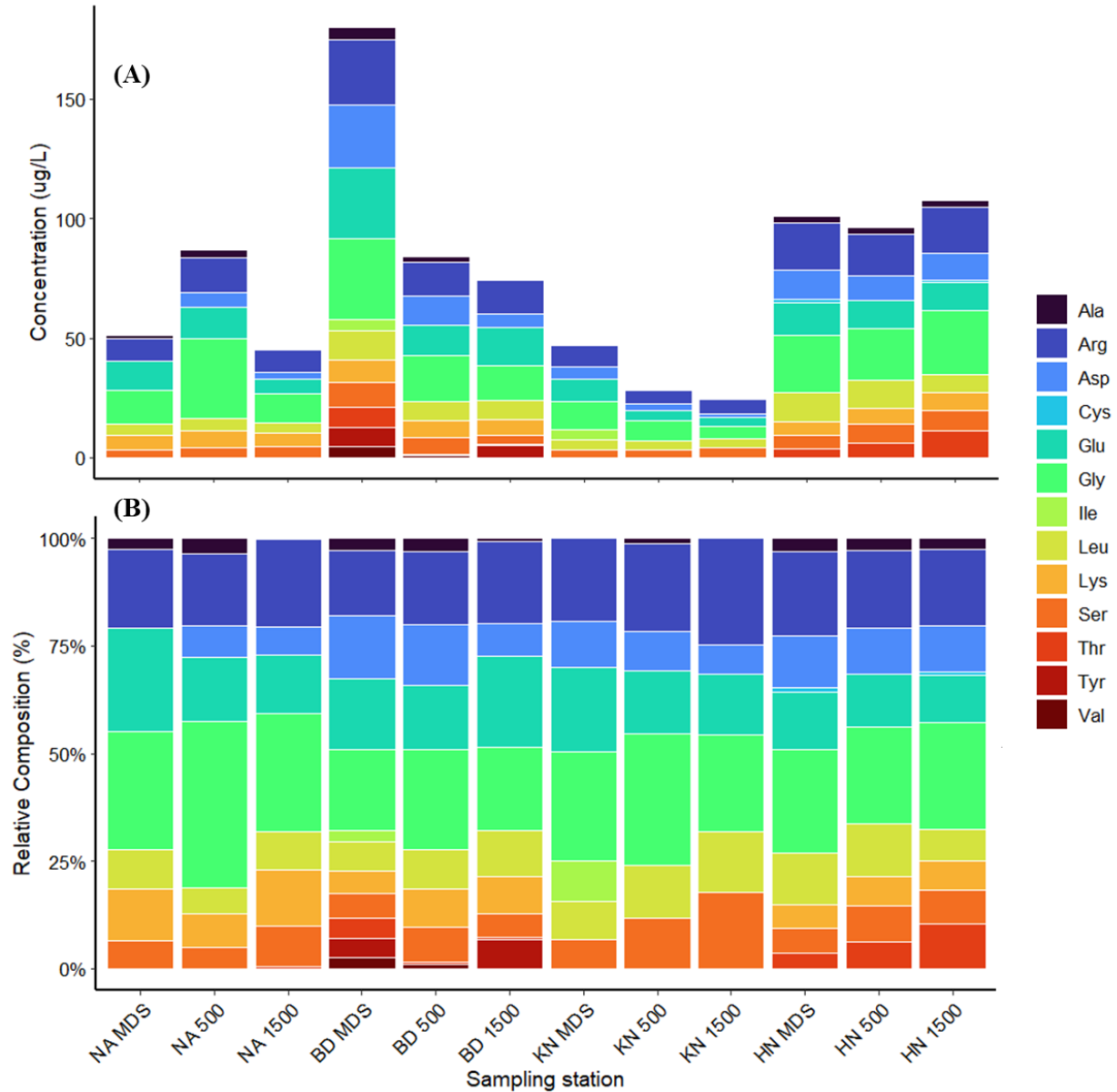
304
 305 **Figure 3.** Spatial variation in monosaccharide composition of surface POM across fjord stations.
 306 (A) Concentrations ($\mu\text{g L}^{-1}$) and (B) relative percentage contributions of individual
 307 monosaccharides at macroalgal bed (MDS), 500 m, and 1500 m sites at NA, BD, KN, and HN.

