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# 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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1 TITLE (21 words / 150 characters) [maximum authorized: 150 characters]

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

4

5 RUNNING PAGE HEAD (6 words) [Editor requirements: 3 to 6 words]

6 Trophic functioning of a Greenland fjord

7

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34 **ABSTRACT** (250 words) [Editor limit length: 250 words]

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

54 **KEY WORDS** (7 key words) [Editor requirement: 3 to 8 key words]

55 Arctic ecosystems, benthic-pelagic coupling, organic matter, climate change, fatty acids, stable  
56 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<sup>-1</sup>  
63 <sup>1</sup>, 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 (N<sub>2</sub>) flux, diluted a second time in a mixture  
162 of methanol and sodium hydroxide (2:1, v:v; [NaOH] = 2 mol.l<sup>-1</sup>), 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 (BF<sub>3</sub>-CH<sub>3</sub>OH 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<sub>FA</sub> is the FA concentration (µg/g), A<sub>FA</sub> is the FA peak area, A<sub>C23</sub> is the 23:0 peak area,  
178 C<sub>23</sub> is the 23:0 quantity (µg) added to each sample, and M<sub>f</sub> 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, Søreide 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  $\delta X$  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 ( $\Sigma$   
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 $\omega$ 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 $\omega$ 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 ( $2.6 \text{ mg.g}^{-1}$ )  
257 <sup>1</sup>) than in Pass Hytten and Kap Breusing (8.0 and  $9.4 \text{ mg.g}^{-1}$  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 $\omega$ 3 and 16:1 $\omega$ 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  $\Sigma$  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 ( $\Sigma$  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 $\omega$ 3 and 16:1 $\omega$ 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 $\omega$ 6, 20:5 $\omega$ 3, and 22:6 $\omega$ 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 $\omega$ 3/22:6 $\omega$ 3 ratio (14.5 vs. 1.3 in  
314 August and May, respectively; Table 4) and for 16:1 $\omega$ 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 $\omega$ 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 $\omega$ 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 $\omega$ 7, 20:5 $\omega$ 3), dinoflagellates (18:4 $\omega$ 3, 22:6 $\omega$ 3), and macroalgae (18:2 $\omega$ 6, 18:3 $\omega$ 3,  
346 18:4 $\omega$ 3, 20:5 $\omega$ 3). Moreover, relative high summer abundances of essential FAs (e.g., 20:5 $\omega$ 3,  
347 22:6 $\omega$ 3, 18:4 $\omega$ 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.,  $\Sigma$  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 $\omega$ 7 and 20:5 $\omega$ 3, whereas  
364 dinoflagellates (18:4 $\omega$ 3, 22:6 $\omega$ 3) and macroalgae markers (18:2 $\omega$ 6, 18:3 $\omega$ 3, 20:4 $\omega$ 6, 20:5 $\omega$ 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  $\Sigma$  SFA and low levels of  $\Sigma$   
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  $\text{CO}_2$ -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  $-23.9\text{‰}$  to  $-20.0\text{‰}$ ; 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  $0.6\text{‰}$ ), 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 ( $18.3 \pm 1.7$ ,  $10.3 \pm 0.2$ , and  $9.1 \pm 0.2$  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 $\omega$ 7, 16:4 $\omega$ 1, and 20:5 $\omega$ 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 ( $-21.6 \pm 0.2\text{‰}$ ,  $-22.7\text{‰}$ , 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 $\omega$ 3 and 22:6 $\omega$ 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 $\omega$ 3 and 22:6 $\omega$ 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 $\omega$ 7 and 20:5 $\omega$ 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 $\omega$ 3 and 22:6 $\omega$ 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  $\omega$ 3/ $\omega$ 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**

