
Coastal waters freshening and extreme seasonality affect organic matter sources, quality, and transfers in a High Arctic fjord (Young Sound, Greenland)

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Abstract :

Arctic benthic ecosystems are expected to experience strong modifications in the dynamics of primary producers and/or benthic-pelagic coupling under climate change. However, lack of knowledge about the influence of physical constraints (e.g. ice-melting associated gradients) on organic matter sources, quality, and transfers in systems such as fjords can impede predictions of the evolution of benthic-pelagic coupling in response to global warming. Here, sources and quality of particulate organic matter (POM) and sedimentary organic matter (SOM) were characterized along an inner-outer gradient in a High Arctic fjord (Young Sound, NE Greenland) exposed to extreme seasonal and physical constraints (ice-melting associated gradients). The influence of the seasonal variability of food sources on 2 dominant filter-feeding bivalves (*Astarte moerchi* and *Mya truncata*) was also investigated. Results revealed the critical impact of long sea ice/snow cover conditions prevailing in Young Sound corresponding to a period of extremely poor and degraded POM and SOM. Freshwater inputs had a very local impact during summer, with relatively more degraded POM at the surface compared to bottom waters that were less nutritionally depleted but more heterogeneous among the sampled stations. Terrestrial inputs contributed to the SOM composition but showed a large variability along the fjord. Finally, diet analyses underlined the contrasted nutritional conditions, showing much higher lipid reserves in *A. moerchi* than in *M. truncata* during winter. Under a scenario with increased freshwater input, such results suggest a decline in organic matter quality and production in Young Sound, with subsequent impacts on benthic food webs.

Keywords : Arctic ecosystems, Benthic-pelagic coupling, Organic matter, Climate change, Fatty acids, Stable isotopes, Young Sound

57 INTRODUCTION

58 The Arctic has been subjected to atmospheric warming in recent decades at a rate that exceeds
59 the global average by a factor of 2–3 (AMAP 2017). This warming induces major modifications
60 in the Arctic marine environment, e.g., a decrease in sea-ice cover (extent and thickness) and
61 an increase in freshwater discharge (AMAP 2017, Kwok & Rothrock 2009, McPhee et al. 2009,
62 Ohashi et al. 2016). The Greenland Ice Sheet annual net loss is currently estimated at 186 Gt.yr⁻¹
63 ¹, which is double the melting rate observed for 1983–2003 (Bamber et al. 2012, Kjeldsen et al.
64 2015). Such changes are expected to impact marine systems through shifts in the spatial
65 distribution of species (Falk-Petersen et al. 2007) and altered food web dynamics via modified
66 quantity, quality, and seasonal timing of primary productivity (Iken et al. 2010, Leu et al. 2011,
67 Ardyna et al. 2014, Arrigo & van Dijken 2015). Moreover, changes in the phenology of primary
68 producers may create mismatches between peak algal blooms and faunal reproductive phases,
69 with major effects on the benthic-pelagic coupling (Søreide et al. 2010, Moran et al. 2012).

70 Several authors have modeled the evolution of food webs and marine wildlife within a changing
71 Arctic (e.g., Wassmann 2011, Kędra et al. 2015). However, recent studies indicate a regionally
72 variable Arctic ecosystem response to global warming depending on specific habitat
73 characteristics (e.g., water depth, exposure to terrestrial runoff; Carmack et al. 2015, De Cesare
74 et al. 2017, Gaillard et al. 2017). For instance, although the generally accepted paradigm states
75 an increase in primary production in the Arctic Ocean, the opposite trend could occur in coastal
76 areas (which represent 35% of the world's coastline) such as fjord systems, due to the increase
77 in freshwater inputs and subsequent turbidity (Carmack et al. 2015, Middelbo et al. 2018).
78 Terrestrial runoff from melting snow and ice increases water column turbidity and diminishes
79 light availability, in turn decreasing primary productivity (Murray et al. 2015, Arimitsu et al.
80 2016). Freshwater inputs also reduce primary productivity in some fjords due to increased
81 stratification, causing nutrient depletion in surface waters (Piquet et al. 2014, Meire et al. 2016,

82 Middelbo et al. 2018). On the other hand, freshwater inputs from glacier melting may provide
83 labile organic carbon, which may be a source of bioavailable carbon in low-productivity
84 ecosystems (Lawson et al. 2014). The impact of increased freshwater loads on the quality of
85 organic matter and transfers in Arctic fjords remains poorly understood.

86 We conducted a sampling program during August 2016 and May 2017 in a High Arctic fjord
87 (Young Sound, NE Greenland) to study how seasonal and physical constraints drive the sources
88 and qualitatively change the organic matter available for dominant benthic primary consumers:
89 the abundant filter-feeding bivalves *Astarte moerchi* and *Mya truncata* (Sejr et al. 2000, Born
90 et al. 2003). Potential bivalve food sources and body tissues were analyzed for fatty acid (FA)
91 and stable isotope (SI) composition. FA analysis can be used to trace the origin of organic
92 matter within an environment, since primary producers often show contrasting FA profiles
93 according to their taxonomic group (e.g., diatoms, dinoflagellates, macroalgae; Meziane &
94 Tsuchiya 2000, Dalsgaard et al. 2003, Kelly & Scheibling 2012). Moreover, biosynthesis of
95 specific FAs, such as polyunsaturated FAs (PUFAs), is usually limited in marine bivalves. This
96 enables the use of FA trophic markers to study diet (Kelly & Scheibling 2012, Thyrring et al.
97 2017). SI analysis may also help to characterize the trophic diet of organisms (Fry 2006,
98 Gaillard et al. 2017) and to investigate environmental processes occurring within an ecosystem,
99 such as inputs of terrestrial carbon (Calleja et al. 2017), organic matter degradation (McTigue
100 et al. 2015), or the dynamics of blooms (Tamelander et al. 2009).

101 The main goals of this study were to (1) understand how seasonal and physical constraints in
102 Young Sound may influence the sources and quality of pelagic organic matter (POM) and
103 sedimentary organic matter (SOM), (2) assess the seasonal patterns (ice/snow cover in May vs.
104 open sea in August) of organic matter transfers within this fjord, and (3) investigate the response
105 of two dominating bivalve species (*A. moerchi* and *M. truncata*) to such seasonality in food
106 availability.

107 MATERIALS AND METHODS

108 Study site and sampling

109 The study was conducted in Young Sound (74°N 20°W, Fig. 1), a High Arctic Greenland fjord
110 characterized by a long sea-ice duration of 9–10 months (Glud et al. 2007). The fjord is
111 approximately 90 km long and 2–7 km wide. The maximum depth is 330 m, but exchange with
112 coastal waters is limited by a shallow sill with a depth of 45 m at the mouth of the fjord
113 (Bendtsen et al. 2007). During land-glacier and snow melting, the surface waters become more
114 turbid and brackish due to freshwater inputs, especially in the inner part of the fjord (Ribeiro et
115 al. 2017). Generally, such freshwater inputs generate a bilayer estuarine water circulation with
116 low-salinity surface flows from the inner to the outer fjord and inflows occurring close to the
117 seabed (Bendtsen et al., 2014). Young Sound has the typical surface current circulation in fjords
118 affected by the Coriolis effect, with the southern part (Clavering Island side) more exposed to
119 freshwater outflow than the northern part (Wolloston Forland side; Bendtsen et al. 2007).

120 Sampling was conducted in August 2016 (open water, early productive period; De Cesare et al.
121 2017) and May 2017 (ice cover, expected “unproductive” period). We sampled three stations
122 in 2016 (Fig. 1), i.e., Pass Hytten (depth = 18 m, 74.41°N 20.33°W), Basalt Island (depth =
123 21.5 m, 74.33°N 20.36°W), and Kap Breusing (depth = 20 m, 74.21°N 20.11°W), but only Pass
124 Hytten and Basalt Island during 2017 for logistical reasons. At each station, ten liters of
125 seawater were collected at two depths corresponding to the surface (s-POM, 1 m below the
126 surface) or bottom (b-POM, 1 m above the seabed), using two 5l Niskin bottles per sample. In
127 parallel, SOM samples were collected at the sediment surface ($\approx 625 \text{ cm}^2$) by scuba divers using
128 a 450 ml syringe. Also, several individuals of *A. moerchi* and *M. truncata* were harvested either
129 by scuba diving or using a triangular biological dredge (KC Denmark A/S) during both seasons.
130 In addition, three macroalgae species (*Desmarestia aculeata*, *Fucus* sp., and *Saccharina*
131 *latissima*) were harvested during summer in order to assess their potential contribution to the

132 bivalves' diet. Statistical analyses were performed on our own results as well as some raw data
133 previously published in De Cesare (2016) and De Cesare et al. (2017) relating summer samples
134 of *A. moerchi* (SI signatures and FA profiles) and macroalgae (SI signatures).

135 **Analyses of Samples**

136 Preliminary treatments

137 POM samples were obtained by filtering collected water on precombusted GF/F Whatman®
138 microfiber filters (diameter: 47 mm, pore size: 0.7 µm) until clogging when possible (mean
139 filtered volume = 7.9 ± 1.9 l, range: 4–8 l). Because syringe-collected samples comprise a
140 mixture of SOM, inorganic particles, and seawater, we let the samples settle for one hour prior
141 to filtering the supernatants until clogging on GF/F filters (mean volume = 0.260 ± 0.100 ml,
142 range: 100–450 ml) in order to remove most of inorganic sedimentary particles. In the field, all
143 samples were directly frozen at -80°C and transferred to the lab for further analyses. Once in
144 the lab, all samples (i.e., POM and SOM filters as well as digestive glands and muscles) were
145 freeze-dried at -50°C for at least 5 hours (30 hours for animal tissues) and directly weighed.
146 The POM and SOM filters were cut in two parts to perform both FA and SI analyses on the
147 same sample. Each half-filter was weighed and the quantity of organic matter for the FA and
148 SI analysis was calculated by the following equation:

$$149 \quad M(X) = \frac{W_{Half\ filter}}{W_{Whole\ filter}} X (W_{Whole\ filter} - W_{Precombusted\ filter})$$

150 Where M (X) is the mass (mg) of POM or SOM used for the FA or SI analysis and W is the
151 dried weight of the half, whole, or precombusted filters.