308
 309 *3.3.4 Amino acid composition of POM*

310 A clear decreasing trend in total amino acid concentrations from MDS to Adj-W was observed at
 311 BD and KN (Fig. 4A and Table S3). In contrast, concentrations at NA increased from NA_MDS
 312 to NA_500 further declined at NA_1500. At HN, total amino acid concentrations decreased

313 slightly from HN_MDS to HN_500 and then increased at HN_1500. Among stations, the average
314 total amino acid concentrations were highest at BD ($113 \mu\text{g L}^{-1}$) followed by HN ($101.6 \mu\text{g L}^{-1}$),
315 NA ($61 \mu\text{g L}^{-1}$) and KN ($33.3 \mu\text{g L}^{-1}$). The average concentrations of individual amino acids were
316 also higher in MDS than in Adj-W (Table S4). The BD station showed the highest concentrations
317 of individual amino acids, with Asp ($26.1 \mu\text{g L}^{-1}$), Glu ($29.8 \mu\text{g L}^{-1}$), Gly ($33.9 \mu\text{g L}^{-1}$), Arg (27.6
318 $\mu\text{g L}^{-1}$), and Lys ($9.4 \mu\text{g L}^{-1}$) peaking at the MDS and declining toward Adj-W (Asp: $5.6 \mu\text{g L}^{-1}$;
319 Glu: $15.9 \mu\text{g L}^{-1}$; Gly: $14.4 \mu\text{g L}^{-1}$; Arg: $14.4 \mu\text{g L}^{-1}$; Lys: $6.5 \mu\text{g L}^{-1}$). A similar decreasing pattern
320 of the individual amino acids was observed for the KN station. Exceptions to the low individual
321 amino acid concentrations at Adj-W (500 and 1500 m locations) included high Gly at NA_500
322 ($33.5 \mu\text{g L}^{-1}$), and high Gly ($26.7 \mu\text{g L}^{-1}$) and Arg ($19.1 \mu\text{g L}^{-1}$) at HN_1500.

323 Mol% concentrations of different amino acids indicated that Gly, Glu, and Arg were the
324 dominant contributors across all sampling stations (Fig. 4B). The mol% concentration of Glu
325 showed a decreasing trend from MDS to Adj-W at NA (24.1 % to 13.7%), KN (19.7% to 14.0%)
326 and HN (13.3% to 10.9%) stations, whereas BD showed an increasing trend (MDS: 16.6%; Adj-
327 W: 21.3%). In contrast, Gly and Arg exhibited similar spatial patterns across stations, with Gly
328 showing its highest mol% contribution at the 500 m station at NA, BD, and KN, while Arg
329 displayed a consistent increase from MDS to Adj-W across these stations.



330

331 **Figure 4.** Spatial variation in amino acid composition of surface POM across fjord stations. (A)

332 Concentrations ($\mu\text{g L}^{-1}$) and (B) relative percentage contributions of individual amino acids at

333 macroalgal beds (MDS), 500 m and 1500 m sites in NA, BD, KN, and HN.

