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## Sources, quality and transfers of organic matter in a highly-stratified sub-Arctic coastal system (Saint-Pierre-et-Miquelon, NW Atlantic)

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1 TITLE (16 words / 137 characters)

2 Sources, quality and transfers of organic matter in a highly-stratified sub-Arctic coastal  
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4 RUNNING PAGE HEAD (8 words)

5 Pelagic-benthic coupling in a highly-stratified sub-Arctic coastal system

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23 **ABSTRACT** (244 words)

24 In response to ongoing global climate change, marine ecosystems in the northwest Atlantic  
25 are experiencing one of the most drastic increases in sea surface temperatures in the world.  
26 This warming can increase water column stratification and decrease surface nutrient  
27 concentrations, in turn impacting primary productivity and phytoplankton assemblages.  
28 However, the exact impacts of these changes on sources and quality of organic matter as well  
29 as its transfers to the benthic compartment remain uncertain. This survey characterized  
30 organic matter sources and quality within a highly-stratified sub-Arctic coastal system (Saint-  
31 Pierre and Miquelon) and described its transfer towards a biomass-dominant primary  
32 consumer, the sand dollar *Echinarachnius parma*. This study analyzed fatty acid and stable  
33 isotope ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) composition of surface and bottom Particulate Organic Matter (s-  
34 POM and b-POM, respectively), Sedimentary Organic Matter (SOM) and sand dollar tissue  
35 along a near shore to offshore gradient during two contrasting seasons associated either with  
36 sharp or weak water column stratification (i.e. High vs Low Stratification Periods). Results  
37 revealed high relative abundances of polyunsaturated fatty acids (notably macro- and  
38 microalgae markers) in POM during the Low Stratification Period while the High  
39 Stratification Period was characterized by elevated relative abundance of saturated fatty acids  
40 indicating a higher organic matter degradation state. In addition, strong seasonal differences  
41 were also observed in food availability with four-fold higher concentrations in total suspended  
42 solids during Low vs High Stratification Periods. These results suggested thus multiple  
43 negative effects of stratification on pelagic-benthic coupling and POM quality. Lower nutrient  
44 repletion of surface waters during period of sharp stratification diminishes pelagic-benthic  
45 coupling by reducing food availability, POM quality and vertical transfer of organic matter.  
46 By contrast, the sediment-based diet of *E. parma* showed a low spatiotemporal variability  
47 reflecting the homogenous composition of the SOM. This study suggests that intensified

48 water column stratification due to increasing sea surface temperatures may modify the  
49 pelagic-benthic coupling and future quality and composition of POM pools.

50 **KEY WORDS** (7 words)

51 Pelagic-benthic coupling – Seasonal stratification – Organic matter – Fatty acids – Stable  
52 isotopes – Subarctic ecosystems – Saint-Pierre et Miquelon archipelago – Newfoundland  
53 Shelf

## 54 1. INTRODUCTION

55 Coastal benthic ecosystems are highly productive areas (e.g. Clavier et al. 2014) that provide  
56 essential ecosystem services such as seafood production and carbon sequestration (Barbier et  
57 al. 2011, Pendleton et al. 2012). However, their functioning and services can strongly depend  
58 on the quality and quantity of organic matter made available in the ecosystem through  
59 processes like bioturbation, nutrient cycling and secondary production (Müller-Navarra et al.  
60 2004, Wieking and Kröncke 2005, Snelgrove et al. 2014, Campanyà-Llovet et al. 2017).  
61 Decreases in the Particulate Organic Matter (POM) quality and quantity for example can  
62 reduce the efficiency of organic matter transfers to higher trophic levels. Benthic food webs  
63 may suffer subsequent impacts (i.e. shift from fresh matter-based to detritus-based food webs)  
64 including a decline in benthic secondary/tertiary production (e.g. Iken et al. 2010). The  
65 dependence of benthic ecosystems on organic matter quality and quantity suggests that  
66 perturbations to organic matter sources and fluxes induced by rising sea surface temperatures  
67 may also perturb pelagic-benthic coupling (defined here as the vertical flow of organic matter  
68 from the surface to the seafloor) (Campanyà-Llovet et al. 2017, Griffiths et al. 2017).