152 Fatty acids analysis

153 The method used for the FA extraction largely follows the Bligh & Dyer method (1959) as
154 adjusted in Meziane & Tsuchiya (2002). To quantify the FA concentrations, a known volume
155 of a commercial standard (23:0, concentration of 5 mg/ml) was introduced in each sample. Half-

156 filters for POM and SOM analyses were diluted in a distilled water-chloroform-methanol
157 solution (1:1:2, v:v:v) and sonicated for 20 minutes for the FA extraction. The samples were
158 then completed by a distilled water-chloroform solution (1:1, v:v) and centrifuged (3000 rpm,
159 5 minutes). Lipid phases were transferred to separate tubes, completed by a distilled water-
160 chloroform solution (1:1, v:v), and sonicated again for 20 minutes to maximize the extraction.
161 Then, samples were evaporated under a dinitrogen (N₂) flux, diluted a second time in a mixture
162 of methanol and sodium hydroxide (2:1, v:v; [NaOH] = 2 mol.l⁻¹), and heated at 90°C for 90
163 minutes for FA saponification. Finally, FAs were converted into FA methyl esters after
164 incubation for ten minutes at 90°C in a methanolic boron trifluoride solution (BF₃-CH₃OH 14%,
165 1 ml). At the end of the reaction, the chloroform phase containing FAs was retrieved and stored
166 at -20°C.

167 The FAs were quantified by gas chromatography (Varian CP-3800 equipped with a Supelco®
168 Omegawax® Capillary GC 320 column [length = 30 m, inside diameter = 0.32 mm, film
169 thickness = 0.25 µm], He as carrier gas). FA pics were identified by comparing with those from
170 an analytical standard (Supelco® 37 Component FAME Mix) and confirmed by mass
171 spectrometry (Varian 220-MS coupled to a Varian 450-GC, He as carrier gas). FA
172 nomenclature is defined as X:YωZ, where X is the number of carbon atoms, Y is the number
173 of double bonds, and Z is the position of the last double bond from the methyl group. The 23:0
174 standard allowed converting each FA methyl esters area into a concentration using the
175 following equation (Schomburg 1987):

176
$$C_{FA} = \left(\frac{A_{FA}}{A_{C23}} \times \frac{C_{23}}{M_f} \right)$$

177 where C_{FA} is the FA concentration (µg/g), A_{FA} is the FA peak area, A_{C23} is the 23:0 peak area,
178 C₂₃ is the 23:0 quantity (µg) added to each sample, and M_f is the mass of matter deposited on
179 the analyzed half-filter.

180 The analytical precision for the samples was generally less than 5% for the total amounts and
181 major components of FA (Meziane pers. com.). Table 1 compiles all the FAs used as organic
182 matter tracers in this study and their related biomarker information.

183 Stable isotope analysis

184 SI analysis was performed on the second half of each POM and SOM filter and on *A. moerchi*
185 and *M. truncata* tissues. Half-filters were fumigated for at least four hours with 35% HCl to
186 remove inorganic carbon (Lorrain et al. 2003). The surface layer, including filtered POM (or
187 SOM), was scraped and 10–30 mg of material was placed in tin capsules. Due to the small
188 amounts of inorganic carbon in digestive glands and muscles, no acidification was performed
189 with these tissues (Jacob et al. 2005, Sørense et al. 2006). The animal tissues were ground and
190 approximately 1 mg was placed in a single tin capsule for each sample. Macroalgae were ground
191 and separated into two subsamples (De Cesare et al. 2017): one subsample was acidified (1M
192 HCl) to remove inorganic carbon and placed in silver capsules for $\delta^{13}\text{C}$ analysis, while the
193 second subsample was directly placed in tin capsules (without prior acidification) for $\delta^{15}\text{N}$
194 analysis.

195 All samples were analyzed at the University of California Davis Stable Isotope Facility
196 (Department of Plant Sciences, UC Davis, Davis, California) by continuous flow isotope ratio
197 mass spectrometry (CF-IRMS). The equipment consisted of an elemental analyzer (PDZ
198 Europa ANCA-GSL [Sercon Ltd., Cheschire, UK] and Elementar Vario EL Cube elemental
199 analyzer [Elementar Analysensysteme GmbH, Hanau, Germany] for animal tissue and filter
200 analysis, respectively) interfaced to an isotope ratio mass spectrometer (PDZ Europa 20-20,
201 Sercon Ltd., Cheschire, UK). Several replicates of laboratory standards, compositionally
202 similar to analyzed samples and calibrated against NIST Standard Reference Materials (IAEA-
203 600, USGS-40, USGS-41, USGS-42, USGS-43, USGS-61, USGS-64, and USGS-65), were
204 inserted between some of the filter and animal samples to correct deviations occurring during

205 the analysis. The standard deviation of the stable isotope measurements was estimated to $\pm 0.2\%$
206 for $\delta^{13}\text{C}$ and $\pm 0.3\%$ for $\delta^{15}\text{N}$ (UC Davis Stable Isotope facility pers. com.). Carbon and nitrogen
207 isotopic ratios were expressed in per mill (‰) and calculated from international standards
208 (Vienna Pee Dee Belemnite and Air, respectively) by the following equation:

$$209 \quad \delta X = \left[\left(\frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \right] \times 1000$$

210 where δX is $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$, and R is the corresponding $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$ ratio (Peterson & Fry
211 1987).

212 **Data analyses**

213 Since pelagic and benthic components usually show different organic matter sources and
214 qualities (e.g., Magen et al. 2010, Kuliński et al. 2014), we chose to separate the SOM and POM
215 samples for statistical analyses. Because our design was not balanced between the two seasons
216 (two stations sampled in winter vs. three in summer), we used two-way PERMANOVAs for
217 each season to study the effects of depth (surface or bottom waters) and station factors on the
218 FA profiles of POM. Since PERMANOVAs are not affected by small differences in dispersion,
219 especially with a balanced design, the PERMDISP test was performed to ensure that data
220 dispersion, possibly highly heterogeneous, would not disturb the interpretation of our analysis
221 (Anderson et al. 2008, Anderson & Walsh 2013).

222 Seasonal differences in FA concentrations were tested by one-way ANOVA, whereas depth
223 and station effects were tested by two-way ANOVA for each season. FA concentrations were
224 log-transformed prior each analysis to validate normality and homoscedasticity assumptions.
225 When significant effects were detected, pairwise Tukey tests were used to determine if the
226 differences were observed among all groups. Similar analyses were performed on carbon and
227 nitrogen isotopic ratios, with either 2 two-way ANOVAs (depth and stations as factors) or 1
228 one-way ANOVA (season as factor), as well as with pairwise tests if needed.

229 Regarding FA data in animal tissues, homoscedasticity and normality were rarely observed
230 between the two factors (e.g., digestive glands from May vs. muscles from August). As data
231 transformation is not recommended for percentage values not derived from count data (as
232 percentage of lipids), we thus performed a one-way PERMANOVA to test each factor
233 separately (e.g., season was tested for each tissue from a single species). Data from the SI
234 analysis on animal tissue were treated similarly with one-way ANOVAs. All statistical analyses
235 were performed using R software (R Core Team 2017).

236 **RESULTS**

237 **Fatty acid profiles from POM and SOM samples**

238 **Particulate Organic Matter (POM)**

239 Sixty-five FAs were identified in POM and SOM samples (44 FAs in August and 47 in May).
240 Only FA percentages higher than 0.2% in at least one sample are shown in Table 2. Strong
241 seasonal differences were observed in the FA profiles of the POM samples. For example, apart
242 from s-POM from Basalt Island, the total percentage of PUFAs was between 9.7% and 22.1%
243 in August and was always less than 1.5% in May. Concomitantly, the sum of saturated FAs (Σ
244 SFA) shows opposite seasonal variations, with higher values in May (range: 82.5%–93.1%)
245 compared to August (range: 49.5%–69.3%).

246 In August, the FA profiles of the POM samples differed significantly depending on site and
247 depth (p-value < 0.01) and without any interaction between these factors (Table 3). The depth
248 variations in the POM FA profiles were not similar between stations. In fact, the FA profiles of
249 s-POM and b-POM samples from Pass Hytten were rather similar (similarity = 73.1%), but
250 those from Basalt Island differed more with depth (e.g., 18:1 ω 9 = 1.9% and 6.2% for s-POM
251 and b-POM, respectively; Table 2). In samples from Kap Breusing, the FA profiles strongly
252 differed between surface and bottom waters (similarity = 64.2%) with 20:5 ω 3 percentages

253 higher in b-POM than in s-POM (9% vs. 2.7%, respectively, Table 2). Considering spatial
254 variability, FA profiles related to the s-POM from Basalt Island in August (Table 2) revealed
255 much more degraded organic matter compared to those from other stations, with a higher sum
256 of SFAs (84.4%), a lower sum of PUFAs (3.1%), and a much lower FA concentration (2.6 mg.g^{-1})
257 ¹) than in Pass Hytten and Kap Breusing (8.0 and 9.4 mg.g^{-1} respectively; pairwise test: p-value
258 < 0.001). In contrast, the b-POM samples were rather similar between Basalt Island and Pass
259 Hytten, while those from Kap Breusing had a distinct FA composition, with high PUFA and
260 monounsaturated FA (MUFA) proportions (22.1% and 25.6% respectively, Table 2). This was
261 particularly clear with FAs 20:5 ω 3 and 16:1 ω 7 reaching 9% and 12% in Kap Breusing,
262 respectively, whereas they were less than 3.7% and 6.9% at the other two sites, respectively
263 (Table 2). However, we did not observe any difference in FA concentration among stations (p-
264 value > 0.05).