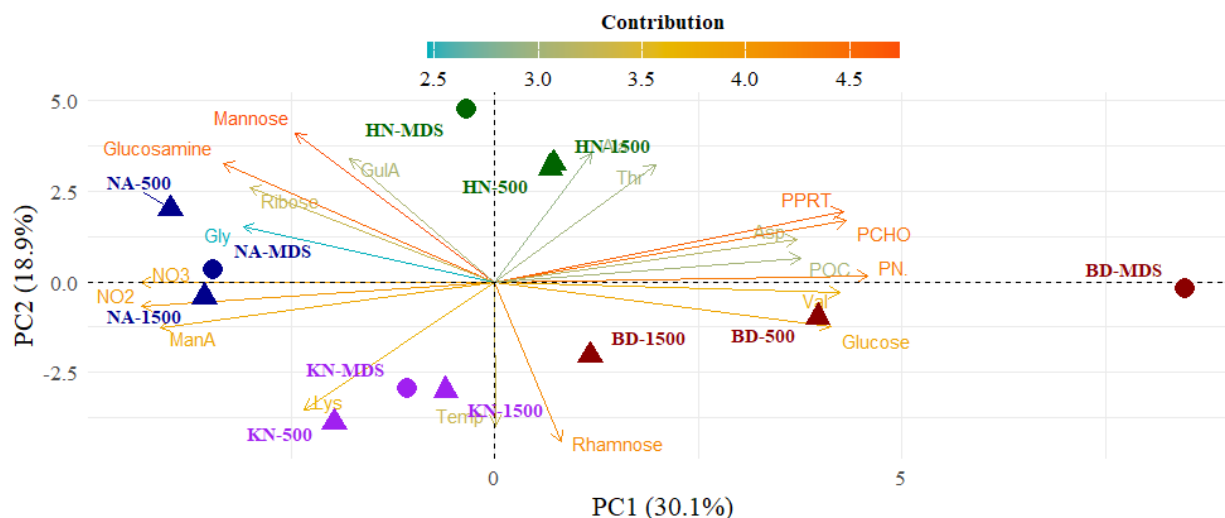
334

335 **3.4 Statistical analysis**

336 Strong positive correlations were observed between PN and POC, PCHO, and PPRT ($r > 0.83$,
337 $p < 0.05$), with an exceptionally high correlation between PPRT and PCHO ($r = 0.96$, $p < 0.05$) (Fig.
338 S2A). In contrast, negative correlations were observed between BPC_LIP% and the non-BPC
339 fraction ($r = -0.95$, $p < 0.05$), and between nitrate and biochemical parameters (POC, PN, PCHO,
340 PPRT) ($r < -0.66$, $p < 0.05$). Despite consistent trends across parameters, ANOVA indicated no
341 significant differences between MDS and Adj-W, suggesting gradual lateral transformations rather
342 than abrupt distance-related changes, together with pronounced spatial heterogeneity among
343 stations (Table S1).

344 Mannuronic acid (ManA) showed strong negative correlations with POC ($r = -0.79$) and
345 PCHO ($r = -0.92$) (Fig. S2B). Glucose and galactose were negatively correlated with several
346 compounds, including glucosamine ($r = -0.72$), mannose ($r = -0.70$), ribose ($r = -0.59$), and ManA
347 ($r = -0.63$). Rhamnose exhibited pronounced negative relationships with guluronic acid (GulA; r
348 $= -0.83$), glucosamine ($r = -0.76$), mannose ($r = -0.85$), and ribose ($r = -0.73$), whereas galactose
349 was positively correlated with fructose ($r = 0.61$) and arabinose ($r = 0.58$). Strong positive
350 associations were also observed among mannose, glucosamine ($r = 0.91$), and ribose ($r = 0.76$),
351 with ribose additionally correlating positively with glucosamine ($r = 0.79$).

352 In PCA, the first two principal components explained 49.0% of the total variance, with PC1
353 and PC2 accounting for 30.1% and 18.9%, respectively (Fig. 5). PC1 was positively loaded by
354 POC, PN, PCHO, PPRT, glucose, galactose, and labile amino acids (Asp, Glu, Thr), whereas
355 negative PC1 loadings were associated with muramic acid, arabinose, fucose, and inorganic
356 nutrients. Sample scores showed a spatial organization, with MDS plotting toward positive PC1
357 values and Adj-W progressively shifting toward negative PC1 values, which was seen more
358 prominently for BD stations.