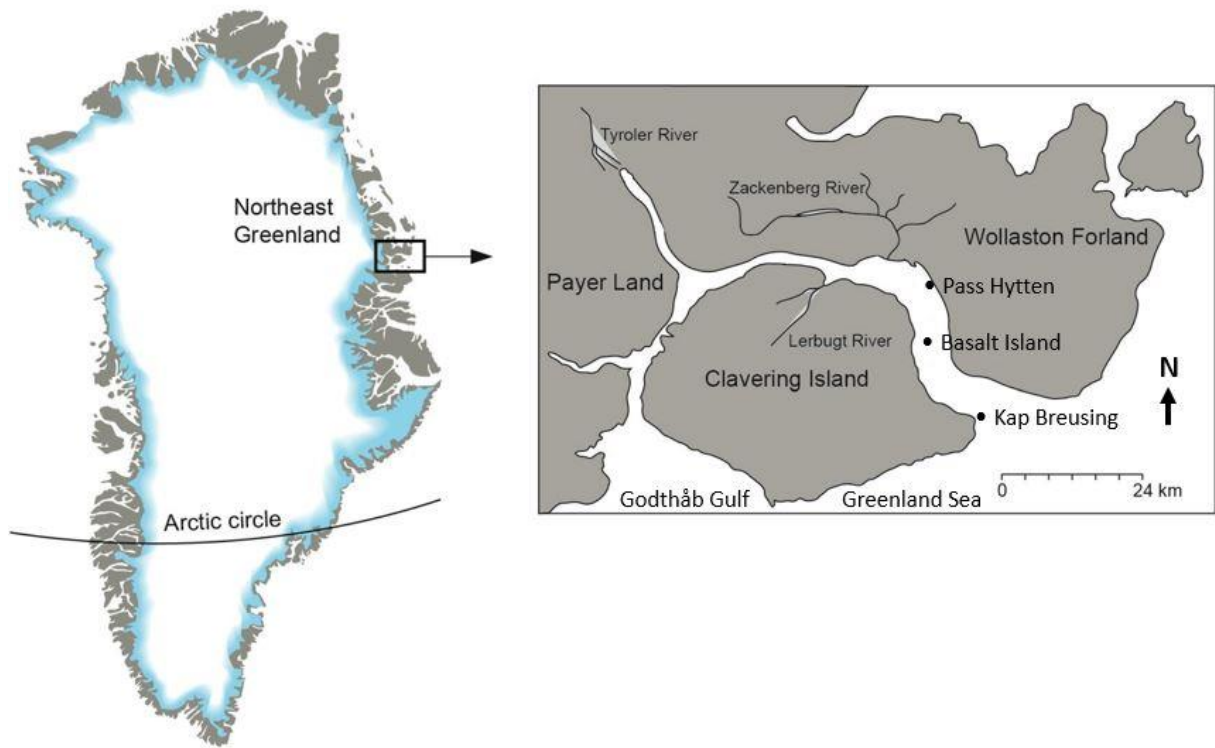
854 Figure 1: Location of the Young Sound's fjord (NE Greenland) and the three sampled stations:  
855 Pass Hytten, Basalt Island, and Kap Breusing (modified from Ribeiro et al. 2017).