265 In May, the FA profiles differed significantly according to both site and depth (p-value < 0.05 ;
266 Table 2) without any interaction between these two factors (p-value = 0.077). At both stations,
267 POM appeared to be slightly more degraded in surface vs. bottom waters, as shown by the
268 higher proportion of SFAs in s-POM (Table 2). Considering spatial variability, a higher
269 proportion of Σ SFA was observed in Pass Hytten than in Basalt Island (93.1 vs. 88.4 for s-
270 POM and 90.4 vs. 82.5 for b-POM, respectively; Table 2). However, such depth and station
271 differences were relatively weak, as attested by the strong similarity between the s-POM and
272 b-POM (84.7% similarity) as well as the Basalt Island and Pass Hytten samples (81.7%
273 similarity).

274 Sedimentary Organic Matter

275 SOM exhibited strong seasonal differences with much higher proportions of SFAs in May; yet,
276 these FAs represented only the half of the summer composition (Σ SFA = 92.2% vs. 56.9% for
277 winter and summer, respectively). Similarly, only some traces of PUFAs were detected in May

278 while their proportion reached 12.9% in August (Table 2). Summer PUFA and MUFA
279 proportions were mainly linked to 20:5 ω 3 and 16:1 ω 7 contributions (18.3% and 6.2%,
280 respectively; Table 2). Strong seasonal differences were also observed in the FA concentrations,
281 which were three-fold more abundant during August (0.7 vs. 0.2 for August and May,
282 respectively, Table 2). In contrast with the POM samples, no differences among stations were
283 observed in SOM during August (p-value = 0.066) and May (p-value = 0.168).

284 **Stable isotopes of POM and SOM samples**

285 In August, depth appeared to be the first discriminating factor in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values among
286 the POM samples. At each station, these $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values differed significantly between
287 surface and bottom waters (p-value < 0.0001), with overall more enriched values by 1‰ for
288 $\delta^{13}\text{C}$ and 2‰ for $\delta^{15}\text{N}$ in b-POM (Fig. 2). Globally, the isotopic signatures were closer between
289 samples for the surface compared to the bottom stations. Moreover, no significant differences
290 were observed between s-POM samples from Kap Breusing and Pass Hytten (for both $\delta^{13}\text{C}$ and
291 $\delta^{15}\text{N}$ values) and between b-POM samples from Pass Hytten and Kap Breusing (only for $\delta^{15}\text{N}$
292 values, p-value > 0.05).

293 In contrast, all isotopic ratios associated with the May samples increased an average of 1.2‰
294 and 2.4‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively. These ratios did not vary significantly with depth
295 within each station (p-value > 0.05, Fig. 2), but for both s-POM and b-POM, they differed
296 significantly between stations (p-value < 0.05, Fig. 2).

297 During summer, mean SOM $\delta^{13}\text{C}$ levels were more enriched, by 2.7‰ and 1.6‰, when
298 compared to s-POM and b-POM, respectively (Fig. 2). Spatial differences were also observed
299 during this season, but they were not significant between Pass Hytten and Basalt Island for $\delta^{13}\text{C}$
300 values and between Basalt Island and Kap Breusing for $\delta^{15}\text{N}$ values (pairwise test: p-value >
301 0.05). During May, the $\delta^{13}\text{C}$ level did not differ between Pass Hytten and Basalt Island (p-value
302 = 0.197), and this level was also similar to that from August (-24.7‰ in average for SOM from

303 Pass Hytten and Basalt Island during both seasons, p-value > 0.05, Fig. 2). $\delta^{15}\text{N}$ values differed
304 significantly between Pass Hytten and Basalt Island (p-value < 0.001) and increased when
305 compared to August levels by 0.9‰ and 2.6‰ for Pass Hytten and Basalt Island, respectively
306 (Fig. 2).

307 **Fatty acids profiles and isotopes values of bivalves**

308 Fatty acids

309 FA signatures associated with the muscle and digestive gland samples of *M. truncata* differed
310 between seasons (p-value < 0.01, Tables 3 and 4). For the muscle samples, such differences
311 were mainly attributable to essential FA (EFA: here, the sum of 20:4 ω 6, 20:5 ω 3, and 22:6 ω 3)
312 variations (41.7% vs. 35.1% for August and May, respectively; Table 4). Temporal differences
313 in the digestive gland data were especially obvious for the 20:5 ω 3/22:6 ω 3 ratio (14.5 vs. 1.3 in
314 August and May, respectively; Table 4) and for 16:1 ω 7 (22.5% vs. 3.4% in August and May,
315 respectively; Table 4). Interestingly, although FA profiles of muscles differed from those of
316 digestives glands during August (p-value < 0.01, Table 5), they were not statistically different
317 during May (p-value = 0.322, Table 5).

318 For *A. moerchi* tissues, both muscles and digestive glands had distinct FA profiles between
319 seasons (p-value < 0.001, Table 5). The highest PUFA and EFA percentages for digestive
320 glands were found in May (Table 4). In contrast, MUFAs were dominant during August, mainly
321 due to twice higher values of 16:1 ω 7 compared to May (Table 4). A similar trend was observed
322 for muscle FA profiles, with May contributions of EFA and PUFA double those of August (e.g.,
323 fivefold higher in May for 22:6 ω 3 = 14.5% vs. 2.8%, Table 4).

324 Isotopes

325 Although isotopic signatures of the digestive glands of *A. moerchi* ($\delta^{13}\text{C}$ = -24.2‰ and $\delta^{15}\text{N}$ =
326 6.5‰) and *M. truncata* ($\delta^{13}\text{C}$ = -24.7‰ and $\delta^{15}\text{N}$ = 6.2‰) were similar during August, they

327 were more distinct in May (Fig. 3). In fact, seasonal differences for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were observed
328 in *M. truncata* (+3‰ and +1.5‰ between August and May for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ [p-value < 0.05],
329 respectively, Fig. 3) but not in *A. moerchi* (+0.4‰ and -0.2‰ between August and May for
330 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ [p-value > 0.05], respectively, Fig. 3). Regarding muscle tissues, no seasonal
331 variations of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were observed in either species (Fig. 3), and no inter-specific
332 variations were observed during each season (p-value > 0.05).

333 In May, carbon and nitrogen isotopic values of s-POM, b-POM, and macroalgae samples clearly
334 differed from those of digestive gland and muscle tissues in both bivalves (Fig. 3B). In contrast,
335 isotopic values of *A. moerchi* and *M. truncata* became closer in summertime to POM and SOM
336 values (Fig. 3A).

337 **DISCUSSION**

338 **Influences of seasonal and spatial constraints on the POM and SOM patterns**

339 **Seasonal patterns**

340 There have been few studies of the seasonal variability between ice cover and open sea periods
341 in the main pelagic and benthic food sources of bivalves in High Arctic coastal areas (but see
342 Connelly et al. 2015, Connelly et al. 2016). This work constitutes the first contribution for the
343 Young Sound fjord. During the productive summer period, FA composition of the POM in
344 bottom waters revealed the dominant contribution of several photosynthetic producers, such as
345 diatoms (16:1 ω 7, 20:5 ω 3), dinoflagellates (18:4 ω 3, 22:6 ω 3), and macroalgae (18:2 ω 6, 18:3 ω 3,
346 18:4 ω 3, 20:5 ω 3). Moreover, relative high summer abundances of essential FAs (e.g., 20:5 ω 3,
347 22:6 ω 3, 18:4 ω 3) in animals and bivalves contrast with the winter situation. In winter, with the
348 absence of *in situ* primary production, POM was highly degraded; this was reflected by the
349 large proportion of total SFA (Rhead et al. 1971, Connelly et al. 2015, Connelly et al. 2016).
350 Very low levels of total PUFAs during May (i.e., <1.5%) indicate that the extended duration of

351 ice and snow cover in Young Sound is paired to the absence of fresh organic matter for primary
352 consumers compared to other Arctic fjords (e.g., Σ PUFA = 14.3%–39.8% in Kongsfjorden,
353 13.4% in Rijpfjorden; Leu et al. 2006, Leu et al. 2011). In fact, in May after 4–5 months in
354 darkness, the POM lipid concentrations measured in Young Sound (2.6–11.3 mg/g) are much
355 lower than in any other Arctic fjord (for example, 95.4–98.6 mg/g in Kobbefjord; Gaillard et
356 al. 2017). In May, despite 24-hour daylight, the presence of snow on the sea ice prevents the
357 transmission of light (Glud et al. 2007), and primary production does not start before mid-July
358 when melt-water ponds that form on the sea ice intensifies light transmission. This in turn
359 triggers a short algal bloom (Rysgaard et al. 1999). PAR sensors fixed at 1 m depth below the
360 sea ice revealed no available PAR for primary producers in May (Mikael Sejr, unpublished
361 data). For SOM, seasonal changes in FA composition show the same trends as in May POM,
362 as shown by low FA and total PUFA concentrations. In contrast, diatoms dominate the SOM
363 during the summer, as revealed by higher relative proportions of 16:1 ω 7 and 20:5 ω 3, whereas
364 dinoflagellates (18:4 ω 3, 22:6 ω 3) and macroalgae markers (18:2 ω 6, 18:3 ω 3, 20:4 ω 6, 20:5 ω 3)
365 suggest additional contributions of these primary sources to the pool of organic matter.

366 The absence of significant primary production in May is confirmed by a general increase in
367 $\delta^{15}\text{N}$ in both POM and SOM. Indeed, food webs from sea ice–covered ecosystems switch to
368 heterotrophy during the polar night due to the development of protozoans and/or microbial
369 planktonic communities (Berge et al. 2015). As heterotrophic microorganisms may be
370 consumers of organic matter, their isotopic signatures should be enriched in $\delta^{15}\text{N}$ when
371 compared to autotrophic algae (Hoch et al. 1996, Tamelander et al. 2009). Hence, such $\delta^{15}\text{N}$
372 enrichment could explain the seasonal increase of the $\delta^{15}\text{N}$ in POM during winter (Tamelander
373 et al. 2009, Kędra et al. 2012), but it also may reflect the increased contribution of animal
374 detritus and fecal pellets (Sampei et al. 2012) and diagenesis (Schulz & Zabel 2006).