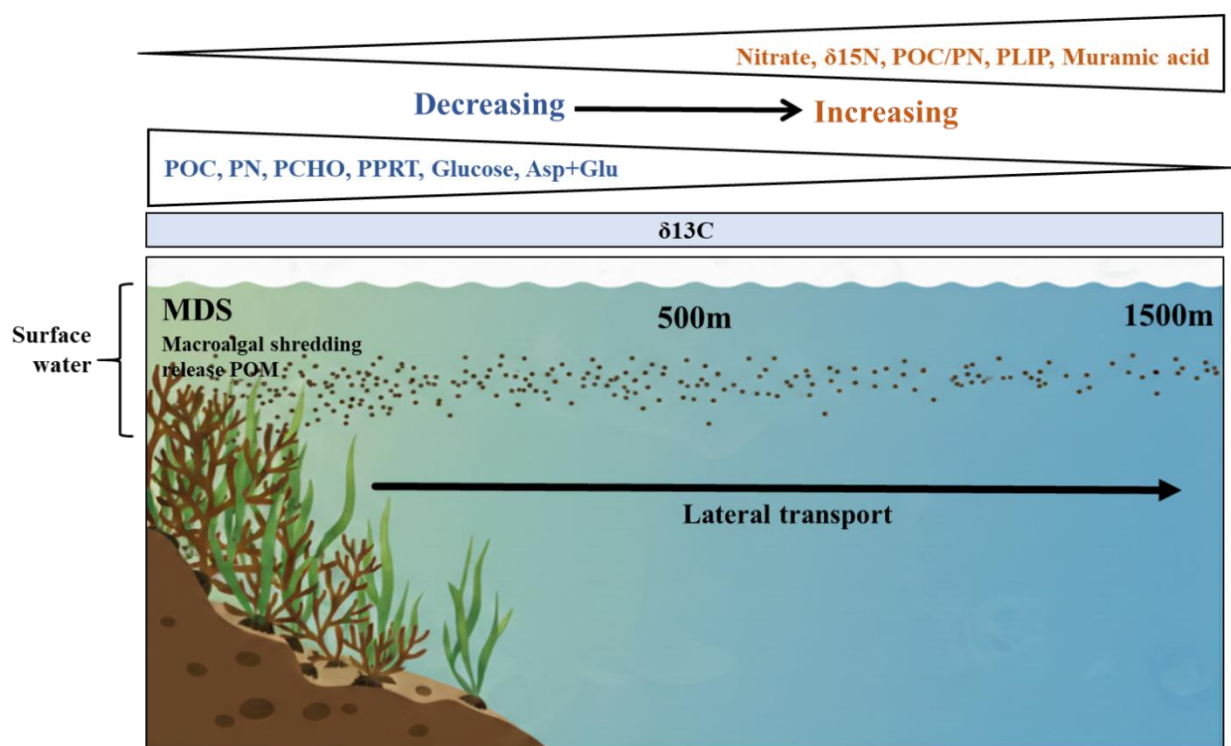


359
 360 **Figure 5.** Principal Component Analysis (PCA) biplot of biogeochemical variables across
 361 different sample sites. The first two principal components (PC1 and PC2) account for 30.1% and
 362 18.9% of the total variance, respectively. Individual samples are represented by colored shapes,
 363 categorized by site (e.g., NA, HN, KN, BD) and location (e.g., MDS, 500, 1500). Vectors (arrows)
 364 indicate the loadings of specific variables, including carbohydrates (e.g., Mannose, Glucose,
 365 Rhamnose), nutrients (NO_2^- , NO_3^-), and organic matter indicators (POC, PN, PCHO, PPRT). The
 366 color scale of the vectors represents the contribution of each variable to the principal components.

367
 368 **4. Discussion**

369 The present study provides a multi-proxy assessment of POM in the surface waters of macroalgal
 370 beds in Kongsfjorden, integrating bulk biochemical, isotopic, biopolymeric composition, and
 371 molecular biomarkers. Elevated bulk (POC, PN, PCHO, and PPRT) and molecular
 372 (monosaccharides and amino acids) concentrations at MDS indicated that macroalgal beds act as
 373 localized sources of biochemically labile organic matter. The results demonstrated that macroalgal
 374 beds imprint surface waters with distinct biochemical and molecular signatures that are

375 redistributed across fjord-scale gradients. The PCA demonstrates that macroalgae influence
 376 surface POM along a continuous multivariate gradient rather than discrete habitat classes. The
 377 systematic offshore decline of these compounds, together with internal reorganization of the
 378 biopolymeric and molecular composition, shows that macroalgal-derived POM is efficiently
 379 exported and selectively transformed during lateral transport (Fig. 6).



380
 381 **Figure 6.** Schematic showing the biochemical nature of POM at macroalgal-dominated sites and
 382 its transformation during lateral transport.

383
 384 **4.1 Influence of Macroalgal Beds on Surface POM Biochemical Composition**

385 Macroalgal beds produce substantial organic carbon via photosynthesis, which enters surrounding
 386 waters (Chen et al., 2020; Filbee-Dexter et al., 2022; Pessarrodona et al., 2022; Watanabe et al.,
 387 2020). The observed higher concentrations of POC and PN at MDS relative to Adj-W, together

388 with consistently higher PCHO and PPRT, indicates localized enrichment of particulate matter
389 near macroalgal beds. The inverse relationship between nitrate and POC, PN, PCHO, and PPRT
390 ($r = -0.82$, $p < 0.05$) reflects biological assimilation of dissolved nutrients into the particulate pool,
391 reinforcing the role of active coastal production in shaping POM composition along the fjord
392 gradient. Macroalgal tissues are structurally rich in polysaccharides and contain substantial protein
393 fractions, and the release of tissue fragments, sloughed material, and epiphyte-associated biomass
394 (Kennedy and Blain, 2025; Watanabe et al., 2020) provides a direct pathway for incorporation of
395 macroalgal carbon into surface POM contributing to Arctic coastal carbon cycling (Ager et al.,
396 2023). Strong positive correlations ($r > 0.83$, $p < 0.05$) between PN and POC, PCHO, and PPRT
397 indicate tightly coupled carbon and nitrogen incorporation during fresh organic matter production.
398 The remarkably strong positive correlation between PPRT and PCHO ($r = 0.96$, $p < 0.05$) further
399 indicates tightly coupled biological production and POM synthesis in macroalgal beds. The
400 multivariate analysis of POM as resolved by PCA showed PC1 (30.1% variance) was dominated
401 by PCHO, PPRT, PN, POC, glucose, and Asp and separated MDS from Adj-W along a continuous
402 biochemical gradient, especially prominent for BD station (Fig. 5). The strong positive loadings
403 of labile carbon and nitrogen compounds supported a distinct organic-rich biochemical state of
404 surface POM at MDS.

