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Climate change and diminishing seasonality in Arctic benthic processes

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1 Summary

1 The iconic picture of Arctic marine ecosystems shows an intense pulse of biological productivity around the
2 spring bloom that is sustained while fresh organic matter (OM) is available, after which ecosystem activity
3 declines to basal levels in autumn and winter. We investigated seasonality in benthic biogeochemical cycling
4 at three stations in a high-Arctic fjord that has recently lost much of its seasonal ice-cover. Unlike observations
5 from other Arctic locations, we find little seasonality in sediment community respiration and bioturbation
6 rates, although different sediment reworking modes varied through the year. Nutrient fluxes did vary,

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7 suggesting that, although OM was processed at similar rates, seasonality in its quality led to spring/summer
8 peaks in inorganic nitrogen and silicate fluxes. These patterns correspond to published information on
9 seasonality in vertical flux at the stations. Largely ice-free Kongsfjorden has a considerable detrital pool in soft
10 sediments which sustains benthic communities over the year. Sources of this include macroalgae and
11 terrestrial runoff. Climate change leading to less ice cover, higher light availability, and expanded benthic
12 habitat, may lead to more detrital carbon in the system, dampening the quantitative importance of seasonal
13 pulses of phytodetritus to seafloor communities in some areas of the Arctic.

14

15 1. INTRODUCTION

16 One of the dominant concepts guiding current understanding of the functioning of Arctic marine ecosystems
17 is the overriding role of dramatic seasonality in physical drivers. Indeed, intense but short-lived algal blooms
18 characterize many Arctic areas and are coupled to the return of sunlight, melting of sea ice, and stratification
19 of the water column. These blooms fuel both pelagic and benthic food-webs, and sustain migratory fish,
20 seabirds, and mammals during the short summer. The lack of primary production during the long polar night
21 has resulted in an assumption of dormancy in many ecosystem elements [1], but this has recently been
22 challenged by evidence of active functioning throughout the ecosystem [2,3], including by seafloor
23 communities [4].

24 For Arctic seafloor communities, generally presumed to be limited by labile carbon [5], ecological functioning
25 shows strong spatial[6,7] and seasonal[8–12] variability linked to patterns of food availability. In spring and
26 summer, intense pulses of fresh material can reach the seafloor, such as ice-derived material or
27 phytodetritus[13,14], upon which benthic communities react in both field and experimental studies by quickly
28 increasing respiration and bioturbation rates[11,15]. These findings are consistent with the paradigm of
29 pelagic-benthic coupling, which posits that stocks and processes in seafloor communities generally mirror
30 spatial and temporal patterns in pelagic production and flux[16,17].

31 Such coupling has been suggested to be more pronounced in high-latitude environments due in large part to
32 the pulsed or spatially discrete nature of food arrival on the seafloor [18]. Many of the pioneering studies of
33 these processes, however, have been conducted on open shelves and areas with considerable sea-ice cover.
34 Climatic change has led to strong declines in sea-ice cover, thickness, and the length of the sea-ice season over
35 the past decades[19], and has resulted in changes in phenology and composition of phytoplankton blooms and
36 flux patterns[20,21]. Further, increased temperature and light availability (due to reduced ice cover) result in
37 increased benthic algal production in nearshore regions[22], with predictions of larger inputs of (macro-) algal
38 detritus to benthic systems in a warmer Arctic. How predicted and observed changes in amount and
39 seasonality of labile carbon will affect Arctic seafloor communities is unclear, but their processes are vital to
40 regenerating nutrients in these otherwise oligo- to meso- trophic systems. Furthermore, fjords are sites of
41 disproportionately high carbon sequestration on a global scale[23], and climate-driven changes in cycling may
42 have implications for climate feedback processes.

43 Kongsfjorden, a high Arctic fjord on the west coast of Svalbard, has observed a dramatic reduction in seasonal
44 ice-cover, and except for inner bays, has been largely ice free in winter since 2006 [24]. The fjord still exhibits
45 strong seasonality in primary production and vertical fluxes to the seafloor [25,26] but little seasonal
46 variability in infaunal community structure [27,28]. Sediment processes, such as oxygen and nutrient fluxes
47 and bioturbation rates, have not been investigated but are critical to understanding ecosystem functioning in
48 rapidly changing Arctic environments.

49 In this study, we quantify seasonal differences in (1) sediment properties, (2) bioturbation and
50 biogeochemical-cycling rates at three locations in Kongsfjorden with different ice-cover and infauna-
51 community composition, and (3) identify mechanisms linking environmental drivers and ecological processes.
52 Results offer insight into the response of benthic communities to a changing Arctic, and how current
53 paradigms of ecosystem functioning may be challenged over the coming decades.

54

2. MATERIAL AND METHODS

2.1 Study area

Kongsfjorden (79°N and 12°E) is 27 km long, 10 km wide, and is located on the Northwestern part of Spitsbergen Island in the Svalbard Archipelago (Figure 1). Because of its open connection to Fram Strait, it is largely influenced by advection of transformed Atlantic waters [29]. In the past, the fjord was regularly covered by sea ice, but because of increased advection of Atlantic water, it experiences variable and reduced sea-ice, with mostly ice-free years since 2005/2006 [29]. The inner part of the fjord is still rather “Arctic” because of the influence of four large tidal glaciers.

Three sampling stations were selected along a gradient from the inner part of the fjord, to the fjord opening: the inner-fjord station (78°54 N, 12°28 E, 80 m deep, Station A) was located at 1.4 km from the head of the fjord under the direct influence of the tidal glacier inputs; the middle-fjord station (78°567 N, 11°56E, 295 m deep, Station B) was located midway between the tidal glacier and the ocean; and the outer station (78°59 N, 11°32 E, 305 m deep, Station C) was located 24 km from the head of the fjord, near the fjord mouth. All stations were visited in May, August and October 2012, and in August 2014 and January 2015. However, due to technical difficulties, it was not possible to perform sediment cores incubations in May and August 2012 at the inner station. The middle and outer stations were also visited in January 2013 period.

2.2 Field sampling

During each field campaign, nine sediment cores (12.7 cm diameter, 10 cm height) were collected from each station with a HAPS corer (KC Denmark), except in January 2013 where the sediment cores were collected using a box corer (45 cm x 45 cm). The top 2 cm of sediment from three cores were sliced after collection for

79 determination of the sedimentary organic matter quantity and quality (e.g., chlorophyll and phaeopigments;
80 total organic carbon and total nitrogen contents: TOC, TN). Sediments were gently homogenized and frozen (-
81 20°C) for further analyses. The six remaining cores were kept in a dark cold room at 2°C for benthic processes
82 measurements.

83

84 2.3 Sediment core incubation for benthic fluxes and bioturbation activities measurements

85

86 Sediment cores were filled (~1L) with recently collected bottom water (2-3 °C, 35 ‰, [30]) and aerated to keep
87 oxygen saturation. The cores were acclimated in the cold room for 24 h (2-3 °C), where upon overlying water
88 was changed to remove the released metabolites, and 5 g of fluorescent luminophores (red, 63–90 µm) were
89 homogeneously introduced to the overlying water to quantify biological sediment reworking activity [7]. In
90 order to measure nutrient fluxes and sediment oxygen demand (SOD), cores were then sealed using tops that
91 provided constant stirring of the overlying water [15]. Oxygen concentrations were monitored every 4 to 6 h
92 using spot sensors (Presens A/S; Germany) [15]. Incubations were terminated after 24 h when 15–20 % of the
93 oxygen had been consumed and SOD was measured as the (negative) slope of the regression line between
94 oxygen concentration and time [15].