69 Numerous studies have investigated how pelagic-benthic coupling may evolve with declining  
70 surface water nutrient concentrations expected from rising sea surface temperatures and  
71 enhanced water column stratification (e.g. Wassmann & Reigstad 2011, Harrison et al. 2013,  
72 Randelhoff et al. 2020). A decrease in surface water nutrient concentrations may lead to a  
73 drop in phytoplankton production (Riebesell et al. 2009, Turner et al. 2015, D'Alelio et al.  
74 2020) associated with pronounced shifts in the composition of phytoplankton communities  
75 (from large diatoms to smaller cells as flagellates; Kiørboe 1993, Finkel et al. 2010). In  
76 addition, warmer surface temperatures in thermally-stratified waters can enhance POM  
77 degradation by increasing heterotrophic bacteria metabolic activity (Piontek et al. 2009,  
78 Wohlers et al. 2009). These reduce carbon fluxes towards bottom waters (Bopp et al. 2005,

79 Turner et al. 2015, Griffiths et al. 2017). In contrast, the impacts of increased stratification on  
80 the quality and composition of the organic matter exported towards the seafloor as well as  
81 their consequences on the benthic food webs remain unknown.

82 This research investigated the quality and sources of organic matter (i.e. surface and bottom  
83 Particulate Organic Matter, or s-POM and b-POM, respectively, and Sedimentary Organic  
84 Matter, or SOM) and their transfers towards a dominant secondary producer, the sand dollar  
85 *Echinarachnius parma* in a highly stratified coastal marine ecosystem of the sub-Arctic  
86 archipelago Saint-Pierre and Miquelon (SPM) in the NW Atlantic. SPM is an ideal study area  
87 due to an exceptionally sharp vertical water column stratification in late-August/mid-  
88 September, when temperatures drop abruptly from 18°C at the surface to 0-2°C at 80 m depth  
89 (Lazure et al. 2018, Poitevin et al. 2018). Climate change is expected to intensify this  
90 stratification. The Newfoundland-Labrador continental shelf is experiencing one of the  
91 highest increase in sea surface temperature in the world (i.e. + 1°C between 1982 and 2006,  
92 Belkin et al. 2009). A recent study also detected diurnal internal waves along SPM's shallow  
93 continental shelf (30 – 60 m depth) during the stratified season (Lazure et al. 2018). Although  
94 these waves remain poorly studied, they play a critical role in near shore ecosystem  
95 functioning by stimulating nutrient replenishment and primary production in surface waters  
96 through increased turbulence and mixing through the pycnocline (Wang et al. 2007, Jantzen et  
97 al. 2013, Woodson 2018). Increased water stratification will make the thermocline less  
98 responsive to perturbations generated by internal waves (i.e. less turbulence and thermocline  
99 vertical motion, Woodson 2018). Given these oceanographic factors, climate change is likely  
100 to modify the quality and sources of organic matter available around SPM through increased  
101 stratification, with potentially cascading effects on benthic food-webs.

102 In order to better understand these impacts, we conducted two sampling surveys around SPM  
103 during periods of either pronounced (August 2017) or weak (July 2018) stratification along a