405 Although macroalgal biomass and detritus are generally carbon-rich, three of the four
406 stations (BD, KN, and HN) exhibited lower POC/PN ratios at the MDS sites than Adj-W. This
407 pattern likely reflects contributions from fresh, nitrogen-rich organic matter produced within
408 macroalgal habitats, possibly including phytoplankton, epiphytic microalgae, and benthic primary
409 producers associated with kelp beds (Burfeid-Castellanos et al., 2021; Stanca and Parsons, 2021),
410 which could be re-suspended into surface waters and become part of POM. Kelp forest POM

411 characteristics are highly variable depending on the water column conditions, which also influence
412 contributions from macroalgal detritus and other autochthonous primary producers (Dyer et al.,
413 2019). In favorable conditions, other primary producers may outweigh the stoichiometric signal of
414 macroalgal tissue itself, resulting in relatively low POC/PN ratios of POM near macroalgal beds
415 (Chen et al., 2020). Similarly, heterotrophic bacteria are typically richer in nitrogen and
416 phosphorus than phytoplankton, and their colonization of particles can lower the bulk POC/PN
417 ratio by contributing nitrogen-rich biomass (Jo et al., 2021). The subsequent increase in POC/PN
418 ratios from MDS to Adj-W is consistent with preferential microbial degradation of labile nitrogen-
419 rich compounds during lateral transport (Vidal et al., 2018), leading to relative enrichment of
420 carbon-rich material with distance from source habitats.

421 $\delta^{13}\text{C}$ values of POM are widely used to trace organic matter sources (Gao et al., 2008;
422 Pineault et al., 2013). Most macroalgae typically exhibit $\delta^{13}\text{C}$ values between -34.6‰ to -2.2‰
423 (Velázquez-Ochoa et al., 2022), though some brown macroalgal species show more negative
424 signatures, ranging from -20‰ to -35‰ (Fredriksen, 2003). In Arctic coastal systems, marine
425 phytoplankton-derived organic matter typically exhibits $\delta^{13}\text{C}$ values between -20‰ and -26‰ ,
426 whereas terrestrial organic matter derived from C3 vegetation is generally more depleted, around
427 -26‰ to -29‰ (Gao et al., 2008; Pineault et al., 2013). However, substantial overlap between
428 marine and terrestrial isotopic ranges complicates source discrimination in Arctic fjord systems
429 (Kumar et al., 2016; Singh et al., 2024b). The similarity of $\delta^{13}\text{C}$ values between MDS and Adj-W
430 indicates that macroalgal material does not dominate bulk POM isotopically; instead, it contributes
431 substantially within a mixed particulate pool of macroalgal, phytoplanktonic, and terrestrial
432 organic matter in Arctic fjords (Ørberg et al., 2023; Roy et al., 2025). This muted isotopic signal
433 likely reflects that macroalgal influence on surface POM is not solely derived from detached kelp

434 tissue, but is also mediated by contributions from epiphytic and benthic microalgal production
435 (Burfeid-Castellanos et al., 2021; Stanca and Parsons, 2021) and biochemically distinct macroalgal
436 fractions, whose $\delta^{13}\text{C}$ values overlap those of pelagic organic matter.

437 $\delta^{15}\text{N}$ values of POM exceeding $\sim 2\text{‰}$ as observed in this study are consistent with marine
438 nitrate-based production and microbial reworking, rather than atmospheric or N_2 -fixation sources
439 (Kuzyk et al., 2010), where intense benthic–pelagic coupling and rapid recycling of dissolved
440 inorganic nitrogen promote isotopic enrichment of the available nitrogen pool (Elliott Smith and
441 Fox, 2022). Reflecting the pattern more prominently, $\delta^{15}\text{N}$ value at BD_MDS (5.0‰), which was
442 already high, further increased toward Adj-W (BD_500: 12.5‰ , BD_1500: 15.9‰), indicating
443 relatively fresher marine-derived organic matter within the macroalgal beds, which is transformed
444 into relatively higher trophic contributions in surrounding waters.