375 Spatial patterns

376 The Marine Basis monitoring program has conducted annual surveys in August since 2003 that
377 documented the strong influence of terrestrial runoff on the water column, especially in surface
378 waters (above 10 m depth), as attested by lower salinity and higher turbidity measurements
379 (Citterio et al. 2017, Middelbo et al. 2018). This influence of direct freshwater inputs is
380 confirmed by s-POM $\delta^{15}\text{N}$ values ($4.2 \pm 0.3\text{‰}$), which are almost identical with riverine $\delta^{15}\text{N}$
381 values ($4.3 \pm 0.3\text{‰}$, Zackenberg River, Rysgaard & Sejr 2007). Poorer organic matter quality
382 in s-POM compared to b-POM (as expressed by the high levels of Σ SFA and low levels of Σ
383 PUFA) suggests an increase in the relative proportion of detrital particles compared to living
384 cells in surface waters (Leu et al. 2006, Mayzaud et al. 2013). Such observations are likely
385 explained by the inflow of nutrient-depleted freshwater (confined to surface waters), which may
386 both discharge a huge amount of terrestrial detrital particles and decrease primary productivity
387 (Mayzaud et al. 2013, Meire et al. 2016, Meire et al. 2017). This hypothesis is consistent with
388 previous findings in Young Sound, which showed lower chlorophyll-*a* concentrations in the
389 most runoff-exposed parts of the fjord (Meire et al. 2016, Arendt et al. 2016, Middelbo et al.
390 2018).

391 Overall, POM from Young Sound bottom waters was nutritionally richer than that from surface
392 waters, as reflected by higher proportions of EFA. However, the related $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values
393 were highly variable among the stations, and we hypothesize that this could be attributable to
394 their differential exposure to freshwater inputs. Thus, higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ found in b-POM in
395 Pass Hytten and Basalt Island could be explained by greater exposure of inner fjord waters to
396 nutrient-depleted and CO_2 -desaturated freshwater inputs (Tamelander et al. 2009, Meire et al.
397 2015, Meire et al. 2016). It also possibly indicates more degraded organic matter at the inner
398 stations due to higher bacterial activity (McTigue et al. 2015). These spatial SI discrepancies
399 may also reflect different bloom dynamics (duration, kinetics) among stations, since isotopic
400 signatures generally show an enrichment during a bloom (Savoie et al. 2003, Tamelander et al.

401 2009). In addition, the higher percentages of diatom and dinoflagellate markers (see above
402 details) in Kap Breusing may reflect local primary productivity that is higher in the outer than
403 in the inner part of the fjord. Accordingly, Meire et al. (2016) showed that upwelling of nitrate
404 and phosphate-rich waters around the fjord's mouth sustains a high phytoplankton biomass
405 throughout the summer.

406 Identifying and quantifying the sources of organic matter in superficial marine sediments is a
407 difficult task, as terrestrial inputs, benthic primary producers (including microphytobenthos and
408 macroalgae), and sedimentation of POM may all be present. For instance, SOM quality and
409 quantity may be affected by benthic organisms through bioturbation, burrowing, use of organic
410 matter, and excretion (e.g., Glud et al. 2000). Although FA analysis results show an input of
411 macroalgae to the SOM, their contributions should be rather limited. Indeed, previous
412 compound-specific isotopic analyses excluded the contribution of *Desmarestia aculeata* to the
413 pelagic and benthic pool of organic matter (De Cesare et al. 2017, Bridier's unpublished data).
414 In addition, the *Fucus* sp. and *Saccharina latissima* contributions seem relatively weak, as $\delta^{13}\text{C}$
415 values of both species ($19.2 \pm 2.2\text{‰}$ and $-21.1 \pm 0.0\text{‰}$, respectively) strongly differ from the
416 SOM $\delta^{13}\text{C}$ value ($-24.9 \pm 0.6\text{‰}$). According to published $\delta^{13}\text{C}$ signatures of Arctic
417 microphytobenthos (from -23.9‰ to -20.0‰ ; Oxtoby et al. 2016), riverine POM ($-25.6 \pm 0.1\text{‰}$,
418 Zackenberg River; Rysgaard & Sejr 2007), and b-POM measured in the present study ($-26.5 \pm$
419 0.6‰), the SOM $\delta^{13}\text{C}$ values probably reflect either (1) a strong contribution of terrestrial
420 organic matter associated with a minor contribution of microphytobenthos, or (2) an equal
421 contribution of marine b-POM and microphytobenthos to SOM. According to the C/N ratios
422 calculated from the Young Sound (18.3 ± 1.7 , 10.3 ± 0.2 , and 9.1 ± 0.2 for the SOM of Pass
423 Hytten, Basalt Island, and Kap Breusing, respectively) and riverine data ($10 < \text{C/N ratio} < 40$,
424 Zackenberg river; Rysgaard & Sejr 2007), the FA composition of Kap Breusing sediment
425 should be less influenced by terrestrial inputs than the other two sites. Moreover, FA profiles

426 of Kap Breusing and Basalt Island sediments display the highest percentages of diatom markers
427 (16:1 ω 7, 16:4 ω 1, and 20:5 ω 3), strongly suggesting that the associated SOM originates from
428 both microphytobenthos and sedimented phytoplankton (second scenario). In contrast,
429 sediments from Pass Hytten should receive organic matter from dominant terrestrial inputs with
430 a low contribution from marine primary producers (first scenario).

431 Comparing marine and riverine POM and SOM $\delta^{13}\text{C}$ values, Rysgaard & Sejr (2007) estimated
432 that half of the Young Sound's sediment organic carbon came from terrestrial sources.
433 However, the marine POM $\delta^{13}\text{C}$ value ($-21.6 \pm 0.3\text{‰}$) used for their estimate originates from a
434 study conducted by Hobson & Welch (1992) in Barrow Strait (NE Canada) that differs from
435 those found here ($-26.5 \pm 0.6\text{‰}$, present study; $-25.5 \pm 0.1\text{‰}$; De Cesare et al. 2017). Although
436 Young Sound's POM $\delta^{13}\text{C}$ isotopic ratios may vary across years, multiannual values relative to
437 a site close to Ny-Ålesund (Kongsfjorden, Svalbard) during May vary slightly between 2007,
438 2012, and 2013 ($-21.6 \pm 0.2\text{‰}$, -22.7‰ , and $-23.1 \pm 0.4\text{‰}$, respectively; Renaud et al. 2011,
439 De Cesare 2016, Calleja et al. 2017). We therefore suggest that differences in POM $\delta^{13}\text{C}$ values
440 between Young Sound and Barrow Strait do not depend on temporal variations, and that future
441 work on the contribution of terrestrial organic matter to SOM should be based on local POM
442 $\delta^{13}\text{C}$ values.

443 **Diet of *Astarte moerchi* and *Mya truncata***

444 Since sampling of bivalves was conducted over two different years, the seasonal comparison of
445 FA profiles and SI signatures probably reflects both seasonal and interannual variabilities of
446 their food sources. However, as the FA profiles of arctic bivalves are usually more sensitive to
447 seasonality than interannual variability (e.g., Birkely et al. 2003), we are confident that the FA
448 profiles from a specific origin and season will be quite stable between years. Moreover, because
449 of the huge seasonality of the Young Sound's physical environment and carbon transport
450 (Rysgaard et al. 2003), the bivalves' food sources should also display much higher seasonal

451 than interannual variations. In contrast, it is more difficult to distinguish seasonal from
452 interannual variability in bivalves' SI signatures, since they vary minimally between seasons
453 and years (Renaud et al. 2011, Kędra et al. 2012, McTigue & Dunton 2014, Gaillard et al. 2017).
454 Thus, seasonal differences in bivalves' SI signatures should be interpreted with caution.

455 Usually, FA associated with neutral lipids (used as energy storage) is directly mobilized from
456 the diet, while polar FA (cell membrane components) is subjected to strong physiological
457 regulation (Jezyk & Penicnak 1966, Napolitano & Ackman 1992, Pazos et al. 2003, Gaillard et
458 al. 2015). Since the digestive gland has a lipid storage function, this tissue displays high levels
459 of neutral compared to polar lipids. In contrast, muscle tissue contains low levels of neutral and
460 thus higher proportions of polar lipids (Napolitano & Ackman 1992, Pazos et al. 2003). For that
461 reason, digestive glands usually have a higher lipid turnover rate and diet sensitivity, whereas
462 muscles are more sensitive to physiological regulation (Napolitano & Ackman 1992,
463 Napolitano et al. 1997, Nérot et al. 2015). Such inter-tissue differences were also evident in the
464 present study; unlike digestive glands for which high levels of 20:5 ω 3 and 22:6 ω 3 are always
465 associated with high levels of diatoms or dinoflagellates dietary FA markers, these two FAs
466 were not associated with high levels of their dietary FA markers in muscle. Therefore, the
467 selective retention of 20:5 ω 3 and 22:6 ω 3, which are two EFAs (Soudant et al. 1996, Parrish
468 2009), confirms that muscle and digestive glands may constitute real proxies of bivalves' diet
469 and physiological conditions, respectively.

470 During summer, the FA compositions and isotopic signatures of the digestive glands of *A.*
471 *moerchi* and *M. truncata* were very similar. This suggests that both bivalves have the same diet
472 dominated by diatoms, as shown by the high proportions of 16:1 ω 7 and 20:5 ω 3, which are also
473 found in POM and SOM during summer (De Cesare et al. 2017). Such strong similarities in FA
474 profiles between bivalves and their food sources indicate tight benthic-pelagic coupling as well
475 as an efficient organic matter transfer from primary producers to primary consumers in the

476 Young Sound food web. If we consider the summer FA composition of muscles, both species
477 exhibit rather good physiological states as indicated by high levels of EFAs, as these are
478 essential for somatic growth, reproduction, and the maintenance of cell membrane fluidity
479 (Soudant et al. 1996, Parrish 2009).