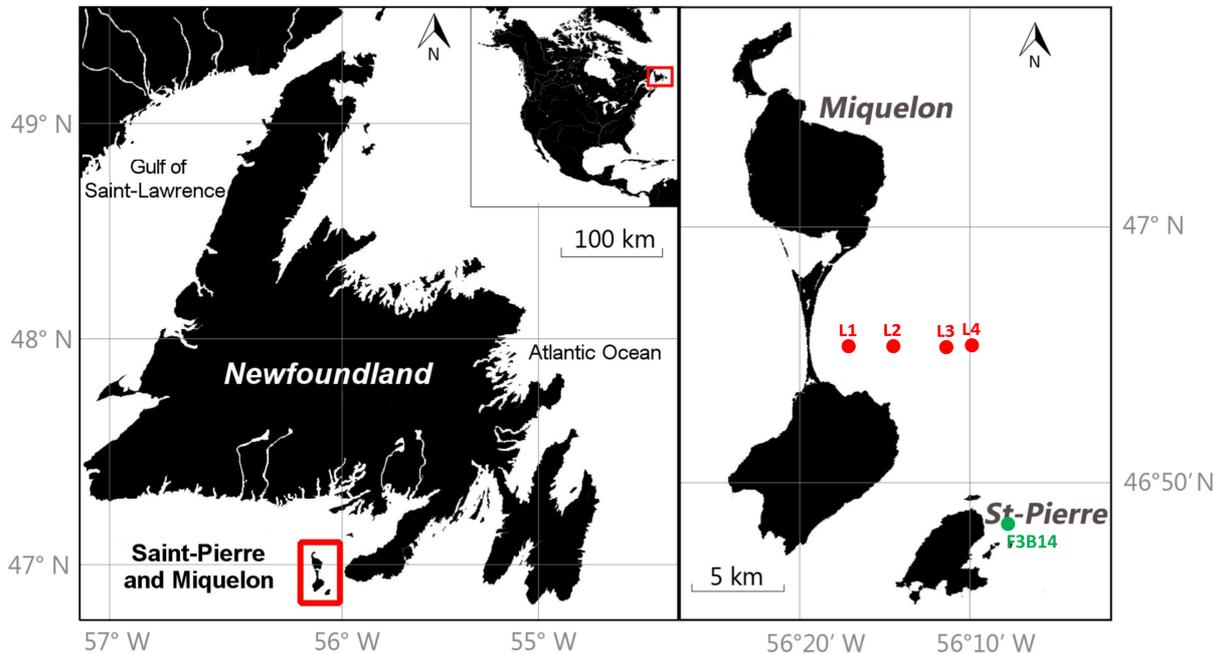
104 near shore to offshore gradient (i.e. pelagic-benthic coupling strength gradient; four stations).  
105 Quality, sources and transfers of organic matter were assessed through fatty acid and stable  
106 isotope analyses since these tools can identify the origin and quality of organic matter at  
107 different trophic levels in aquatic ecosystems (e.g. Søreide et al. 2013, Connelly et al. 2015,  
108 Mathieu-Resuge et al. 2019). The main goals of this study were to (1) describe spatial  
109 variability and seasonality (i.e. periods of strong versus weak stratification) in POM and SOM  
110 from a poorly studied sub-Arctic ecosystem, (2) assess the potential impact of seasonal sea  
111 surface temperature increases on quality and sources of POM and SOM, and their transfers to  
112 a dominant primary consumer (i.e. *E. parma*).

## 113 **2. MATERIALS AND METHODS**

### 114 **2.1 Study site**

115 The study was conducted in SPM (46°50'N, 56°20'W), a sub-Arctic archipelago located  
116 about 20 km south of Newfoundland (Figure 1). Sea surface temperatures usually show large  
117 seasonal variations (from sub-zero temperatures in March – April to 18°C in August –  
118 September) while bottom water temperatures (i.e. below 80 m) remain stable throughout the  
119 year (0 to 2°C; Lazure et al. 2018, Poitevin et al. 2018). The annual primary production  
120 occurs mainly during the phytoplankton bloom in April (Harrison et al. 2013, Pepin et al.  
121 2017). Aqua MODIS satellite data (OCI algorithm) over the last two decades have revealed  
122 inter-annual variations in which a second phytoplankton bloom may occur in  
123 September/October (Appendix, Figure S1). SPM is a costal oligotrophic environment  
124 deprived of major surface nutrient inputs from local rivers (C. Jauzein pers. com., Doré et al.  
125 2020). Although the Saint-Lawrence River is a major source of freshwater for the NW  
126 Atlantic, its outflows are deflected toward the western part of Cabot Strait and do not  
127 influence SPM waters (e.g. Wu et al. 2012). The absence of river influence on SPM

128 environments has been further confirmed by two recent paleoecology studies using primary  
129 production proxies (Poitevin et al. 2019, Doré et al. 2020).