445

446 **4.2 Transformation of surface POM during lateral transport from macroalgal beds** 447 **to adjacent waters**

448 The biochemical composition of POM provides valuable insights into the nature of organic carbon
449 and its benthic–pelagic coupling in macroalgal beds (Elliott Smith and Fox, 2022; Renaud et al.,
450 2015). The observed systematic offshore changes in POM composition revealed both lateral
451 transport and early transformation of macroalgal beds derived particles across the fjord (Vidal et
452 al., 2018). The concentrations of PCHO and PPRT declined consistently from MDS to Adj-W,
453 indicating progressive dilution of organic matter with distance sourced from macroalgal beds and
454 associated autochthonous production (Ørberg et al., 2023; Smale et al., 2022; Simpkins et al.,
455 2025). These labile compounds are preferentially consumed by particle-associated and free-living
456 microbes (Jain et al., 2019), serving as indicators of freshly produced, easily degradable organic

457 matter (Li et al., 2025). In contrast, PLIP generally increased offshore (except at BD), indicating
458 a relative enrichment of lipid-rich pelagic material and/or the preferential preservation of more
459 stable lipid compounds during transport. This pattern likely reflects selective microbial
460 degradation of labile carbohydrates and proteins during lateral transport, combined with mixing
461 with newly produced pelagic material (Li et al., 2025), highlighting dynamic compositional
462 transformation of POM from MDS to Adj-W.

463 The compositional shift in POM was further supported by changes observed in BPC
464 fractions. BPC represents the labile fraction of POM, mainly comprising proteins, carbohydrates,
465 and a lipid fraction, whereas the non-BPC fraction includes more refractory components such as
466 lignin, humic substances, black carbon, and cellulose (Fabiano et al., 1993; Lobbes et al., 2000;
467 Tselepidis et al., 2000). Among BPC constituents, %BPC_lipid increased markedly from MDS
468 ($17.8 \pm 2.8\%$) to Adj-W ($25.1 \pm 8.6\%$), whereas the labile fraction (proteins and carbohydrates)
469 showed minor differences between MDS ($23.1 \pm 3.6\%$) and Adj-W ($21.5 \pm 2.5\%$). This pattern
470 suggests a relative enrichment of more stable organic matter within POC, accompanied by lateral
471 degradation of labile components, consistent with the observed decline in POC from MDS to Adj-
472 W. Further, the strong inverse relationship between %BPC_LIP and the non-BPC fraction ($r =$
473 -0.95 , $p < 0.05$) suggested biochemical reorganization of POM during lateral transport, consistent
474 with selective degradation and compositional restructuring rather than just uniform bulk loss. In
475 support, PCA also showed a progressive leftward shift from MDS to Adj-W along PC1 (Fig. 5)
476 demonstrating lateral export of POM from macroalgal beds to surrounding waters as a gradient,
477 consistent with progressive dilution and selective transformation during fjord-scale transport of
478 POM.

479

480 **4.3 Molecular-level evidence for macroalgal imprint and early transformation of POM**

481 Molecular fingerprints based on monosaccharides and amino acids offer direct insight into the
482 origin, bioavailability, and early diagenetic transformation of organic matter (Grosse et al., 2021;
483 Jo et al., 2022). Glucose is a common constituent of the macroalgal storage polysaccharide
484 laminarin, while fucose, galactose, and uronic acids (glucuronic, mannuronic, and guluronic acids)
485 are key monomers of structural polysaccharides such as alginates and fucans (Singh et al., 2024a).
486 This carbohydrate pool of macroalgae is bound within structurally complex cell-wall polymers
487 that are relatively resistant to microbial degradation (Kennedy and Blain, 2025). In contrast,
488 phytoplankton cell walls and extracellular matrices are dominated by cellulose, and species-
489 specific storage glucans, which are recycled relatively rapidly in surface waters (Biersmith and
490 Benner, 1998). Glucose and galactose were observed to be the dominant monosaccharides
491 throughout the samples, reflecting a shared baseline of organic matter likely derived from a
492 mixture of macroalgal detritus, phytoplankton, and bacterial biomass (Li et al., 2025; Smale et al.,
493 2022). However, the positive correlation of glucose with POC and PCHO indicated a relative
494 enrichment of a labile, carbohydrate-rich organic matter pool at MDS where POC and PCHO were
495 higher than Adj-W. On the other hand, the negative correlation between glucose and other
496 monosaccharides such as galactose, mannose, mannuronic acid, ribose, and glucosamine reflected
497 a relative increase in structurally complex, algal, microbial, and zooplankton-associated sugars
498 during lateral transport and early diagenesis.