95 Sixty milliliters of overlying waters were sampled with a syringe at the beginning and at the end of the 24h
96 incubation for nutrient analyses. Nutrient fluxes were measured as a difference in nutrient concentration
97 between the two sampling times [15]. Water samples for nitrate + nitrite ($\text{NO}_3^- + \text{NO}_2^-$), ammonium (NH_4^+) and
98 phosphate (PO_4^{3-}) were filtered (0.2 µm) and directly frozen for future analyses, while filtered samples for
99 silicate ($\text{Si}(\text{OH})_4$) were kept at +4°C. Cores were then reopened and kept with constant aeration by bubbling
100 and by renewing overlying water every three days. Cores were incubated in those conditions with the
101 luminophores for 10 days [7]. At the end of the experiment, the sediment cores were sliced into 0.5-cm layers

102 from 0 to 5 cm depth, 1-cm layers from 5 to 10 cm depth and 2-cm layers from 10 to 18 cm depth. Each slice
103 was carefully homogenized and kept for luminophores quantification.

104

105 2.4 Laboratory analyses

106

107 2.4.1: Bulk sediment analyses

108 At the laboratory, sediments were freeze-dried and gently crushed to powder and homogenized for bulk
109 sediment analyses. Dry bulk sediment density (δ) was determined for each sample by using the known
110 sediment volume. Pigments (chlorophyll *a* (chl*a*) and phaeopigments (phaeo)) were analyzed fluorometrically
111 [15]. Organic matter (OM) content was measured as loss on ignition (450°C, 4 h). Total organic carbon (TOC)
112 and total nitrogen (TN) contents were measured by the Thermo Quest Flash EA 1112 CHN analyser [15].
113 Biomass of TOC and pigments contents was calculated (TOC_{bm}, chl_{abm}, and phaeo_{bm}) as ratios (Chl*a*/phaeo; C-
114 Chl*a*/TOC) over the 0-2 cm sediment layer.

115

116 2.4.2: Nutrient fluxes

117 Nitrate + nitrite, silicate, and phosphate were analyzed by colorimetry on a Bran+Luebbe Autoanalyzer 3, and
118 ammonium was analyzed by fluorometry [15]. Analytical precision for nutrient analyses was 0.05 μ M. Fluxes
119 were calculated from the slopes of the linear regressions of nutrient concentrations against time.

120

121 2.4.3: Bioturbation measurements

122 Luminophore detection and counting for quantification of the tracer transport modes were made following to
123 [7]. This model simultaneously quantifies the biodiffusion-like transport (*Db* coefficient; $\text{cm}^2\cdot\text{y}^{-1}$) and the non-
124 local transport of the tracers (*r* coefficient; y^{-1}). It adjusts a theoretical curve of the tracer distribution with
125 depth on experimental data. The best fit between the observed and modeled tracer distribution is estimated by
126 the least squares method and produces the best *Db* and *r* coefficients.

127

128 2.5 Data analyses

129

130 The influences of time and location on biogeochemical fluxes, sediment variables and bioturbation coefficients
131 were tested using a two-way analysis of variance with season (January, May, August, October from 2012 to
132 2015) and stations (inner, middle, outer) as fixed factors. To satisfy homoscedasticity and normality
133 requirements, oxygen and silicate fluxes were $\log(x+1)$ and square-roots transformed, respectively. Parametric
134 analyses (ANOVA) and pairwise comparison tests (Tukey's HSD) were then applied to these variables and to
135 TOC and TN. Differences in other parameters (C/N, TOC_{biom} , Chl_{biom} , $PhaeO_{biom}$, C-Chla/TOC, Chla/Phaeo,
136 ammonia, nitrate+nitrite, and phosphate fluxes, Db and r coefficients) were tested using the non-parametric
137 two-way analysis of variances (Sheirer-Ray-Hare test) followed by the Wilcoxon pairwise comparison test
138 with Bonferroni corrections, due to the non-homoscedasticity of the data and the unbalanced design [31].

139 In order to determine which biogeochemical variables, benthic fluxes, and bioturbation coefficients explained
140 most variability among studied stations between 2012 and 2015, a principle components analysis (PCA) was
141 performed using the "factomine" Rstudio package[32]. Data were normalized prior to analysis.

142 Correlation analyses were then used to quantify the relatedness between variables using the non-parametric
143 Spearman coefficient after data normality verification.

144

145 **3. RESULTS**

146

147 3.1 Sediment organic matter and pigments

148

149 OM (9%), TOC (1.6%) and TN (0.2%) were significantly higher at outer Station "C", followed by the middle
150 Station "B" and the inner station "A" (Table 1, supplementary figure 1, S1). No temporal changes in % OM,
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151 TOC and TN were observed at Station A. In the outer station, OM, TOC and TN contents were significantly
152 higher in January 2015 than in August 2014 and October 2012 (table 1, Suppl. Material. 1). OM followed the
153 same trends in the middle station, but TOC was lower there in January 2015 than in August 2012, 2014 and
154 May 2012 (Table 1, supplementary figure 1, S1). Significantly lower biomass of TOC ($\text{TOC}_{\text{bm}} \sim 50\text{-}100 \text{ mg m}^{-2}$)
155 was found at Station A compared to the two other stations for each date (Table 1, Figure 2a, supplementary
156 figure 1, S1). Seasonal decreasing of TOC_{bm} was only statistically significant at Station B in January 2015
157 (figure 2a). Biomass of Chl-a (Chl_{abm}) was highest (60-70 mg m^{-2}) near the glacier in May and August 2012
158 (table 1, figure 2b). While the Chl_{abm} remained stable over time at station B, it significantly decreased in
159 January 2015 in stations A and C (10 mg m^{-2} ; figure 2b, table 1). Biomass of phaeopigments (PhaeO_{bm}) was
160 significantly different between all station pairs, being significantly the lowest near the glacier (50 mg m^{-2}),
161 followed by the outer ($\sim 120 \text{ mg m}^{-2}$) and middle ($\sim 150 \text{ mg m}^{-2}$) stations (figure 2c). PhaeO_{bm} did not change
162 seasonally at station B, but significantly decreased in January 2015 at the two other stations (table 1, figure 2c).
163 $\text{Chl}_a:\text{phaeo}$ and C- $\text{Chl}_a:\text{TOC}$ ratios were both significantly higher at the station near the glacier in May and
164 August 2012, whereas it decreased significantly in January 2015. $\text{Chl}_a:\text{phaeo}$ ratios and C- $\text{Chl}_a:\text{TOC}$ ratios
165 were consistent at the middle and outer stations for the entire sampling period. Pigment biomass and their
166 respective ratios were highly variable in October between the sediment cores at station A (Table 1, Figure 2).