480 During winter, $\delta^{13}\text{C}$ values associated with POM, SOM, and macroalgae sources were too
481 distinct from those of digestive glands and muscles, thus these sources were unlikely to
482 contribute to the bivalves' diet. Although macroalgae $\delta^{13}\text{C}$ values may slightly fluctuate
483 between seasons (Vizzini & Mazzola 2003), the lack of macroalgal FA markers in bivalve
484 tissues provides evidence that macroalgae were not consumed during winter. We thus suggest
485 that poor trophic environmental winter conditions, evidenced by highly degraded organic
486 matter sources, induce a drastic decrease and more likely an interruption in the feeding activity
487 of both bivalves. Such winter quiescence has previously been observed in bivalves (Pernet et
488 al. 2007, Comeau et al. 2012) but contrasts with numerous studies reporting the persistence of
489 long-term "food banks" in polar benthic ecosystems (e.g., Mincks et al. 2005) that fuel many
490 organisms by labile detritus (McClintock 1994, Mincks et al. 2008, McMeans et al. 2015,
491 Silberberger et al. 2018). This is not the case in Young Sound fjord, where the survival of *A.*
492 *moerchi* and *M. truncata* individuals relates to their reliance on energetic reserves under a poor
493 trophic winter environment. Moreover, each species displays a distinct pattern in its ability to
494 use these lipids. Hence, the similar FA profiles observed during winter between digestive glands
495 and muscle tissues of *M. truncata* may reflect a depletion of its lipid reserves. This phenomenon
496 will induce a decrease in the concentration of neutral lipids (constituent of the lipid reserves in
497 digestive glands) and will mechanically increase the proportion of polar lipids in this tissue (i.e.,
498 there will be a higher proportion of polar lipids in winter for a similar concentration between
499 the two seasons). Hence, the similar lipid class composition between digestive glands and
500 muscles may increase the similarity in their lipid profiles. The seasonal increase of digestive

501 gland $\delta^{13}\text{C}$ values may strengthen this hypothesis, since lipids are more depleted in $\delta^{13}\text{C}$ than
502 in other compounds (Lorrain et al. 2002). The increase in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ may also reflect the
503 impact of starvation on *M. truncata* metabolism (Hertz et al. 2015, Doi et al. 2017). A
504 simultaneous percentage decrease in 20:5 ω 3 and 22:6 ω 3 with a percentage increase in 20:2
505 NMI (non-methylene-interrupted) FA also confirms the poor physiological state of *M. truncata*
506 during winter. In fact, NMI biosynthesis should be critical for this species for maintaining both
507 structure and fluidity of their cell membranes in the face of a decrease in PUFA levels (Pernet
508 et al. 2007, Gaillard et al. 2015). The lipid reserves were less depleted in winter for *A. moerchi*
509 than *M. truncata*. In fact, the winter FA concentration in digestive glands for *A. moerchi* was
510 twice as high as for *M. truncata*, and the proportions of EFA and FA trophic markers remain
511 high compared to those in summer. Such species-specific seasonal patterns of lipid reserves
512 could be explained by (1) differential lipid mobilization during winter, or (2) the differential
513 ability to build lipid reserves during the rise in primary production. Data from the present study
514 do not support one hypothesis over the other. For instance, the first hypothesis may reflect the
515 bivalves' ability to reduce their metabolic rate or their reproduction investment. However, both
516 species show a similar decrease in their ω 3/ ω 6 ratio during winter, which may indicate that they
517 devote similar efforts to reproduction (Leroy et al. 2013, De Cesare 2016). Likewise, little
518 information is available about their ability to reduce their metabolic rate during starvation or
519 any other physiological stress (e.g., Abele-Oeschger & Oeschger 1995, Camus et al. 2003).
520 Hence, further studies, such as *in situ* measurements of bivalve metabolic rate or clearance rates
521 during winter or observations about their ability to store lipid during a short food supply (e.g.,
522 as for *Yoldia hyperborea*; Stead et al. 2013), will be thus helpful to better explore such
523 hypotheses.

524 Finally, about 30% of Young Sound's seafloor is below 100 m depth (Rysgaard et al. 2003),
525 and the link between filter feeders and primary producers in deeper basins may differ from our

526 results from shallow areas. Although vertical carbon fluxes at both shallow and deeper depths
527 have not been quantified in this fjord, the very low abundance of benthic macrofauna at 85 m
528 depth (Glud et al. 2000, Sejr et al. 2000) suggests a decrease in carbon transfer to deeper areas
529 via pelagic-benthic coupling (Ambrose & Renaud 1995). However, because similar C/N ratios
530 were found at 20 and 163 m depth (Glud et al. 2000), we hypothesize that organic matter transfer
531 from the surface to deeper basins would be fast enough to fuel benthic filter-feeding species
532 with relatively fresh organic matter (i.e., similar to that in shallow waters). Such tight pelagic-
533 benthic coupling has previously been reported up to 600 m depth in the High Arctic Canadian
534 archipelago for the filter-feeding bivalve *Bathyarca glacialis* (Gaillard et al. 2015).

535 **Conclusion and outlooks**

536 Extremely long sea-ice cover deprives Young Sound of fresh primary production during most
537 of the year, while freshwater inputs strongly degrade the quality of organic matter in surface
538 waters and seems to control the primary production dynamics within bottom waters during
539 summer. However, distinct adaptations are observed among filter-feeding bivalves to cope with
540 the long winter conditions: *A. moerchi* seems to be best adapted to live on stored energy
541 reserves, whereas the depletion of *M. truncata*'s lipid reserves during May suggest it has less
542 energetic margin to survive the winter.

543 In the face of climate change, Young Sound will be exposed to a continued freshening of its
544 surface water masses, preventing the renewal of deeper basin water masses in the inner fjord
545 (e.g., Sejr et al. 2017, Boone et al. 2018). Numerous studies have highlighted the effect of such
546 a freshening on the Young Sound's primary productivity through a decrease in light (Murray et
547 al. 2015) and nutrient availability (Meire et al. 2016). Results from our study suggest that this
548 decrease in primary productivity may be amplified by a decrease in organic matter quality in
549 the inner parts of this fjord. In contrast, the outer part of Young Sound may be less affected by
550 this freshening due to its sill, which allows nutrient replenishment through vertical mixing

551 (Meire et al. 2016). However, such impoverishment of the trophic environment in the inner
552 fjord may weaken the ability of some primary consumers (e.g., *Mya truncata*) to accumulate
553 enough lipid reserves during summer to cope with winter conditions, and this might have
554 cascading effects on their survival and renewal potential. Considering the key functional role
555 of such filter-feeding bivalves for the transfer of organic matter toward higher trophic levels,
556 such a shift could impact the entire benthic food web from primary producers to mammals,
557 especially walrus that can consume up to 57 kg of fresh *Mya truncata* per day (Born et al. 2003).

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569

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853 **FIGURE LEGENDS**

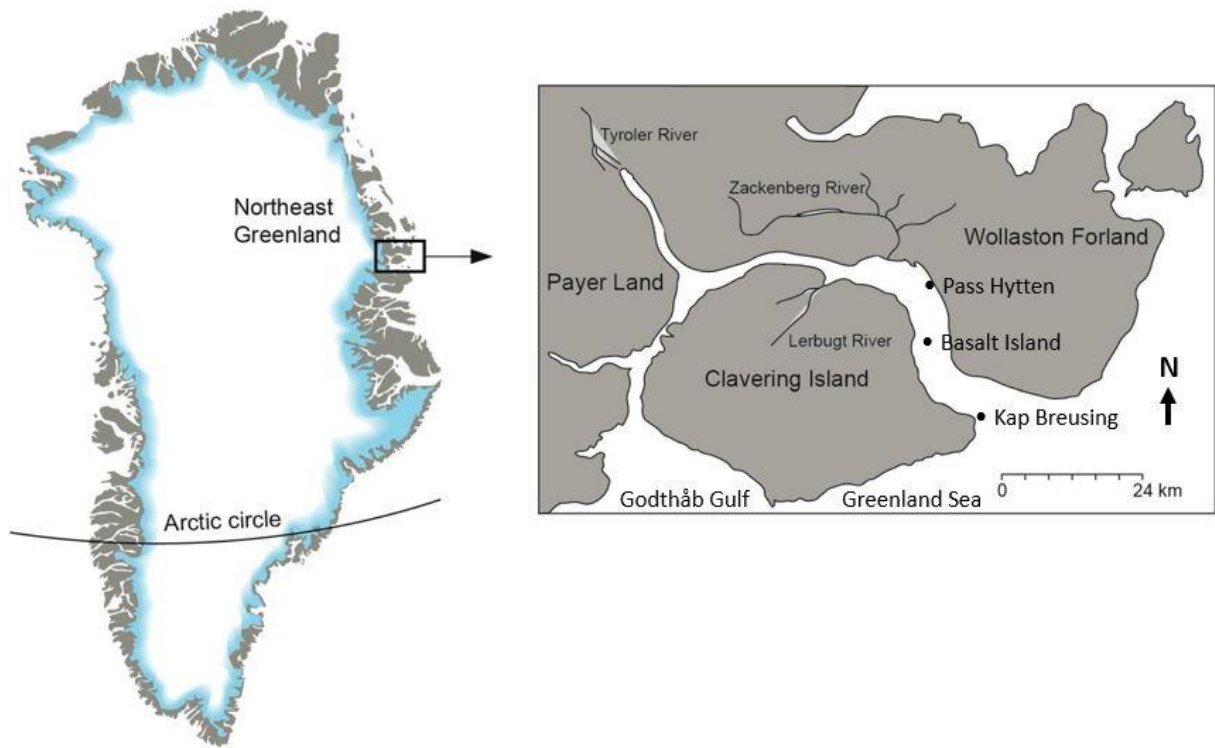
854 Figure 1: Location of the Young Sound's fjord (NE Greenland) and the three sampled stations:
855 Pass Hytten, Basalt Island, and Kap Breusing (modified from Ribeiro et al. 2017).