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

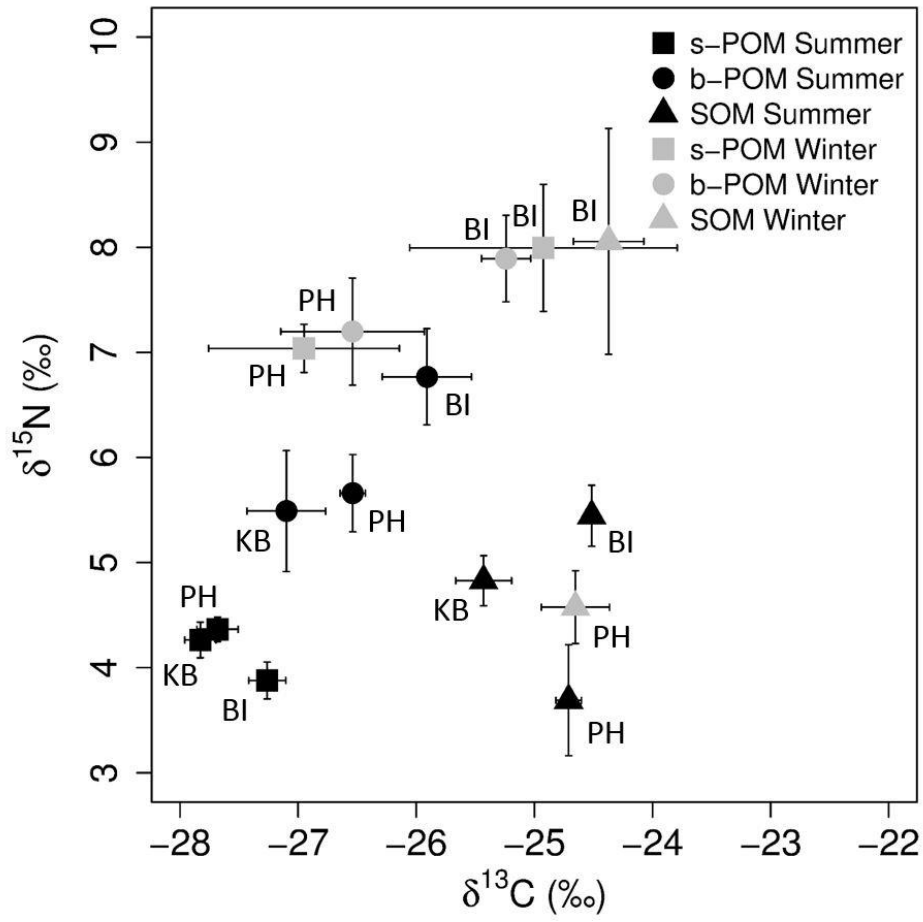
865 **Figure 1**



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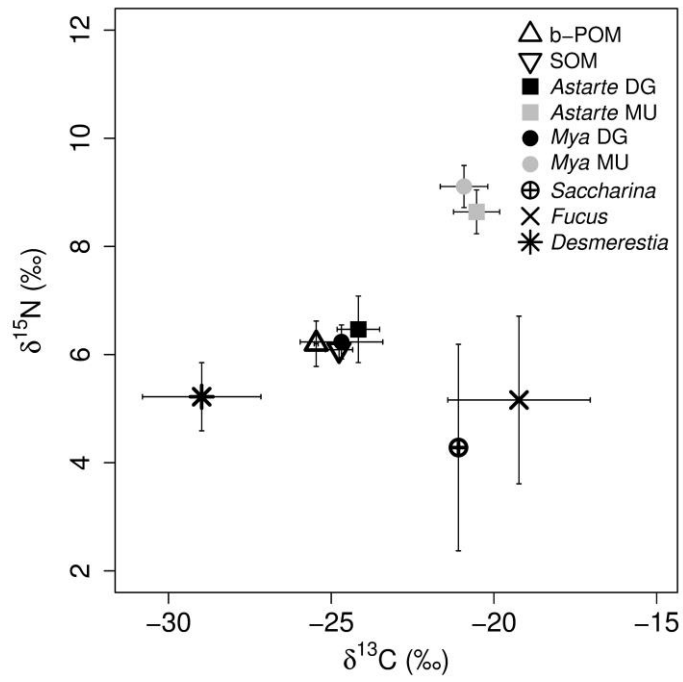
867 **Figure 2**