167

168 3.2 Bioturbation coefficients

169

170 The biodiffusion coefficient D_b ranged from 0 to 3 $\text{cm}^2 \text{ y}^{-1}$ along the fjord; mean values were significantly
171 higher in May 2012 (2-3 $\text{cm}^2 \text{ y}^{-1}$), than in August 2012, 2014, October 2012 and January 2015 ($D_b < 0.5 \text{ cm}^2 \text{ y}^{-1}$;
172 $p < 0.00002$) for middle and outer stations (table 1, figure 3). The non-local transport coefficient (r) ranged from
173 0 to 8 y^{-1} over the study area and was significantly lowest at the inner station in October 2012, August 2014
174 and January 2015 (table 1, figure 3). While the mean r remained stable over time at the middle station, it was
175 significantly higher in October 2012 for the outer station ($p < 0.01$) (table 1, figure 3).

176

177 3.3 Oxygen and nutrient fluxes

178

179 Station A presented no data (nd) in May, August 2012, and January 2013 since core incubation at this station
180 was not possible during these months. SOD was lowest at the inner station in October 2012, August 2014 and
181 in January 2015 (Figure 4a, Table 1) and remained stable over the three sampling periods (6-7 mmol O₂ m⁻² d⁻¹).
182 For the middle and outer stations, SOD was similar (10-12 mmol m⁻² d⁻¹) and did not vary seasonally (p>0.12,
183 Table 1), although SOD tended to be higher in the months of August 2012 and 2014 at the middle station.
184 Nutrient fluxes were measured at the middle and outer stations in May, August, October 2012, and January
185 2015 and during October 2012 and January 2015 at the inner station (Figure 4 b-e, Table 1). Silicate was always
186 released from the sediment and significant highest rates were at the middle and outer stations (1.5 - 2 mmol m⁻²
187 d⁻¹, p<0.05), mainly in August and October 2012 (Figure 4b, table 1). Ammonium uptake was significant and
188 consistent at the outer station (-0.1 mmol m⁻² d⁻¹; p<0.05, table 1, figure 4c). Low levels of ammonium release
189 were measured in the middle station (0.1 mmol m⁻² d⁻¹) with no significant seasonal change. At station A,
190 ammonia fluxes were opposite with high ammonia release in October 2012 (0.4 mmol m⁻² d⁻¹) and ammonia
191 uptake in January 2015 (- 0.5 mmol m⁻² d⁻¹). Nitrate + nitrite showed a consistent pattern going from
192 significant NO₃+NO₂ uptake in May 2012 (p<0.05, table 1) at stations B and C to release in October, August
193 2012 and January 2015 for all stations (Figure 4d). Net phosphate fluxes were quite low (< 0.04 mmol m⁻² d⁻¹)
194 and showed different significant seasonal patterns among the three stations (Figure 4e, Table 1, p<0.05).
195 Phosphate influxes were measured at station A in October 2012 and in January, and in station C in May and
196 January (Figure 4d). Phosphate was released and significantly highest in October 2012 at the stations B and C
197 (p<0.05, table 1).

198

199 3.4 Environmental variables

200

201 The PCA analysis explained 59% of the variability among sampling stations and dates: the first axis explained
202 37% and the second axis 22% (Figure 5, supplementary figure 2, S2). The most important variables (and their
203 loadings) defining the first axis were TOC_{bm} (0.89), silicate fluxes (0.80), r (0.76), phaeo_{bm} (0.75), PO_4^{3-} fluxes
204 (0.46), SOD (-0.54), NH_4^+ fluxes (-0.54), C-chla:TOC (-0.75), chla:phaeo (-0.83), while chl_{abm} (0.96), chla (0.93),
205 NH_4^+ fluxes (0.63), C-chla:TOC (0.60), phaeo_{bm} (0.51), and C:N (-0.46) defined the second axis. Stations were
206 separated into two groups on the basis of PCA results: Station A alone and stations B and C together. Time
207 points at Sta A are distributed along a gradient from lowest values of chla and NH_4^+ flux in January to highest
208 in October. The opposite gradient was observed for C/N. Sampling date for stations B and C had little effect on
209 station groupings, and these stations were characterized by the PCA as having high SOD, phaeo_{bm} , TOC_{bm} ,
210 nitrate+nitrite, phosphate and silicate fluxes, and non-local bioturbation rates. Biogeochemical fluxes were
211 significantly inter-correlated, SOD was positively correlated with ammonium uptake, and silicate and
212 phosphate efflux to overlying waters as well as chla:phaeo and C-chla:TOC ratios (table 2). SOD was
213 negatively correlated with phaeo_{bm} and non-local bioturbation (table 2). Chl_{abm} was positively correlated with
214 ammonium flux (table 2). Both biodiffusion and nitrate+nitrite fluxes were not correlated with any measured
215 variables.

216

217

218 4. DISCUSSION

219

220 4.1 Spatial and temporal differences in sediment properties

221

222 In Kongsfjorden, previous studies have shown seasonal changes in pelagic production. In 2012, a mooring in
223 mid-Kongsfjorden registered a strong diatom-dominated spring bloom from April to mid-May, with moderate

224 fluorescence from mid-June until July [26]. A seasonal sediment-trap study conducted from 2012-2013
225 documented a sedimenting bloom in May as increased POC and chl a flux at all three stations, continuing into
226 August at the glacier station (Station A) [25]. Another study [33] found that the sediments near the glacier
227 were lithogenic-dominant depleted in biopolymeric carbon (the sum of the main macromolecules: lipids,
228 proteins and carbohydrates) compared to the entrance of the fjord and that the sedimentary isotopic signature
229 showed different sources between the inner (fresh diatoms, lithogenic material with calcareous benthic
230 foraminifers) and outer (faecal pellets, degraded phytoplankton cells) stations. Recently, non-pelagic sources
231 of organic carbon have been suggested to be important for biogeochemical cycling in Kongsfjorden and many
232 coastal sites in the Arctic. These other sources, including macroalgal detritus [11], terrestrially-derived carbon
233 [34,35], and microphytobenthos [36], may be partly responsible for the higher sedimentary TOC at middle and
234 outer Kongsfjorden stations, whereas the high inorganic sediment load at the glacier station dilutes any of
235 these inputs resulting in consistently low TOC levels. These sources were not measured in this study,
236 however.

237 It has been suggested that changes in the quality of the organic matter on the seafloor can be reflected in
238 sedimentary TOC or pigments [37]. Although sediment OM, TC, TN contents and TOC_{biom} were higher in the
239 middle and outer stations in our study, biogenic silica and fecal-pellet carbon fluxes, indicating zooplankton
240 grazing of diatoms at these same stations in May [25], likely explain the low chl a/Phaeo and C-chl/TOC ratios
241 in sediments at Stations B and C year-round. Low zooplankton grazing is suggested for Station A [25,33],
242 allowing fresher sedimenting material at this station.