856 Figure 2: Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of surface particulate organic matter (s-POM), bottom
857 POM (b-POM), and sedimentary organic matter (SOM) from Pass Hytten (PH), Basalt Island
858 (BI), and Kap Breusing (KB) collected during summer and winter.

859 Figure 3: Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of *Astarte moerchi* and *Mya truncata* tissues and their
860 potential food sources during (A) summer and (B) winter. b-POM: bottom-particulate organic
861 matter, SOM: sedimentary organic matter, DG: digestive gland, MU: muscle. Errors bars
862 represent the standard deviation. Stable isotope values from macroalgae and b-POM, SOM, and
863 *Astarte*'s tissues from wintertime originated from De Cesare (2016) and De Cesare et al. (2017).

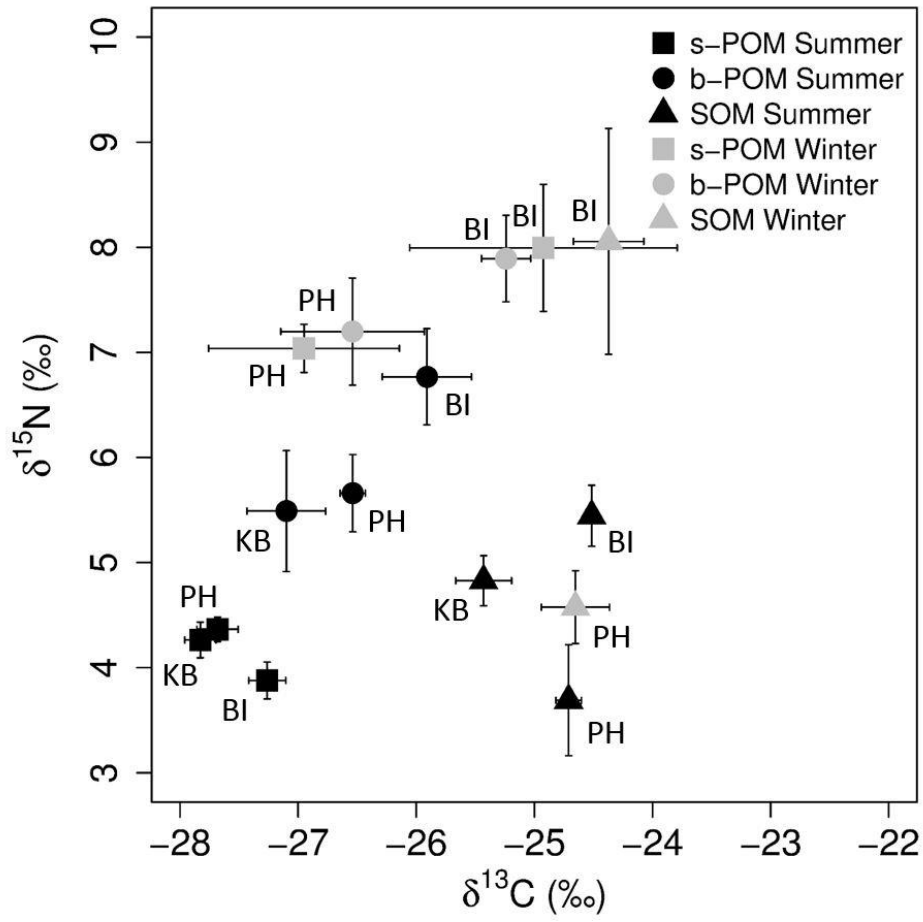
864

865 **Figure 1**



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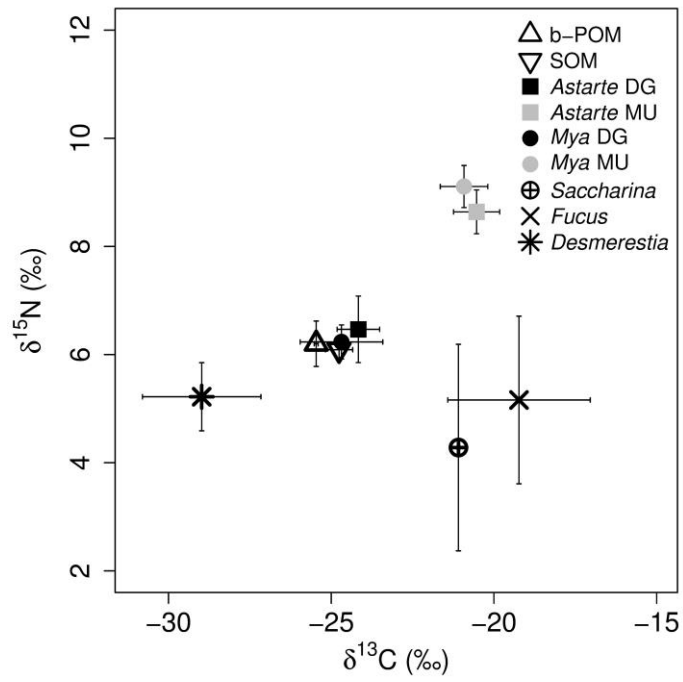
867 **Figure 2**



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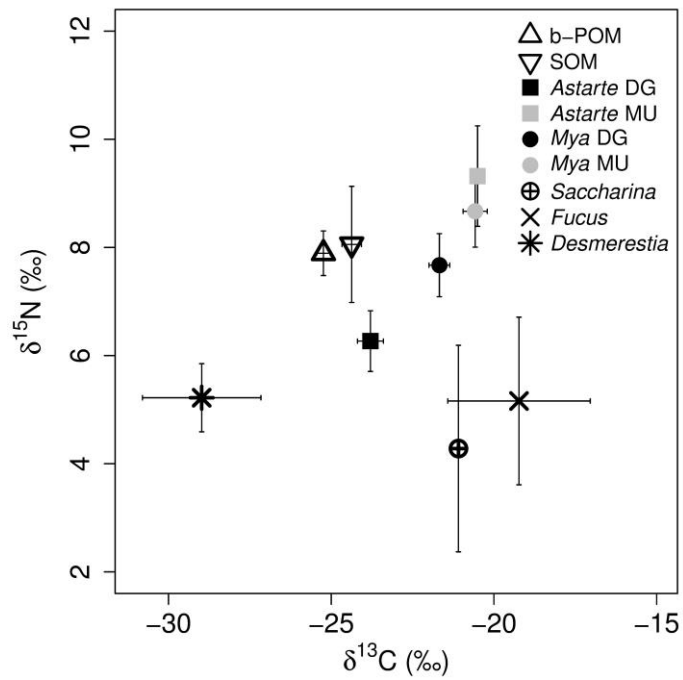
870 **Figure 3**



871

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A)



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B)

876 TABLE LEGENDS

877 Table 1: Fatty acids (FAs) used in this study as markers to describe the origin and quality of
878 organic matter.

879 Table 2: Fatty acid (FA) composition of particulate organic matter (POM) and sedimentary
880 organic matter (SOM) from summer and winter seasons. s-POM: surface POM, b-POM: bottom
881 POM, SFA: saturated FA, MUFA: monounsaturated FA, PUFA: polyunsaturated FA, BrFA:
882 branched FA, EFA: essential FA (sum of 20:4 ω 6, 20:5 ω 3, and 22:6 ω 3 proportions), nd: not
883 detected, tr: trace (FA percentage <0.2%). Standard deviations are represented within brackets.
884 FA percentages lower than 0.2% in all samples were not included in this table.

885 Table 3: Result of the two-way permutational multivariate analysis of variance
886 (PERMANOVA) realized on the FA composition of summer and winter POM samples based
887 the Bray Curtis dissimilarity matrix. Site (S) and depth (D) are tested as fixed factors.
888 Significant p-values are displayed in bold.

889 Table 4: Fatty acid (FA) composition of digestive gland (DG) and muscle (MU) tissues of
890 *Astarte moerchi* and *Mya truncata* collected from Basalt Island and Daneborg during summer
891 and winter. SFA: saturated FA, MUFA: monounsaturated FA, PUFA: polyunsaturated FA,
892 BrFA: branched FA, EFA: essential FA (sum of 20:4 ω 6, 20:5 ω 3, and 22:6 ω 3 proportions),
893 EPA/DHA: 20:5 ω 3/22:6 ω 3, nd: not detected, tr: trace (FA percentage <0.2%). Standard
894 deviations are represented within brackets. FA percentages lower than 1% in all samples are
895 not included in this table. Winter FA compositions of digestive glands and muscles from *A.*
896 *moerchi* originated from De Cesare (2016) and De Cesare et al. (2017).

897 Table 5: Result of the one-way permutational multivariate analyses of variance
898 (PERMANOVA). The upper part relates to the FA composition of digestive gland (DG) and
899 muscle (MU) tissues of *Astarte moerchi* and *Mya truncata*, with season as a fixed factor. The

900 lower part relates to the FA composition of *A. moerchi* and *M. truncata* from summer (Sum.)
901 and winter (Win.) seasons, with tissue as a fixed factor.