499 Amino acid distributions provide complementary evidence for POM source and lability
500 patterns, as their composition reflects both the origin and degree of degradation (Grosse et al.,
501 2021; Jo et al., 2022). The total amino acid concentrations observed in this study (24–180 $\mu\text{g L}^{-1}$)
502 fall within the reported values from coastal Kongsfjorden (Zhu et al., 2016) and across Fram-Strait

503 (Grosse et al., 2021). The average total amino acids were higher at MDS ($94.8 \mu\text{g L}^{-1}$) than at Adj-
504 W ($68.4 \mu\text{g L}^{-1}$), with BD exhibiting the highest average concentration ($113.0 \mu\text{g L}^{-1}$), indicating
505 fresher, nitrogen-rich, proteinaceous POM in surface waters, along with elevated PPRT and low
506 C:N ratios observed near macroalgal beds. At BD and KN, total amino acids drop by ~60–50%
507 from MDS to Adj-W, indicating preferential microbial utilization of proteinaceous, nitrogen-rich
508 matter during lateral transport, consistent with the observed offshore increase in POC/PN and PLIP
509 enrichment. NA and HN show mid-station or distal increases (NA_500, HN_1500), likely
510 reflecting local resuspension or secondary production, supporting spatial heterogeneity as
511 discussed before. The combined Asp + Glu content, reflecting the freshness of organic matter and
512 the diagnostic Asp/Gly ratio, indicates the degradation state of organic matter (Machado et al.,
513 2020; Yao et al., 2023). The decline in Glu, Asp, and Asp/Gly ratio, and the relative enrichment
514 of Gly and Arg from MDS to Adj-W for most of the stations further provide molecular signatures
515 for early-stage protein degradation and microbial reworking of macroalgal-derived POM during
516 lateral transport.

517 Together, the coupled behavior of carbohydrates and amino acids demonstrated that
518 macroalgal beds imprint surface POM with a distinct molecular signature that is progressively
519 modified during fjord-scale export. These molecular patterns corroborate the bulk biochemical and
520 isotopic evidence, indicating that macroalgal-derived organic matter is redistributed across coastal
521 gradients while undergoing selective early transformation. The pronounced total monosaccharides
522 and amino acid enrichment at BD (especially BD_MDS), which also exhibited the highest POC
523 and PPRT concentrations, identifies this site as a biogeochemical hotspot of macroalgal influence,
524 reinforcing the spatial coherence of macroalgal signatures across independent biochemical proxies.
525

526 **4.4 Brandal (BD) as a biogeochemical hotspot of macroalgal influence in Kongsfjorden**

527 BD station, among all studied stations, consistently emerged as an organic-rich site, showing
528 characteristics of macroalgal-influenced surface POM, highlighting its role as a biogeochemical
529 hotspot within Kongsfjorden. With the highest concentrations of POC, PN, PCHO, PPRT, total
530 monosaccharides, and total amino acids, the BD station contributed the most in the PCA biplot
531 (Fig. 5), which demonstrated local production and accumulation of biochemically labile organic
532 matter within this macroalgal-dominated habitat. The strong gradient observed across PN, $\delta^{15}\text{N}$,
533 C:N, PPRT, and amino acid composition from MDS to Adj-W at BD indicated nitrogen
534 assimilation, dominance of fresh marine organic matter in macroalgal bed, and their progressive
535 downstream alteration. At the molecular level as well, BD_MDS was strongly enriched in glucose
536 and other macroalgal sugars (fucose, galactose, mannuronic acid), with total monosaccharides and
537 glucose declining offshore. Similarly, the offshore decrease in labile amino acids (e.g., Asp, Glu)
538 provides a molecular signature for early degradation during export, indicating that the BD
539 macroalgal bed is a major source of biochemically active POM and a key contributor to fjord-scale
540 redistribution (Van der Mheen et al., 2024).

541 Situated on the westernmost part of the south shore, BD is influenced by Atlantic water
542 inflow, which creates relatively warmer and more saline conditions (Williams, 2017; Wilson,
543 2022; Woelfel et al., 2014), supporting abundant micro-phytobenthic and benthic mosses (Woelfel
544 et al., 2014). At BD, macroalgal cover is not higher than at other sites, yet detritus accumulation
545 is substantial, supporting elevated benthic faunal diversity. The presence of a deep trench,
546 combined with storm-driven transport, concentrates detritus at BD (Schimani Katherina, 2019).
547 Habitat heterogeneity further drives microbial community assembly and functional differentiation
548 (Huang et al., 2026), reflected in high macroalgal detrital cover and meiofaunal density (Schimani

549 et al., 2022). Additionally, BD exhibits significantly lower turbidity than glacier-proximal sites,
550 which prevents mineral masking of organic signatures and provides a stable light regime for
551 primary producers (Bianchi et al., 2020). Collectively, these features make BD a retention zone
552 for macroalgal detritus, acting as a biogeochemical hotspot and a critical repository for macroalgal-
553 derived carbon. While Brandal represents a biogeochemical hotspot, its broader representativeness
554 is constrained due to spatial variability in macroalgal structure and function across high Arctic
555 fjords, driven by variation in latitude, ice scour, light availability, terrestrial runoff, and glacier-
556 induced salinity and turbidity gradients (Bartsch et al., 2016). Thus, although Brandal provides a
557 high-resolution case study, caution is required when extrapolating its biogeochemical fluxes to
558 fjords characterized by intense glacial runoff, seasonal sea-ice cover, and a different community
559 composition.