243 Although temporal changes were not reflected in sediment organic parameters (OM, TC, TN, TOC_{biom}) at
244 station A (glacier station), temporal decline in sediment pigments (chl a, phaeopigments, chl a/Phaeo and C-
245 chl/TOC ratios) were observed at this station. This is perhaps to be expected due to the seasonal sources of
246 phytopigments relative to the larger pool of OC of mixed lability in the sediments. This shows that sediment
247 pigment content and biomass are determined by the intensity of POC (grazed, faecal pellets) and

248 phytoplankton (ungrazed) downward export fluxes over the year. Elevated export fluxes observed in May
249 2012 near the station result from the phytoplankton bloom and the release of particles from glacier melting,
250 while during the important melt period in August the turbid waters likely dampen phytoplankton
251 development [25]. This is more obvious in August 2014, which was a warm year for the Kongsfjorden with the
252 inner section receiving warm Atlantic waters accelerating the glacier melt [38–40]. The month of January in
253 this region is marked by a decline in the development of autotrophic organisms and in glacial melt both
254 caused by the colder temperatures and polar night [25]. Once deposited at the sediment surface, fresh organic
255 material (ungrazed) is slowly consumed over the following months since the benthic biomass and diversity
256 [27], and bioturbation activities (this study) remain low at this station. In contrast, the export fluxes observed
257 in the middle and outer stations remained elevated and stable over time due to the continuous intrusion of
258 warm Atlantic waters and associated phytoplankton communities until the mid-fjord [25,39], favouring the
259 match between phytoplankton bloom and copepod grazing, and POM fluxes. However, sedimenting OM does
260 not accumulate at Stations B and C, suggesting it is consumed and processed rapidly by seafloor communities.
261 These two stations have higher faunal abundance, species and functional diversity than Station A [27]. Higher
262 bioturbation rates at these stations than at Station A also suggest that benthic communities at these stations are
263 more efficient at consuming material upon its arrival on the sediment surface. A similar finding was made in a
264 study on the Beaufort shelf, where, despite strong seasonal signals in vertical flux and sediment community
265 oxygen consumption, little change in sediment pigments was found [11].

266

267 4.2 Spatial and temporal differences in bioturbation activities

268

269 Bioturbation showed strong spatial variability in the fjord, with very low biodiffusion and non-local mixing at
270 Station A. This station has no deep burrowing polychaetes (e.g. maldanids) and is dominated by small
271 surface-deposit feeders (cirratulid and cossurid polychaetes) throughout the year [27]. Non-local mixing rates
272 at Station A were similar to those for the deep stations (over 400 m) Barents Sea region dominated by small-

273 sized organisms [7]. The middle and outer stations showed similar rates of both biodiffusion and non-local
274 mixing, and these rates were 2-4x those from previous studies in Arctic [7]. Active burrowers and deep-
275 dwelling tubeworms were found at Stations B and C [27], and organic content was 3-4 x higher at the middle
276 and outer stations than at Station A (Figure 3).

277 There was little obvious seasonal change in non-local transport at any of the stations, and non-local transports
278 are positively correlated to degraded sedimentary organic matter (phaeopigment biomass). This is consistent
279 with the lack of accumulation of a pulse of phytopygments at the mid and outer stations (Figure 3), and the
280 lower richness and abundance of burrowers at Station A [27], particularly those most often involved in non-
281 local mixing (oweniid and maldanid polychaetes). Biodiffusion was highest in May at Stations B and C and
282 was a factor of >4 lower during the rest of the year. POC, chl a, biogenic silica, and fecal pellet fluxes,
283 indicators of deposition of organic material, were considerably (2-15 x) higher in May than during other
284 seasons at these stations [25], and likely led to enhanced biodiffusion activities, as observed in other studies
285 [15,41].

286 Diversity and size-structure of meio- and macrobenthic communities are similar through the year at each
287 station [27], probably due to sedimentary organic matter remaining available during a large part of the year.
288 Thus, it is supposed here that communities at each station change their bioturbation behavior through the year
289 depending on phytodetritus pulses and stock of degraded OM. Biodiffusion is dominant in May at the
290 stations B&C but non-local (conveyer-like) mixing dominates from August to January. The quality of OM
291 between May and August at the two stations may explain these changes, where sub-surface activities are
292 dominant after rapid processing of the freshest phytodetritus.

293

294 Although we don't have bioturbation data in May and August at the Station A, bioturbation intensity there is
295 lower than in stations B&C during the other seasons. This is caused by the impoverishment of benthic
296 communities by conditions at the glacier front (hydrodynamics, erosion), although the sedimentary pigments

297 are less degraded at this station from spring to fall. Stations B&C have more diverse benthic communities and
298 higher functional-trait diversity and bioturbation. This can explain why the two modes of bioturbation are
299 observed at these two stations.

300

301 4.3 Spatial and temporal differences in benthic fluxes

302

303 The remineralization of carbon and nutrients by Arctic seafloor communities has been shown to depend
304 primarily on organic matter availability [41–45]. At deep Arctic basin stations, depth is as important as
305 pigment concentration [33] but the depth range in this study was relatively narrow (80 - 305 m). SOD
306 measured in this study is similar to other measurements of SOD from Kongsfjorden [42,46], and generally
307 higher than colder Svalbard fjords [15,45,46] and deep-sea Arctic sediments [44]. SOD, stable over the year at
308 each station, was higher at Stations B&C where Phaeo_{bm} and TOC_{bm} are highest, although chl *a* was higher at
309 Station A. The lack of significant seasonal variability in SOD at any of our stations is in direct contrast to
310 findings in a number of empirical studies [8–11] showing SOD was linked with seasonal cycles of pelagic
311 production. Only in deep areas such as the central Arctic basin, where the seasonal pelagic signals is likely
312 reduced due to great depths and generally lower primary production, was no seasonality in SOD identified
313 [7]. Response to pulsed food inputs can be realized in elevated SOD within days and persist for several weeks
314 (e.g. [11]), and nutrient fluxes and bioturbation may respond at different time scales. Peak vertical flux of both
315 POC and chl *a* in 2012 was in May [25], simultaneous with the sediment flux and bioturbation measurements,
316 so we would have expected a peak in one or more of these parameters if there was a response to seasonal
317 inputs. In the other studies cited, however, the timing of sampling relative to a food pulse may influence
318 whether a response is observed.

319

320 Maintaining high SOD at stations throughout the year necessitates storage of organic material within
321 sediments and/or significant presence of other labile carbon sources. The presence of a 'food bank' within the

322 sediment that is available for use throughout the year was the explanation for little seasonality in SOD
323 observed along the western Antarctic Peninsula [47]. Alternately, more than 40% of carbon assimilation by
324 soft-sediment benthos in another boreal, ice-free fjord in west Svalbard came from macroalgal detritus, even at
325 depths up to 400 m [48], and an average of 60% of sediment organic carbon in Kongsfjorden comes from
326 macroalgae [49]. We have no reason to exclude either of these possibilities and, indeed, both may contribute to
327 the lack of seasonality in SOD.

328

329 Fauna associated with higher bioturbation rates at Stations B&C may also explain higher SOD [50]. The
330 correlation of SOD with non-local transport might result from intensification of microbial processes in
331 subsurface sediments at Stations B&C caused by maldanid and spionid burrowing here [27]. Change in
332 bioturbation mode between May and August at Stations B&C is not perceptible in SOD. This may indicate
333 either compensation in SOD between bioturbation functional groups and their associated microbial processes,
334 or a dominance of maintenance respiration in fauna that overwhelms enhanced seasonal activities by diffusers
335 or non-local mixers. Higher non-local transport in August likely stimulates the release of silicate to the
336 overlying water and enhances sedimentary silicate dissolution [51]. Silicate dissolution, usually most efficient
337 on grazed OM [52], is higher in stations with high $PhaeO_{bm}$ and enriched in diatoms. Thus, sediment microbes
338 can accelerate biogenic silica dissolution by colonizing and enzymatically degrading the organic coating of
339 diatom frustules.