902 **Table 1**

Descriptor of	Fatty acids (FAs)	References
Organic matter origin		
Diatoms	16:1 ω 7, 16:4 ω 1, 20:5 ω 3	Reuss & Poulsen (2002), Dalsgaard et al. (2003), Kelly & Scheibling (2012)
Dinoflagellates	18:4 ω 3, 22:6 ω 3	Napolitano et al. (1997), Kelly & Scheibling (2012)
Macroalgae (Phaeophyceae)	18:2 ω 6, 18:3 ω 3, 18:4 ω 3, 20:5 ω 3	Kelly & Scheibling (2012), De Cesare et al. (2017), Gaillard et al. (2017)
Organic matter quality		
Degraded organic matter	Dominance of SFA (e.g., 14:0, 16:0, 18:0)	Rhead et al. (1971), Connelly et al. (2015), Connelly et al. (2016)
Labile and nutritionally rich organic matter	Dominance of PUFA and EFA (here, sum of 20:4 ω 6, 20:5 ω 3, and 22:6 ω 3)	Soudant et al. (1996), Parrish et al. (2005), Parrish (2009)

903

904 **Table 2**

	August							May				
	Pass Hytten		Basalt Island		Kap Breusing		SOM	Pass Hytten		Basalt Island		SOM
	s-POM N = 5	b-POM N = 5	s-POM N = 5	b-POM N = 4	s-POM N = 5	b-POM N = 4		s-POM N = 4	b-POM N = 4	s-POM N = 5	b-POM N = 5	
12:0	nd	nd	nd	nd	nd	nd	nd	1.6 (0.7)	3.7 (1.3)	6.6 (4.8)	2.4 (0.6)	1.6 (1.1)
13:0	nd	nd	nd	nd	nd	nd	nd	tr	0.3 (0.2)	tr	tr	0.3 (0.1)
14:0	17.8 (6.2)	7.1 (1.6)	19.9 (7)	8.5 (1.6)	12.9 (3.6)	8.4 (0.8)	9.7 (3.7)	7.5 (0.3)	7.4 (0.9)	13.2 (2.7)	9 (1)	6.3 (1.7)
15:0	1.3 (0.3)	1.8 (0.3)	1.5 (0.3)	2.1 (0.5)	1.3 (0.3)	1.3 (0.2)	1 (0.3)	2.7 (0.3)	2.3 (0.4)	2.5 (0.4)	2.8 (0.5)	1.7 (0.3)
16:0	35.3 (9.8)	32.9 (4.9)	45.1 (8.7)	36 (7.9)	31.5 (3.3)	27.1 (4.8)	34.2 (6.4)	43 (0.8)	41.1 (1.7)	38.6 (5.3)	39.5 (6.3)	46 (3)
17:0	0.8 (0.2)	1.1 (0.2)	1.1 (0.5)	1.5 (0.6)	0.8 (0.2)	0.8 (0.2)	0.6 (0.6)	1.6 (0.1)	1.3 (0.1)	1.3 (0.2)	1.6 (0.3)	1.3 (0.2)
18:0	7.5 (2.8)	20.1 (4.2)	13.5 (4.8)	17.6 (3.4)	8.7 (1.3)	9.8 (2)	9 (7.7)	31.8 (3)	30.5 (6.4)	21.6 (3.7)	22.5 (3.4)	30.5 (4.2)
19:0	0.5 (0.2)	0.3 (0.2)	0.7 (0.2)	0.9 (0.5)	0.5 (0.1)	0.3 (0.2)	0.5 (0.5)	nd	nd	tr	nd	nd
20:0	0.3 (0.1)	0.9 (0.1)	0.5 (0.4)	0.8 (0.2)	0.5 (0.2)	0.5 (0.1)	0.4 (0.4)	1.6 (0.0)	1.3 (0.1)	1.1 (0.2)	1.2 (0.1)	1.4 (0.1)
21:0	0.3 (0.3)	0.2 (0.1)	0.6 (0.4)	0.3 (0.3)	0.4 (0.5)	tr	0.3 (0.4)	tr	0.2 (0.2)	0.3 (0.2)	0.3 (0)	tr
22:0	0.5 (0.2)	0.8 (0.1)	0.8 (0.3)	0.6 (0.2)	0.5 (0.1)	0.5 (0.1)	0.5 (0.4)	1.2 (0.1)	1.0 (0.1)	1 (0.3)	1.2 (0.3)	1.2 (0.1)
24:0	0.3 (0)	0.7 (0.3)	0.5 (0.2)	0.9 (0.2)	0.4 (0.2)	0.6 (0.1)	0.7 (0.5)	1.7 (0.1)	1.1 (0.3)	1.5 (0.4)	1.5 (0.3)	1.5 (0.3)
25:0	nd	nd	nd	nd	nd	nd	nd	0.3 (0.0)	0.2 (0.0)	0.2 (0.1)	0.3 (0.1)	0.8 (1.3)
Σ SFA	64.5 (15.2)	65.8 (9.5)	84.4 (14.2)	69.3 (14.2)	57.4 (6.7)	49.5 (6.9)	56.9 (15.7)	93.1 (2.6)	90.4 (5.4)	88.4 (10.1)	82.5 (11.3)	92.8 (2.6)
14:1ω5	nd	nd	nd	nd	nd	nd	nd	tr	0.2 (0.2)	0.2 (0.1)	tr	0.2 (0.2)
15:1ω1	nd	nd	nd	nd	nd	nd	nd	0.3 (0.7)	1.0 (1.4)	1.1 (0.6)	0.6 (0.5)	0.7 (0.8)
16:1ω5	1.1 (0.5)	0.6 (0.3)	0.3 (0.3)	0.4 (0.2)	1.2 (0.2)	0.8 (0.1)	0.3 (0.2)	nd	nd	nd	nd	nd
16:1ω7	7.8 (3.3)	6.9 (1.6)	4 (5.4)	6.6 (4.6)	9.4 (1.6)	12 (1.2)	18.3 (7.8)	0.4 (0.3)	0.4 (0.4)	0.6 (0.7)	0.9 (0.6)	tr
16:1ω9	0.7 (0.2)	1.7 (0.5)	0.4 (0.5)	1.9 (1.2)	0.9 (0.1)	1.2 (0.4)	0.9 (0.5)	0.3 (0.1)	0.3 (0.1)	0.6 (0.9)	1.2 (1)	0.3 (0.2)
17:1ω7	0.2 (0.1)	0.2 (0.1)	tr	0.2 (0.2)	0.2 (0.1)	0.2 (0.1)	tr	nd	nd	tr	nd	nd
17:1ω9	tr	tr	tr	tr	tr	tr	tr	tr	0.2 (0.1)	0.2 (0.1)	tr	tr
18:1ω5	tr	0.3 (0.2)	0.2 (0.2)	0.3 (0.1)	0.2 (0)	0.3 (0.1)	tr	tr	tr	tr	0.3 (0.2)	tr
18:1ω7	1.9 (0.7)	2.2 (0.6)	1 (1.3)	1.4 (0.7)	3 (1.1)	2.5 (0.9)	2.4 (1)	0.2 (0.2)	0.4 (0.3)	0.5 (0.6)	1.1 (0.4)	0.3 (0.5)
18:1ω9	7.1 (2.7)	6.7 (2)	1.9 (2.7)	6.2 (4.1)	9.7 (2.2)	6.4 (0.9)	6 (2.1)	0.7 (0.8)	2.9 (4.8)	3.2 (6.2)	7.3 (8)	0.5 (1)
20:1ω7	0.3 (0.3)	tr	tr	0.2 (0.1)	0.5 (0.3)	0.8 (0.6)	tr	tr	0.4 (0.4)	0.3 (0.2)	0.5 (0.2)	nd
20:1ω9	0.3 (0.2)	0.2 (0.1)	nd	tr	tr	0.2 (0.1)	tr	0.8 (1.4)	0.5 (0.8)	0.2 (0.3)	0.2 (0.2)	0.2 (0.3)
22:1ω9	tr	tr	tr	tr	tr	0.3 (0.1)	tr	nd	nd	tr	tr	nd
22:1ω11	0.4 (0.3)	tr	tr	tr	0.4 (0.3)	0.7 (0.5)	tr	nd	nd	0.5 (0.8)	0.2 (0.1)	nd
Σ MUFA	20.1 (7)	19.4 (4.9)	8 (10.9)	17.9 (10.3)	26 (4.4)	25.6 (1.6)	28.6 (10.7)	3.2 (1.4)	6.2 (5.2)	8 (8.5)	13.1 (10.3)	2.8 (2.3)
16:2ω4	tr	tr	tr	tr	tr	0.4 (0.1)	0.3 (0.2)	nd	nd	nd	nd	nd
16:2ω6	tr	tr	tr	tr	tr	tr	0.2 (0.3)	nd	nd	nd	nd	nd
16:3ω3	tr	tr	nd	tr	nd	0.3 (0.2)	0.2 (0.2)	nd	nd	nd	nd	nd
16:4ω1	tr	0.2 (0.1)	tr	0.4 (0.2)	tr	1.1 (0.5)	0.6 (0.3)	nd	nd	nd	nd	nd
16:4ω3	0.6 (0.3)	0.4 (0.2)	0.2 (0.2)	0.4 (0.1)	0.6 (0.1)	0.7 (0.2)	0.4 (0.3)	nd	nd	nd	nd	nd
18:2ω6	1.3 (0.8)	1.9 (0.7)	0.5 (0.8)	2.8 (1.4)	1.9 (0.4)	2.6 (0.3)	2 (0.9)	tr	0.3 (0.4)	0.5 (0.9)	1.1 (1.3)	tr
18:3ω3	0.9 (0.7)	0.6 (0.2)	0.3 (0.5)	0.7 (0.2)	1.2 (0.3)	0.8 (0.1)	0.5 (0.3)	tr	tr	0.2 (0.1)	0.2 (0.1)	tr
18:4ω3	1.7 (1.4)	1.3 (0.4)	0.3 (0.5)	0.7 (0.3)	1.9 (0.6)	2.4 (0.2)	0.5 (0.4)	nd	nd	tr	nd	nd
20:4ω6	tr	tr	nd	tr	nd	tr	0.2 (0.2)	nd	nd	tr	nd	nd
20:5ω3	2.6 (2.2)	3.7 (2.1)	0.7 (1)	2.7 (2.5)	2.7 (1)	9 (4.9)	6.2 (3.3)	nd	nd	tr	nd	nd
22:2ω9	tr	tr	0.4 (0.5)	0.3 (0.3)	tr	0.2 (0.1)	0.5 (0.4)	nd	nd	nd	nd	nd
22:5ω3	tr	0.3 (0.2)	nd	0.5 (0.2)	tr	0.4 (0.1)	0.3 (0.6)	nd	nd	tr	nd	nd
22:6ω3	3.7 (3.5)	2.4 (1.3)	0.6 (0.9)	0.9 (0.6)	4 (1.4)	3.6 (0.9)	0.8 (0.7)	tr	nd	tr	tr	tr
Σ PUFA	11.6 (9.2)	11.4 (5)	3.1 (4)	9.7 (5.1)	13 (3.9)	22.1 (6.7)	12.9 (5.9)	0.2 (0.1)	0.3 (0.4)	1.1 (1.6)	1.5 (1.5)	tr
Σ BrFA	3.8 (0.7)	3.4 (0.4)	4.5 (0.6)	3.2 (0.9)	3.6 (0.5)	2.8 (0.6)	1.6 (0.5)	3.5 (1.9)	3.1 (1.2)	2.5 (0.2)	2.9 (0.9)	4.2 (1)
Σ PUFA/Σ SFA	0.2 (0.3)	0.2 (0.1)	0.0 (0.1)	0.2 (0.1)	0.2 (0.1)	0.5 (0.2)	0.3 (0.2)	tr	tr	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Σ EFA	6.4 (5.7)	6.2 (3.4)	1.2 (1.9)	3.6 (3.1)	6.8 (2.4)	12.7 (5.8)	7.2 (3.9)	tr	nd	tr	tr	tr
16:1ω7/16:0	0.3 (0.2)	0.2 (0.1)	0.1 (0.2)	0.2 (0.2)	0.3 (0.1)	0.5 (0.1)	0.6 (0.3)	tr	tr	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
[FA] (mg/g)	8.0 (2.1)	9.5 (5.0)	2.6 (0.9)	11.3 (4.4)	9.4 (2.3)	7.2 (5.7)	0.7 (0.4)	3.9 (0.5)	4.9 (2.5)	5.8 (2.4)	8.4 (4.4)	0.2 (0.0)