130

131 *Figure 1: Map of the Saint-Pierre and Miquelon's archipelago (SPM) showing station F3B14*  
132 *and the four Langle's stations (L1, L2, L3 and L4; modified from Poitevin et al. 2018).*

133 Considering the physical characteristics, SPM is located within the contiguous part of the  
134 coastal branch of the Labrador Current flowing through the Avalon channel towards the NW,  
135 south of Newfoundland (De Young and Hay 1987, White and Hay 1994, Wu et al., 2012,  
136 Lazure et al., 2018). This current speed varies seasonally (strongest in fall/winter, weakest in  
137 summer; Wu et al., 2012) with an annual mean value of  $10 \text{ cm s}^{-1}$  in the middle of Saint-  
138 Pierre's Channel (Hay and De Young, 1989). Although mean currents were not measured  
139 within our study area, they are probably weaker than average due to higher bottom friction in  
140 shallow water areas. Sedimentation rates have not been estimated for SPM but global  
141 estimates (usually ranging from 1 to  $150 \text{ m d}^{-1}$ , Turner et al. 2015) suggest POM  
142 sedimentation time is much shorter than one season (e.g. minimum estimates of  $1 \text{ m d}^{-1}$   
143 implying that POM would settle in 80 days at the deepest station).

144 Lazure et al. (2018) reported remarkably large near-daily oscillations of near-bottom  
145 temperatures around SPM. During the stratification period (July-September), the interaction  
146 of surface tides with local bathymetric features generates diurnal internal waves, which  
147 propagate around the archipelago guided by bathymetry. The large amplitude of these internal  
148 waves (40 – 60 m) and the sharp thermocline can generate temperature gradients along the  
149 seafloor of as much as 11°C over a period of hours in mid-September. The 15-25 m depth of  
150 the thermocline and internal wave amplitudes lead to strong perturbations between 30 to 60 m  
151 depth (respective depths of thermocline elevations and depressions). Water column zones  
152 above 30 m and below 60 m do not appear to experience the direct effects of these internal  
153 waves.

## 154 **2.2 Sampling strategy**

155 Sampling was conducted in late August 2017 and early July 2018. These timeframes  
156 respectively correspond to a “High Stratification Period” and a “Low Stratification Period”  
157 observed for the study area (see Lazure et al. 2018). During both sampling campaigns, four  
158 stations were sampled along a bathymetric gradient labeled L1 (10 m) to L4 (80 m) and  
159 spanning contrasted zones of pelagic-benthic coupling (Figure 1, Table 1). At each station, 10  
160 liters of seawater per replicate were collected by Niskin bottles at one meter below the surface  
161 for surface POM samples (s-POM) and one meter above the seafloor for bottom POM  
162 samples (b-POM). CTD probes (Seabird 911plus, coupled to a Wetlab ECO FL chlorophyll-a  
163 fluorescence sensor in 2017; RBR *concerto* in 2018) were deployed during sampling at each  
164 station to record depth profiles of temperature, salinity and fluorescence. Salinity was not  
165 measured from station L4 in July 2018 due to logistical reasons and fluorescence was not  
166 measured in July 2018 due to the absence of a fluorescence sensor. An oceanographic  
167 mooring (composed of 28 TidbiT® temperature sensors ranging from 15 m below the surface  
168 to 120m) was deployed from May 2017 to May 2018 to assess water circulation as well as