340

341 Nutrient fluxes (in the same range of values from the Svalbard area [46] and in the Canadian Arctic [53])
342 indicate that fjord sediments are an important source of inorganic nutrients for driving primary production in
343 the fjord. The seasonality of nutrient fluxes is further evidence of rapid processing of the sedimenting spring
344 bloom/fecal pellet carbon. Higher NH_4^+ release at Station A might be the result of faster mineralization of the

345 fresher sediment organic material, compared to at Stations B&C, where degraded organic matter slows
346 microbial mineralization rates and perhaps leads to denitrification at the outer station.

347

348 4.4 Seasonality in a changing Arctic

349

350 Whereas strong seasonality of pelagic production and export of OM persists in a warmer, ice-free
351 Kongsfjorden, the benthic system does not show a dramatic response. Such seasonality in Arctic benthic
352 processes is most often observed in open shelf systems [8]. In one of the very few seasonal studies of benthic
353 processes performed in fjords [15] a strong response to experimental food addition was observed in a high-
354 Arctic system with up to 8 months of ice cover per year. We argue that the results from Kongsfjorden may be a
355 model for many areas on Arctic shelves undergoing loss of sea-ice and warming waters. Thus, it is important
356 to explore potential mechanisms for this loss of strong seasonality in some processes, and possible
357 consequences for Arctic benthic ecology.

358

359 There is considerable observational evidence that reductions in sea-ice and warming temperatures are
360 strongly linked to increased macroalgal production due in large part to increased light availability [54].
361 Macroalgae, particularly kelps, undergo seasonal growth and senescence cycles, generating considerable
362 amounts of detritus [55]. Production of this detritus, however, is temporally distinct from pulses of pelagic
363 phytodetritus as it arrives in autumn and winter due to natural senescence cycles and seasonal storms that
364 detach living kelps from the sea floor. Increased light levels in a warming Arctic may also lead to enhanced
365 growth of microphytobenthos, an as yet understudied source of organic matter to the coastal marine system
366 [36]. Additionally, inputs of terrestrial carbon via rivers, melting glaciers, and coastal erosion are also
367 predicted to increase considerably as the Arctic and surrounding systems warm [56]. It is already clear that
368 much of this carbon is labile and is processed rapidly when it reaches the marine system [35], and is not
369 restricted to coastal areas [57]. Thus, elevated levels and processing of detrital material in warming, ice-free

370 fjords relative to cold, seasonally ice-covered fjords [48,49] suggest sediment communities in the future Arctic
371 may function differently than at present.

372

373 How, then, will increased detritus content affect system functioning, aside from reduced seasonality? Detritus
374 has been suggested to dampen seasonal fluctuations in carbon supply, leading to more stable food-chains and
375 higher resilience to interannual variability in pelagic primary production [58]. Deposit-feeding taxa may be
376 favored over suspension-feeders in many of these systems with potential implications for bioturbation modes
377 and intensity, and at a longer time scales, decreasing functional traits diversity within benthic communities.
378 Monitoring programs could target these questions in detailed comparative studies. Such food-web shifts have
379 not been well studied but could have strong consequences for sustenance of top predators, including
380 subsistence human populations. Finally, fjords have been identified as sites of disproportionately high carbon
381 burial [23]. It is unclear whether increased detrital carbon and its impacts on seafloor processing will enhance
382 or reduce this role. It is possible, however, that greater inputs of labile macroalgal detritus will enhance
383 remineralization of more refractory sedimentary carbon that would otherwise be buried [59]. This 'organic
384 priming' can be promoted by bioturbation, enabling fresher material and oxidants to reach buried carbon, and
385 such processes demand both observational and experimental attention.

386

387 Responses to pulsed pelagic inputs will continue to be strong and pelagic-benthic coupling can still be quite
388 tight, but the addition of detrital carbon from macroalgae, benthic microalgae, and terrestrial sources can
389 make it harder to track seasonality in benthic activity. Benthic processes may remain quite seasonal on
390 oligotrophic shelves and ice covered coastal regions, but increases in organic matter inputs from terrestrial
391 and coastal systems may change this over time. The interaction of processes, including changes in relative
392 inputs of different carbon sources, declining seasonality in benthic activity, and potential changes in
393 bioturbation functional traits and food-web structure (i.e., decoupling of separate energy channels by

394 enhancing detrital food web [60]), will likely result in ecosystem instability and in alteration of carbon cycling
395 pathways. The potential consequences of fundamental changes in how organic matter is processed by Arctic
396 benthos imply a need for development of biomarkers and experimental approaches to tease apart these
397 interactions.

398

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406

407 **Data Accessibility**

408 The datasets supporting this article have been uploaded as part of the Supplementary Material.

409

410 **Competing Interests**

411 *We have no competing interests.*

412

413 **Authors' Contributions**

414 Substantial contributions to conception and design (NM, EM, PR), acquisition of data (NM, RC, PR), analysis
415 and interpretation of data (NM, EM, MAP, JD, MLG, RC, PR); 2) drafting the article or revising it critically for
416 important intellectual content (NM, EM, PR); and 3) final approval of the version to be published (NM, EM,
417 MAP, JD, MLG, RC, PR).

418

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Tables

Table 1: Differences in the bulk sediment variables, benthic fluxes and bioturbation coefficients at the three stations of Svalbard (Inner (A), Middle (B), Outer (C)) between 2012 (May, August, October), 2014 (August) and 2015 (January), after two-way ANOVAs (A; F and p values) or Sheirer-Ray-Hare (SRH; H and p values) tests. Significant differences ($p < 0.05$) are indicated by asterisk (*). Last column indicates the pair wise comparisons between the three stations.

	<i>Main Effect</i>			<i>Main Effect</i>		<i>Interaction</i>		<i>Pair wise comparison between stations</i>		
	test	<i>time</i>		<i>Station</i>		<i>time × Station</i>		<i>Inner Station</i>	<i>Middle Station</i>	<i>Outer Station</i>
		stat	p	stat	p	stat	p			
OM (%)	A	5.7	0.004**	26.6	0.00001***	5.4	0.001**	a	b	c
TOC (%)	A	12.7	0.00001***	849	0.00001***	7.3	0.00001***	a	b	c
TON (%)	A	12	0.00001***	1112	0.00001***	4.8	0.001**	a	b	c
C:N (mol:mol)	SRH	30	0.00001***	36	0.00001***	39	0.00001***	a	a	a
TOC _{bm} (mg.m ⁻²)	SRH	14	0.006**	70	0.00001***	15	0.04*	a	b	b
Chla _{bm} (mg.m ⁻²)	SRH	24	0.00001***	24	0.00001***	38	0.00001***	a	b	b
Phaeo _{bm} (mg.m ⁻²)	SRH	6.7	0.10	54	0.00001***	17	0.03*	a	b	c
C-Chla:TOC	SRH	7.6	0.1	70.4	0.00001***	31.6	0.0001**	a	b	b
Chla:Phaeo	SRH	6.5	0.16	36.5	0.00001***	35	0.00001***	a	b	b
O ₂ (mmol.m ⁻² .d ⁻¹)	A	2	0.12	6.5	0.002**	2.8		a	b	b
NH ₄ ⁺ (mmol.m ⁻² .d ⁻¹)	SRH	47	0.001**	88	0.0001**	53	0.01*	a	a	b
NO ₃ ⁻ (mmol.m ⁻² .d ⁻¹)	SRH	69	0.01*	12		52		a	a	a
Si(OH) ₄ ³⁻ (mmol.m ⁻² .d ⁻¹)	A	30	0.001**	28	0.0001**	4.5	0.0001**	a	b	c
PO ₄ ³⁻ (mmol.m ⁻² .d ⁻¹)	SRH	62	0.001**	41	0.01*	112	0.01*	a	b	a
Db (cm ² .y ⁻¹)	SRH	68	0.001**	11	0.004**	7		a	b	b
R (y ⁻¹)	SRH	65	0.001**	74	0.001**	12		a	b	b