906 **Table 3**

Source of variation	df	MeanSqs	POM - Summer		
			F Model	R ²	p-value
Site (S)	2	0.1360	5.7102	0.2809	0.0014
Depth (D)	1	0.1327	5.5725	0.1371	0.0052
S x D	2	0.0198	0.8324	0.0410	0.5088
Residuals	22	0.0238		0.5411	
	df	MeanSqs	POM - Winter		
			F Model	R ²	p-value
Site (S)	1	0.0494	4.7766	0.2137	0.0014
Depth (D)	1	0.0251	2.4328	0.1088	0.0494
S x D	1	0.0222	2.1470	0.0960	0.0766
Residuals	13	0.0103		0.5815	

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909 **Table 4**

	<i>Mya truncata</i>				<i>Astarte moerchi</i>			
	August		May		August		May	
	Basalt Island		Basalt Island		Daneborg		Basalt Island	
	DG	MU	DG	MU	DG	MU	DG	MU
	N = 5	N = 5	N = 4	N = 5	N = 10	N = 6	N = 5	N = 4
14:0	2.7 (0.6)	0.9 (0.1)	1.1 (0.4)	1.2 (0.1)	2.5 (0.7)	1.7 (0.7)	2.4 (0.4)	0.7 (0.2)
16:0	14.7 (0.5)	13.5 (1.1)	12.1 (2.9)	13.7 (1.2)	10.4 (0.4)	21.9 (5.8)	11.5 (1.3)	16.1 (1.5)
17:0	0.3 (0)	0.5 (0)	0.6 (0.1)	0.6 (0.1)	0.3 (0.1)	1.2 (0.4)	0.5 (0.1)	1.3 (0.1)
18:0	2.3 (0.5)	5.9 (1)	6.1 (1.7)	6.6 (1.7)	1.2 (0.4)	15.6 (11.2)	1.7 (0.6)	4.7 (0.5)
Σ SFA	20.3 (0.7)	21.3 (1.3)	20.7 (3.3)	22.8 (2.7)	14.6 (0.5)	42 (18.8)	16.6 (1.8)	23.3 (2.3)
16:1ω5	0.4 (0)	tr	tr	tr	1.6 (0.4)	1.1 (0.3)	1.2 (0.2)	0.3 (0)
16:1ω7	22.5 (4.3)	5.4 (0.8)	3.4 (1)	4.5 (0.8)	22.6 (5.5)	11.9 (4.5)	12.7 (3.2)	3.6 (0.8)
18:1ω5	0.5 (0.1)	0.3 (0)	0.4 (0)	0.3 (0.1)	4.5 (0.5)	5.5 (1.9)	4.6 (0.6)	5.7 (0.5)
18:1ω7	6.9 (0.7)	2.5 (0.2)	2 (0.6)	2.1 (0.4)	6.9 (1)	5.3 (1.8)	5.6 (0.5)	3.7 (0.5)
18:1ω9	0.8 (0.3)	2.6 (0.4)	2.6 (1.3)	2.9 (0.3)	1.3 (0.1)	2.9 (0.8)	2 (0.3)	2.3 (0.2)
20:1	1.7 (0.7)	6.9 (0.4)	nd	nd	1.3 (0.4)	1 (0.8)	nd	nd
20:1ω11	nd	nd	2.2 (0.4)	2.2 (0.4)	1.5 (0.8)	1 (0.7)	2.3 (0.6)	2.2 (0.2)
20:1ω7	1.7 (0.8)	3.5 (0.4)	5.1 (0.9)	4.1 (0.3)	2.9 (0.9)	3 (1.2)	3 (0.4)	3.7 (0.3)
20:1ω9	nd	nd	2.8 (0.4)	4.9 (0.8)	0.4 (0.2)	0.2 (0.2)	0.7 (0.2)	0.4 (0.1)
22:1ω9	nd	nd	2.3 (3.7)	0.4 (0.5)	tr	nd	0.4 (0.2)	0.3 (0.2)
Σ MUFA	35 (3.9)	21.5 (1.3)	22.1 (5.8)	23.3 (0.7)	43.6 (2.4)	32.2 (9.7)	33.2 (2.2)	22.6 (1.8)
18:4ω3	1.4 (0.2)	0.8 (0.4)	2.7 (1.2)	2.8 (1.2)	1.4 (0.3)	0.6 (0.6)	1.2 (0.1)	0.7 (0.4)
20:2 NMI	1 (0.7)	5.9 (0.8)	8.8 (3)	7.5 (2.7)	0.3 (0.1)	tr	0.2 (0.1)	tr
20:2ω9	nd	nd	nd	nd	1.1 (0.6)	1.1 (0.6)	1.3 (0.4)	2.5 (0.8)
20:4ω6	0.7 (0.2)	2.7 (0.2)	3.5 (0.5)	2.9 (0.2)	1.2 (0.9)	1.9 (1.1)	1.8 (0.3)	5.8 (0.5)
20:5ω3	32 (2.2)	22.4 (1)	17.8 (6.9)	17 (2.8)	25.9 (1.1)	12.5 (6.1)	29.5 (1.9)	17.8 (1.6)
21:5ω3	0.8 (0.2)	1.2 (0.2)	0.9 (0.6)	1.2 (0.3)	0.6 (0)	0.4 (0.4)	0.7 (0.1)	1 (0.1)
22:2ω6	tr	0.4 (0.1)	tr	tr	1.2 (0.5)	0.7 (0.6)	1.4 (0.4)	1.8 (0.2)
22:2ω9	tr	0.6 (0.1)	0.2 (0.3)	0.3 (0.2)	0.7 (0.4)	0.5 (0.4)	1 (0.3)	1.2 (0.3)
22:4ω6	tr	1.5 (0.3)	3.5 (1.6)	2.1 (0.3)	nd	nd	0.3 (0.1)	0.4 (0.1)
22:5ω3	tr	2 (1.1)	2.2 (0.6)	2.9 (0.5)	0.6 (0.4)	0.7 (0.9)	1 (0.2)	4.1 (0.7)
22:5ω6	tr	0.4 (0.1)	0.9 (0.5)	0.8 (0.5)	tr	1 (1.3)	0.3 (0.1)	0.8 (0.4)
22:6ω3	3.4 (2.4)	16.6 (1.3)	13.8 (2.6)	13.8 (1.5)	3.2 (0.5)	2.8 (2)	6.7 (1.6)	14.5 (1.9)
Σ PUFA	44.5 (4.1)	56.2 (1.6)	55.9 (6.6)	52.7 (3.2)	41.1 (2.4)	24.1 (11.3)	49.3 (1.1)	52.7 (3.9)
Σ BrFA	0.3 (0.1)	1 (0.1)	1.3 (0.5)	1.1 (0.3)	0.6 (0.2)	1.7 (1.1)	0.9 (0.2)	1.4 (0.2)
Σ EFA	36.1 (4)	41.7 (2.2)	35.1 (8.4)	33.8 (2.7)	30.3 (1.4)	17.2 (8.7)	38 (0.6)	38 (3.2)
Σ PUFA/Σ SFA	2.2 (0.2)	2.7 (0.2)	2.8 (0.6)	2.4 (0.5)	2.8 (0.2)	0.8 (0.6)	3 (0.3)	2.3 (0.4)
EPA/DHA	14.5 (10.9)	1.4 (0.1)	1.3 (0.4)	1.3 (0.3)	8.4 (1.4)	5 (1.2)	4.7 (1.7)	1.2 (0.2)
[FA] mg/g	NA	NA	21.9 (21.1)	4.5 (2.4)	123.4 (48.3)	19.9 (7.5)	51.8 (24.5)	3.9 (0.4)

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912 **Table 5**

Tested group	Season as fixed factor				
	df	MeanSqs	F Model	R ²	p-value
<i>M. truncata</i> DG	1	0.4866	36.8920	0.8405	0.0062
<i>M. truncata</i> MU	1	0.0931	20.9360	0.7235	0.0074
<i>A. moerchi</i> DG	2	0.1092	16.6220	0.6129	0.0001
<i>A. moerchi</i> MU	2	0.2220	7.2209	0.4593	0.0005
	Tissue as fixed factor				
	df	MeanSqs	F Model	R ²	p-value
<i>M. truncata</i> May.	1	0.0166	1.175	0.1437	0.3220
<i>M. truncata</i> Aug.	1	0.3589	99.035	0.9253	0.0084
<i>A. moerchi</i> May.	1	0.3243	48.958	0.7776	0.0001
<i>A. moerchi</i> Aug.	1	0.4510	19.831	0.5862	0.0001

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