169 water column stratification seasonality and short-term variability around SPM (i.e. down to  
170 hourly timescales). Temperature profiles sampled at 10 min intervals were then averaged on a  
171 weekly basis for the first week of July and the last week of August 2017. The mooring was  
172 deployed to the northeast of Saint-Pierre island at 125 m depth (F3B14 in Figure 1). Scuba  
173 divers collected SOM samples at stations L1 and L2 in 2017 and only at L2 in 2018 (Table 1).  
174 SOM was collected using a 450 ml syringe sucking the upper millimeters of the sediment  
175 surface (i.e. 0-3 mm, surface area  $\approx 625 \text{ cm}^2$ ). The upper few millimeters of the sediment are  
176 expected to be highly-responsive to particle fluxes (e.g. Danovaro et al. 1999) and are more  
177 likely to be resuspended and thus assimilated by benthic invertebrates than deeper sediment  
178 layers. In order to track organic matter transfers to primary consumers, several sand dollar  
179 individuals (i.e. 3 – 9) were collected at each station by either scuba divers or using a “Rallier  
180 du Baty” dredge. *E. parma* was selected in our study as a model species for two reasons: (1)  
181 *E. parma* is a biomass-dominant species in SPM benthic habitat (i.e. this species has therefore  
182 a preponderant role on the organic matter flowing through the benthic food web) and (2) *E.*  
183 *parma* was the only species found at every stations from 10 to 80 m (J. Grall per. obs.). Five  
184 macroalgae species (*Agarum clathratum*, *Desmarestia viridis*, *Halosiphon tomentosus*,  
185 *Porphyra* spp., *Saccharina latissima*) were also collected in 2017 to assess their potential  
186 contribution to POM, SOM and sand dollar diet (Table 1). These five palatable macroalgae  
187 represent a major part of the seaweed biomass around SPM and are known to be potentially  
188 major food sources for benthic invertebrates (Perez et al. 2013, Renaud et al. 2015, Gaillard et  
189 al. 2017).

190 *Table 1: Site coordinates, date and biological material sampled in August 2017 and July*  
191 *2018 around Saint-Pierre and Miquelon.*

Station	Latitude	Longitude	Sampling dates	Depth (m)	Biological material / Physical parameters
L1	46°55.514' N	56°17.279' W	29/08/2017 & 04/07/2018	11	s-POM, b-POM, SOM (only in 2017), <i>E. parma</i> , macroalgae, CTD
L2	46°55.678' N	56°14.654' W	30/08/2017 & 02/07/2018	25	s-POM, b-POM, SOM, <i>E. parma</i> , macroalgae, CTD
L3	46°55.468' N	56°11.549' W	28/08/2017 & 05/07/2018	60	s-POM, b-POM, <i>E. parma</i> (only in 2018), CTD
L4	46°55.909' N	56°09.936' W	28/08/2017 & 07/07/2018	88	s-POM, b-POM, <i>E. parma</i> (only in 2017), CTD (only in 2017)
F3B14	46°48' N	56°05' W	01/07/2017 to 31/08/2017	125	CTD

192

## 193 **2.3 Sample analyses**

### 194 2.3.1 Preliminary information

195 We decided to investigate seasonal variations in quality, composition and transfers of organic  
196 matter between High and Low Stratification Periods by analyzing fatty acid and stable isotope  
197 composition of *E. parma* as well as various sources of organic matter (i.e. POM, SOM and  
198 macroalgae). Fatty acids have been shown to constitute powerful tools to identify the origin of  
199 the organic matter in aquatic ecosystems (e.g. Meziane & Tsuchiya 2000) since fatty acid  
200 profiles (i.e. the list and relative contributions [%] of all fatty acids contained in one lipid  
201 sample) of primary producers are usually characteristics of specific taxonomic groups (see  
202 Table 2). Moreover, some fatty acids as PolyUnsaturated Fatty Acids (PUFAs) can be used to  
203 describe the diet of secondary consumers since they are generally transferred conservatively  
204 (Dalsgaard et al. 2003, Gaillard et al. 2017, Thyrring et al. 2017). Stable isotopes are a useful  
205 complementary tools to study organic matter transfers in secondary producers (Fry 2006,  
206 Perez et al. 2013, De Cesare et al. 2017, Gaillard et al. 2017). Their high sensitivity to  
207 biological and physical processes allow also to distinguish organic matter sources according  
208 to their compartment (pelagic vs benthic), freshness (fresh vs refractory) or origin  
209 (phytoplankton, microphytobenthos, macroalgae, seagrass, Kharlamenko et al. 2001,  
210 McTigue et al. 2015, Mathieu-Resuge et al. 2019). Although POM and SOM pools are  
211 inherently highly variable and relate on environmental variations occurring in the ecosystem  
212 (e.g. variations in primary production or river inputs), fatty acid and stable isotope analyses  
213 are generally adapted to track high temporal variations within 1-2 weeks (Riera and Richard