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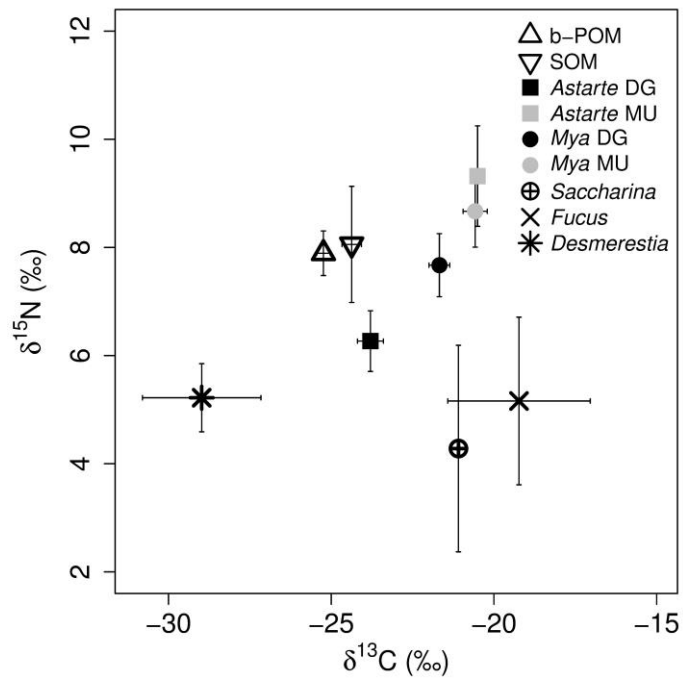
870 **Figure 3**



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 $\omega$ 6, 20:5 $\omega$ 3, and 22:6 $\omega$ 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 $\omega$ 6, 20:5 $\omega$ 3, and 22:6 $\omega$ 3 proportions),  
893 EPA/DHA: 20:5 $\omega$ 3/22:6 $\omega$ 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
<b>Organic matter origin</b>		
Diatoms	16:1 $\omega$ 7, 16:4 $\omega$ 1, 20:5 $\omega$ 3	Reuss & Poulsen (2002), Dalsgaard et al. (2003), Kelly & Scheibling (2012)
Dinoflagellates	18:4 $\omega$ 3, 22:6 $\omega$ 3	Napolitano et al. (1997), Kelly & Scheibling (2012)
Macroalgae (Phaeophyceae)	18:2 $\omega$ 6, 18:3 $\omega$ 3, 18:4 $\omega$ 3, 20:5 $\omega$ 3	Kelly & Scheibling (2012), De Cesare et al. (2017), Gaillard et al. (2017)
<b>Organic matter quality</b>		
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 $\omega$ 6, 20:5 $\omega$ 3, and 22:6 $\omega$ 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	b-POM	s-POM	b-POM	s-POM	b-POM		s-POM	b-POM	s-POM	b-POM	
	N = 5	N = 5	N = 5	N = 4	N = 5	N = 4	N = 10	N = 4	N = 4	N = 5	N = 5	N = 9
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 <sup>2</sup>	p-value
Site (S)	2	0.1360	5.7102	0.2809	<b>0.0014</b>
Depth (D)	1	0.1327	5.5725	0.1371	<b>0.0052</b>
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 <sup>2</sup>	p-value
Site (S)	1	0.0494	4.7766	0.2137	<b>0.0014</b>
Depth (D)	1	0.0251	2.4328	0.1088	<b>0.0494</b>
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 <sup>2</sup>	p-value
<i>M. truncata</i> DG	1	0.4866	36.8920	0.8405	<b>0.0062</b>
<i>M. truncata</i> MU	1	0.0931	20.9360	0.7235	<b>0.0074</b>
<i>A. moerchi</i> DG	2	0.1092	16.6220	0.6129	<b>0.0001</b>
<i>A. moerchi</i> MU	2	0.2220	7.2209	0.4593	<b>0.0005</b>
	Tissue as fixed factor				
	df	MeanSqs	F Model	R <sup>2</sup>	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	<b>0.0084</b>
<i>A. moerchi</i> May.	1	0.3243	48.958	0.7776	<b>0.0001</b>
<i>A. moerchi</i> Aug.	1	0.4510	19.831	0.5862	<b>0.0001</b>

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