Table 2: Spearman's rank correlation analyses between biogeochemical fluxes (O_2 , $NO_3^-+NO_2^-$, PO_4^{3-} , NH_4^+), sediment biomarkers (C:N, C-Chla:TOC, Chla:Phaeo ratios, and biomass of TOC, chla and phaeopigments), and bioturbation variables (Db, r). Significant values are marked in bold ($p < 0.05$).

	Db	r	O_2	$NO_3^-+NO_2^-$	$Si(OH)_4$	NH_4^+	PO_4^{3-}	C:N	chla:phaeo	C-Chla:TOC	TOC_{bm}	$chla_{bm}$	$Phaeo_{bm}$
Db	1.00	-0.20	-0.12	-0.27	-0.08	-0.43	-0.29	-0.18	-0.04	-0.16	0.34	-0.07	0.19
r	-0.20	1.00	-0.86	0.49	0.94	-0.42	0.80	0.06	-0.72	-0.69	0.77	-0.30	0.76
O_2	-0.12	-0.86	1.00	-0.38	-0.94	0.59	-0.65	0.00	0.71	0.72	-0.92	0.24	-0.91
$NO_3^-+NO_2^-$	-0.27	0.49	-0.38	1.00	0.45	0.08	0.15	-0.53	0.08	0.08	0.17	0.36	0.41
$Si(OH)_4$	-0.08	0.94	-0.94	0.45	1.00	-0.47	0.80	0.01	-0.72	-0.71	0.83	-0.21	0.87
NH_4^+	-0.43	-0.42	0.59	0.08	-0.47	1.00	-0.10	-0.37	0.82	0.86	-0.73	0.79	-0.36
PO_4^{3-}	-0.29	0.80	-0.65	0.15	0.80	-0.10	1.00	0.18	-0.59	-0.51	0.59	-0.16	0.66
C:N	-0.18	0.06	0.00	-0.53	0.01	-0.37	0.18	1.00	-0.48	-0.44	0.12	-0.71	-0.26
chla:phaeo	-0.04	-0.72	0.71	0.08	-0.72	0.82	-0.59	-0.48	1.00	0.98	-0.79	0.81	-0.50
C-Chla:TOC	-0.16	-0.69	0.72	0.08	-0.71	0.86	-0.51	-0.44	0.98	1.00	-0.82	0.80	-0.53
TOC_{bm}	0.34	0.77	-0.92	0.17	0.83	-0.73	0.59	0.12	-0.79	-0.82	1.00	-0.43	0.86
$chla_{bm}$	-0.07	-0.30	0.24	0.36	-0.21	0.79	-0.16	-0.71	0.81	0.80	-0.43	1.00	0.04
$Phaeo_{bm}$	0.19	0.76	-0.91	0.41	0.87	-0.36	0.66	-0.26	-0.50	-0.53	0.86	0.04	1.00

Figures captions

Figure 1: Locations of the three stations at Inner (station A), Middle (station B), Outer (station C) in Kongsfjorden (Svalbard).

Figure 2: Mean biomass (mg m^{-2}) of total organic carbon (TOC) (a), Chla (b), Phaeopigments (c) and mean ratios of chla:phaeo (d) and C-Chla:TOC (%) (e) over the 2 first cm of sediment (\pm SD) at the three stations in Kongsfjorden, Svalbard (Inner (A), Middle (B), Outer (C)) in 2012 (May, August, October), 2014 (August) and 2015 (January) (mean \pm SD, $n=3$). * indicate biomass or ratios that significantly differ with station and with time ($p<0.05$).

Figure 3 : Mean biodiffusion (Db in $\text{cm}^2 \text{y}^{-1}$) and non-local (r in y^{-1}) transports measured at the three stations in Kongsfjorden (Inner (A), Middle (B), Outer (C)) between 2012 and 2015 (mean \pm SD, $n=6$). * indicates bioturbation coefficients that significantly differ with station and with time ($p<0.05$). The station A presented no data (nd) in May and August 2012 since sediment cores incubations were not possible at this period. Absence of bars in August 2014 and January 2015 at station A and in May 2012 at stations B and C means that no bioturbation was measured.

Figure 4 : Mean oxygen (a) and nutrient net fluxes (b-e) ($\text{mmol m}^{-2} \text{d}^{-1}$) at the sediment-water interfaces at the three stations in Kongsfjorden (Inner (A), Middle (B), Outer (C)) between 2012 and 2015 (mean \pm SD, $n=6$). * indicates biogeochemical fluxes that significantly differ with station and with time ($p<0.05$). The station A presented no data (nd) when core sampling was not feasible.

Figure 5: Principal component analysis based on the sediment variables (C:N, Chla:phaeo and C-Chla:TOC ratios, biomass of TOC, Chla and Phaeo pigments), benthic fluxes (oxygen, ammonium (NH_4), nitrate+nitrite (NO_3+NO_2), phosphate (PO_4^{3-}), silicate ($\text{Si}(\text{OH})_4^{3-}$), and bioturbation coefficients (biodiffusion, Db and bioadvection, r) along the Kongsfjorden area between 2012 and 2015. The two axes pictured explain 58.8% of the variance in station data.