1997, Lorrain et al. 2002, Leu et al. 2006, Mayzaud et al. 2013). Similarly, turnover rates of animal organs (e.g. digestive gland, stomach) are usually sufficiently high to identify monthly variations of diets of benthic invertebrates (e.g. Pazos et al. 2003, Paulet et al. 2006). Therefore, such a high response of organic matter fatty acid profiles and stable isotope signatures to environmental fluctuations should allow us to track high-frequency variations in organic matter quality and composition related to seasonal changes in stratification conditions. Conversely, the short temporal resolution of these trophic markers eliminates any influences of the spring phytoplankton bloom on our results (occurring usually in April; Pepin et al. 2017, Maillet et al. 2019).

*Table 2: List of fatty acids used in this study as tracer and descriptor of the organic matter origin and quality (modified from Bridier et al. 2019). SFA, PUFA and EFA refer to*

Descriptor of	Fatty acids	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)

*Saturated, PolyUnsaturated and Essential Fatty Acid, respectively.*

226

### 227 2.3.2 Preliminary treatments

228 POM samples were obtained by filtering seawater samples on precombusted GF/F  
 229 Whatman® microfiber filters (diameter: 47 mm; pore: 0.7  $\mu$ m) until clogging when possible  
 230 (mean filtered volume =  $8.9 \pm 1.4$  l; range: 4.2 – 10.0 l max). SOM samples represented a  
 231 mixture of organic matter (including microphytobenthos and detritus), inorganic particles and  
 232 seawater. SOM samples were agitated and allowed to settled for one hour before filtration on

233 GF/F filters (mean filtered volume = 0.450 ml). All filters and biological samples (i.e. urchins  
234 and macroalgae) were stored at -20°C in the field laboratory (Ifremer/DTAM, Saint-Pierre)  
235 and transferred frozen by boat and train (-20°C) to the MNHN-Paris where they were stored  
236 at -80°C until further analyses. Prior to analysis, all samples were freeze-dried at - 50 °C for  
237 at least 5 h (48 h for animal and macroalgae tissues) and then immediately weighed. Urchin  
238 stomachs (i.e. intestinal tissues and gut content) were dissected and ground prior to stable  
239 isotope and fatty acid analyses. POM and SOM GF/F filters were divided into two fractions  
240 for stable isotope and fatty acid analyses. The mass of organic matter on each half-filter was  
241 estimated using the equation given in Bridier et al. (2019):

$$242 \quad M(X) = \frac{W_{Half\ filter}}{W_{Whole\ filter}} X (W_{Whole\ filter} - W_{Precombusted\ filter})$$

243 Where M (X) is the mass (mg) of POM or SOM used for the fatty acid or stable isotope  
244 analysis, and W is the dry weight of half, whole or precombusted filters.

### 245 2.3.3 Fatty acid analyses

246 Fatty acid extraction followed the Bligh and Dyer method (1959) as modified in Meziane &  
247 Tsuchiya (2002). Samples were sonicated in a distilled water-chloroform-methanol solution  
248 (1:1:2, v:v:v) for 20 minutes. After this extraction, samples were dissolved in a 1:1 (v:v)  
249 distilled water-chloroform solution and then centrifuged (1409 X g, 5 min). After this physical  
250 separation, the solution containing lipid phases (i.e. 2 ml) was transferred into separate tubes,  
251 and subjected to additional rounds of phase transfer, sonication and centrifugation. Lipid were  
252 then dried under a dinitrogen (N<sub>2</sub>), diluted in a sodium hydroxide-methanol solution (1:2, v:v,  
253 [NaOH] = 2 mol.l<sup>-1</sup>) and heated at 90°C for 90 min for fatty acid saponification. This reaction  
254 was stopped by the addition of 500 µl of hydrochloric acid (37 %). Lipid fractions were then  
255 dissolved in 3 ml chloroform, transferred in separate tubes and dried under a dinitrogen (N<sub>2</sub>)  
256 gas. Finally, lipid extracts were heated at 90°C for 10 min with 1 ml of a methanolic boron

257 trifluoride solution (BF<sub>3</sub>-CH<sub>3</sub>OH, 14%) in order to convert fatty acids into Fatty Acid Methyl  
258 Esters (FAMES). At the end of the reaction, lipids were retrieved in 2 ml of chloroform and  
259 stored at – 20 °C.