560

561 **4.5 Implications of macroalgal-beds for Arctic coastal carbon cycling**

562 Unlike previous studies on POM in Kongsfjorden that primarily used bulk isotopes (e.g., $\delta^{13}\text{C}$,
563 $\delta^{15}\text{N}$) and their ratios for source apportionment (Kuliński et al., 2014; Singh et al., 2024b), our
564 study advances the biochemical perspective by integrating molecular level biomarkers (amino
565 acids, sugars) with a spatially resolved transect. This approach shifts the focus from POM origin
566 to its functional quality, enabling differentiation between labile and refractory pools. Our study
567 demonstrates that macroalgal-dominated sites in Kongsfjorden act as hotspots of labile and
568 bioavailable organic matter, significantly shaping the composition and lability of POM in adjacent
569 waters. The intermediate and variable patterns observed at the few stations highlight that the
570 influence of MDS was not uniform but forms a gradient shaped by local hydrodynamics,
571 freshwater inputs, and nutrient availability. The strong spatial heterogeneity observed, particularly

572 the emergence of Brandal as a biogeochemical hotspot, emphasizes that macroalgal impacts on
573 coastal carbon cycling are unevenly distributed within fjord systems. Such localized but persistent
574 sources of organic carbon from macroalgal beds to surrounding waters, thereby dampening the
575 seasonal variability in carbon availability (Norkko et al., 2007), enhancing benthic-pelagic food-
576 web stability and increase ecosystem resilience to inter-annual fluctuations in pelagic primary
577 production (Norkko et al., 2007; Renaud et al., 2015).

578 Although our study focused on surface waters, future research should include vertical
579 fluxes of POM near macroalgal beds and their coupling to hydrodynamics. Additionally, the
580 effects of seasonal variability driven by glacial melt, riverine runoff, and episodic nutrient inputs
581 at the coast are important because they can alter carbon concentrations and biochemical
582 composition, particularly in nearshore macroalgal habitats (Ager et al., 2023). Experimental
583 studies at model sites like BD could further help elucidate the rates of labile carbon turnover,
584 microbial utilization, and nutrient remineralization at these sites. As macroalgal habitats are
585 expanding under ongoing warming, resolving the contribution of macroalgal biomass and beds-
586 associated organic matter dynamics in coastal biogeochemistry would be important for estimating
587 Arctic carbon budgets and ecosystem functioning.

588

589 **Conclusion**

590 The present study provides new insights into the role of Arctic macroalgal beds as active drivers
591 of coastal particulate organic matter dynamics in Kongsfjorden, an Arctic fjord. By integrating
592 bulk biogeochemical composition, stable isotopes, biopolymeric composition, and molecular
593 biomarkers, we demonstrate that macroalgal habitats imprint surface waters with a distinct
594 biochemical and molecular signature. Elevated concentrations of POC, PN, carbohydrates,

595 proteins, monosaccharides, and amino acids at macroalgal-dominated sites indicate that
596 macroalgal beds act as localized sources of biochemically labile organic matter to the overlying
597 water column. Systematic offshore declines in bulk parameters, together with internal
598 reorganization of biopolymeric and molecular composition, reveal that macroalgal-beds derived
599 POM is efficiently exported across fjord-scale gradients and undergoes selective early-stage
600 transformation during lateral transport. The muted bulk isotopic gradients further indicate that
601 macroalgal influence is expressed through continuous mixing and biochemical restructuring of a
602 heterogeneous particulate pool rather than simple replacement of pelagic organic matter. A
603 pronounced spatial gradient was observed across the stations, within which Brandal emerged as a
604 distinct biogeochemical hotspot of macroalgal-associated organic matter dynamics, as supported
605 by our multiproxy study. Overall, our findings show that macroalgal beds function as dynamic
606 benthic–pelagic coupling zones that redistribute and transform organic carbon beyond their
607 immediate habitat. As macroalgal cover continues to expand along Arctic coastlines under climate
608 warming, their contribution to coastal carbon fluxes is likely to intensify, with important
609 implications for Arctic carbon budgets and ecosystem functioning.

610

611 **Data availability.** The data are available in the Zenodo repository at:
612 <https://doi.org/10.5281/zenodo.18457176> (Jagtap et al., 2026).

613

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618

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621

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