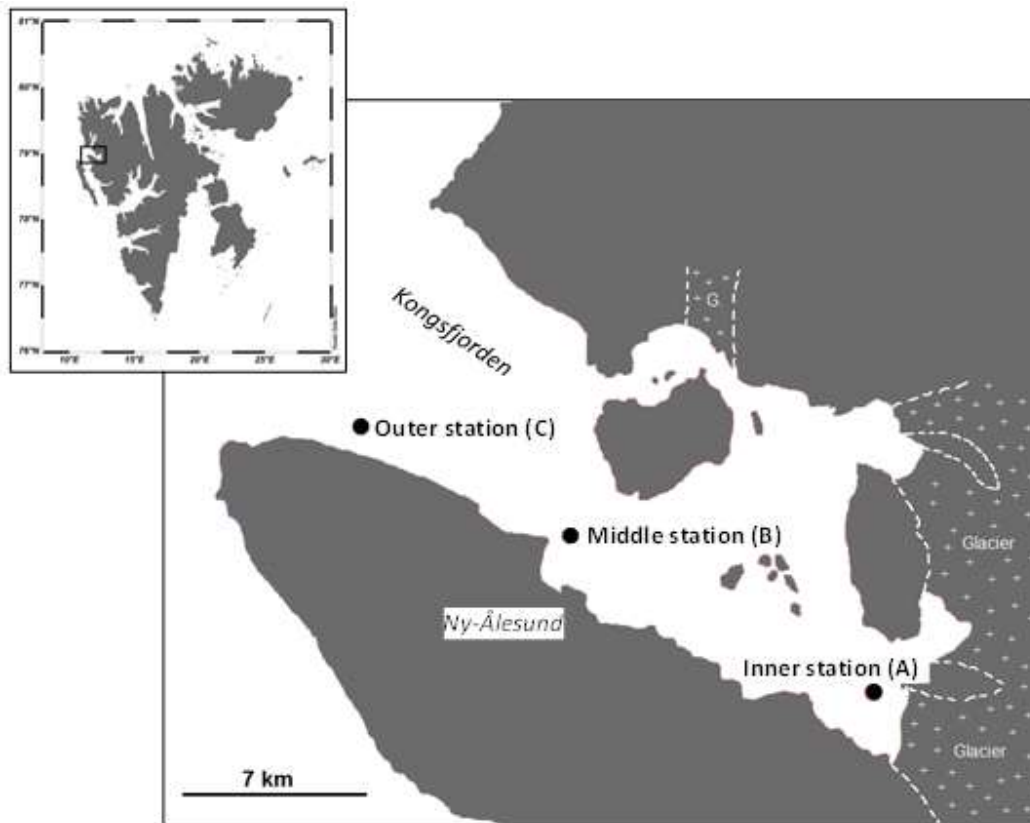


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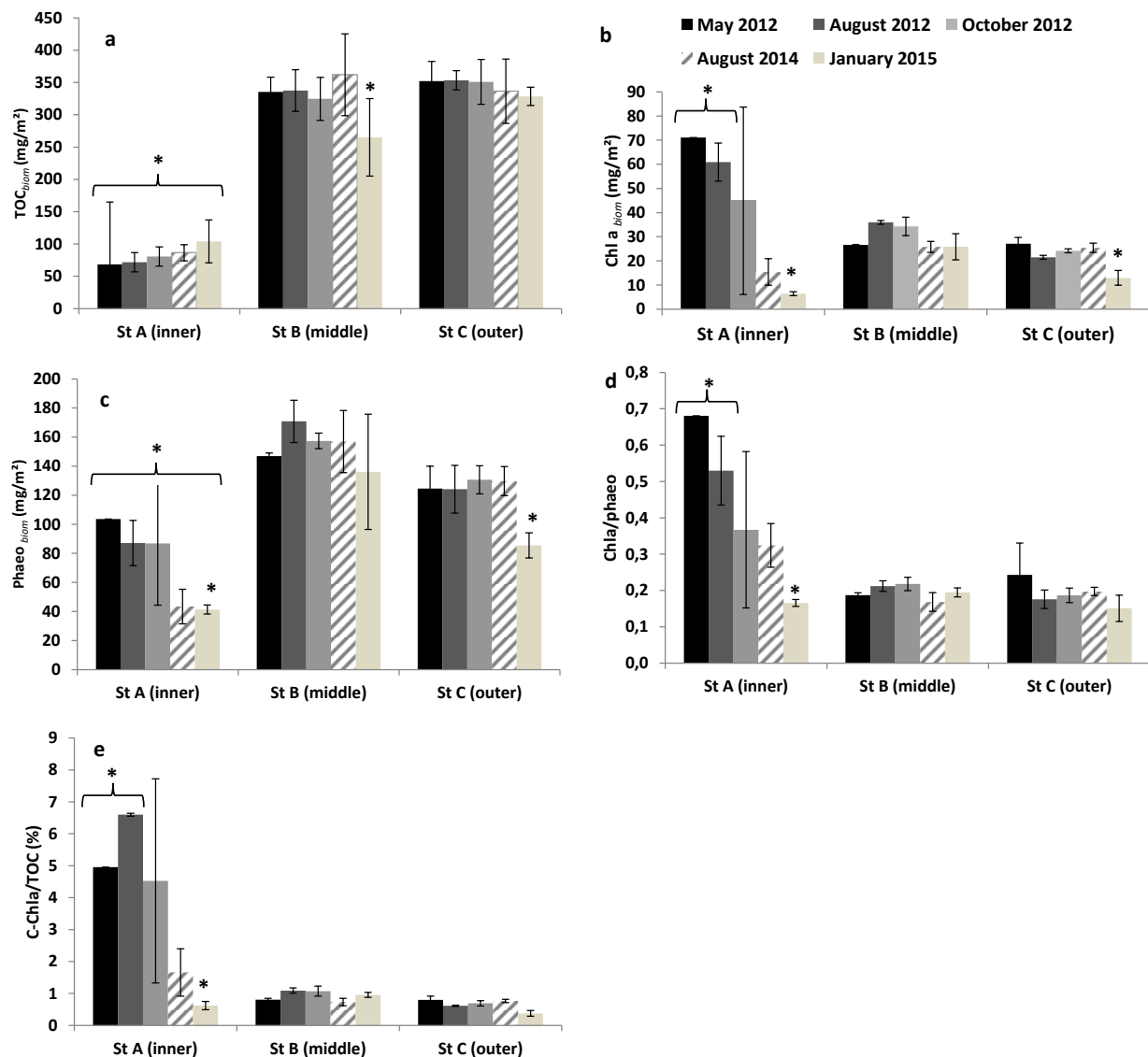


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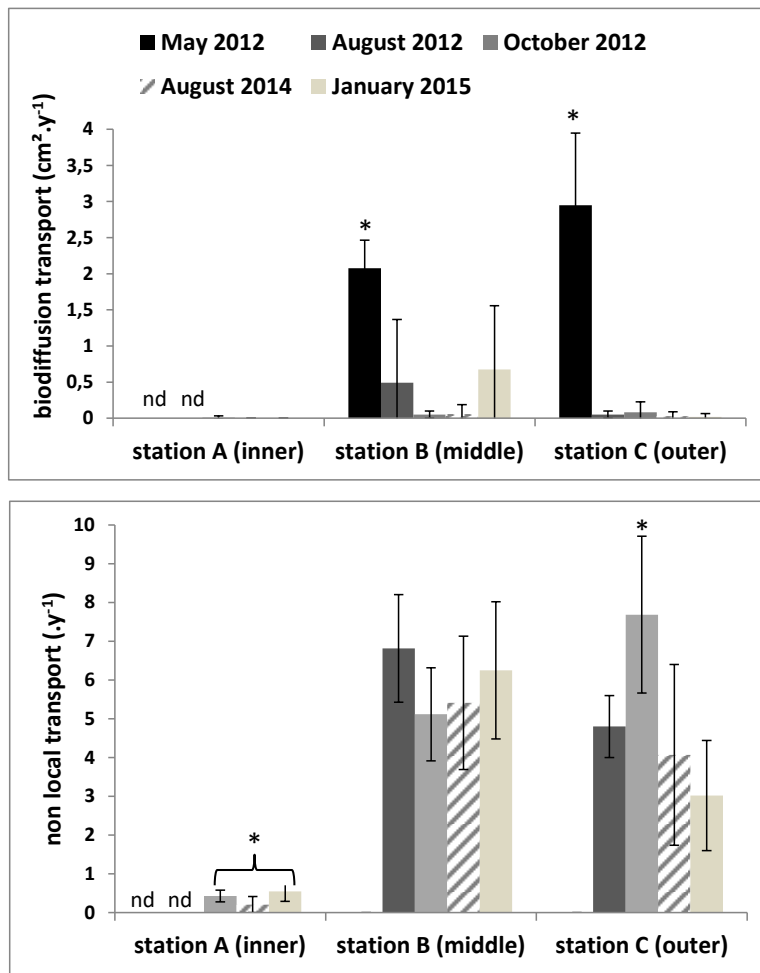


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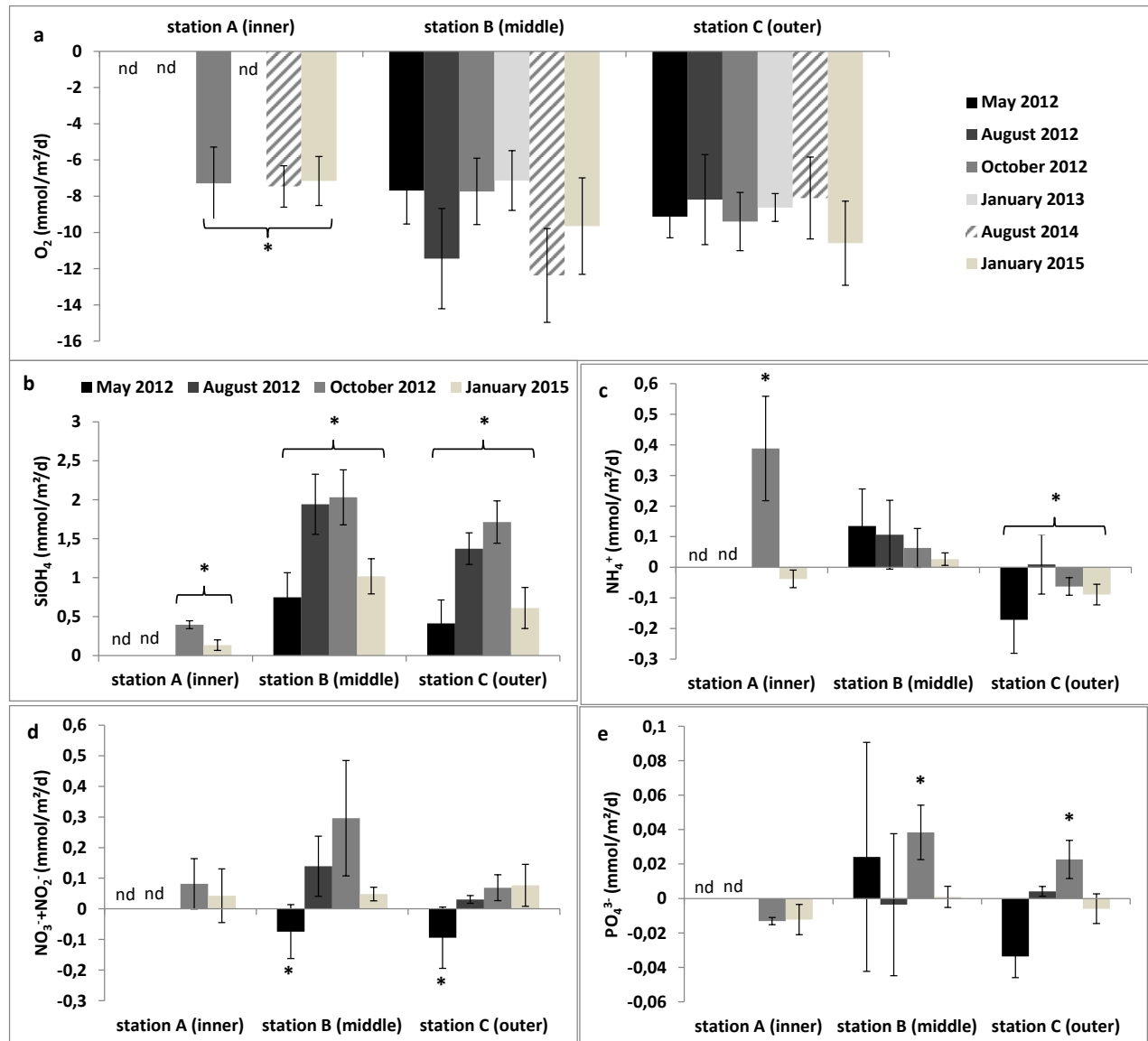


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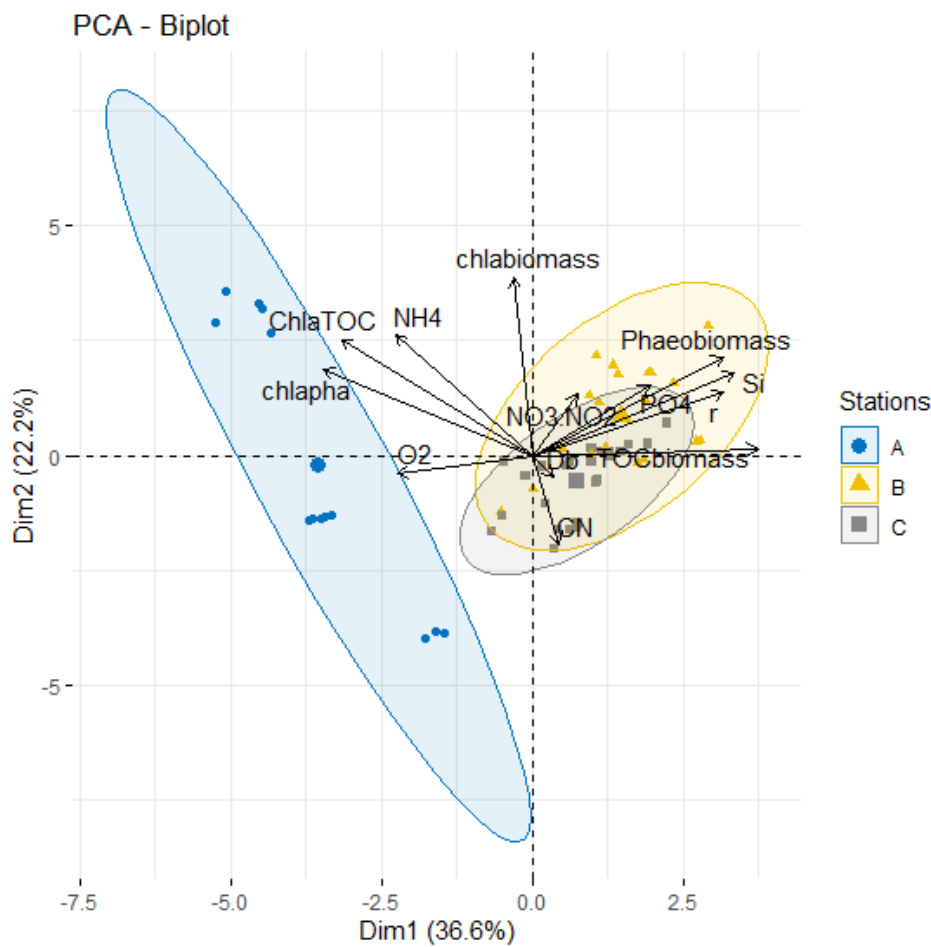


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