260 Fatty acid quantification was performed using a Varian CP-3800 gas chromatograph equipped  
261 with a Supelco® Omegawax® Capillary GC 320 column and He carrier gas. Fatty acid  
262 identifications were validated using retention times and mass spectra measured from a  
263 commercial reference standard (Supelco® 37 Component FAME Mix). Mass spectra were  
264 measured with a Varian 220-MS coupled to a Varian 450-GC using a He carrier gas. Fatty  
265 acid nomenclature is defined as X:YωZ where X is the number of carbon atoms, Y the  
266 number of double bonds and Z the position of the last double bond relative to the methyl  
267 group. Concentration of each fatty acid peak was determined using an internal commercial  
268 standard (23:0, 5 mg.l<sup>-1</sup>) and the equation given in Schomburg et al. (1987):

$$269 \quad C_{FA} = \left( \frac{A_{FA}}{A_{C23}} \times \frac{C_{23}}{M_f} \right)$$

270 Where C<sub>FA</sub> is the fatty acid concentration (μg.g<sup>-1</sup>), A<sub>FA</sub> is the fatty acid peak area, A<sub>C23</sub> is the  
271 23:0 peak area, C<sub>23</sub> is the 23:0 quantity (μg) added to each sample and M<sub>f</sub> is the mass of  
272 organic matter measured from the half-filter.

#### 273 2.3.4 Stable isotope analyses

274 Half-filters and sand dollar guts were fumigated over 4 and 48 h, respectively, with 37% HCl  
275 to remove inorganic carbon (Lorrain et al. 2003, Søreide et al. 2006). The surface layer of  
276 POM and SOM filters were scraped into 10-30 mg fragments which were then transferred to  
277 tin capsules. Macroalgae and gut samples were first ground into a fine powder using a ball  
278 mill. Fractions of about 1 mg were then transferred to tin capsules.

279 Samples were analyzed at the University of California Davis Stable Isotope Facility (UC  
280 Davis SIF) using two different elemental analyzers (PDZ Europa ANCA-GSL, Sercon  
281 macroalgae/animal tissues and an Elementar Vario EL Cube elemental analyzer for filters)  
282 interfaced with an isotope ratio mass spectrometer (PDZ Europa 20-20, Sercon). Isotopic  
283 ratios are expressed using  $\delta$  notation corresponding to deviation (‰) in  $^{13}\text{C}/^{12}\text{C}$  and  $^{15}\text{N}/^{14}\text{N}$   
284 ratios from the international standards (Vienna PeeDee Belemnite and Air, respectively). The  
285  $\delta$  notation from Peterson & Fry (1987) is as follows:

$$286 \quad \delta X = \left[ \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \right] \times 1000$$

287 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.

## 288 **2.4 Statistical analyses**

289 Detecting meaningful covariation in the different datasets collected required the application of  
290 PERMANOVA statistical tests frequently used in marine ecological surveys. Statistical  
291 analyses were performed using the R software (R Core Team 2017) and “vegan” package  
292 (Oksanen et al. 2019). In contrast to ANOVAs, well designed PERMANOVA analyses do  
293 not depend on assumptions of normality and homoscedasticity (Anderson & Walsh 2013).  
294 Three-factor PERMANOVA was not appropriate given strong interactions among factors. We  
295 applied one-way PERMANOVA to test the seasonal variability of POM fatty acid profiles. A  
296 two-way PERMANOVA procedure was applied to test the effects of station and depth on  
297 POM fatty acid profiles for both seasons. We also used pairwise PERMANOVA to test for  
298 interactions between station and depth factors for both seasons. The effect of season on SOM  
299 fatty acid profiles could not be tested due to the low number of replicates (i.e. only 2  
300 replicates in July 2018). Spatial variability of SOM fatty profiles was tested through one one-  
301 way PERMANOVA. Similar to fatty acid profiles, effects of seasons and stations-depth on  
302 POM stable isotope signatures were tested by one-way and two-way PERMANOVAs,

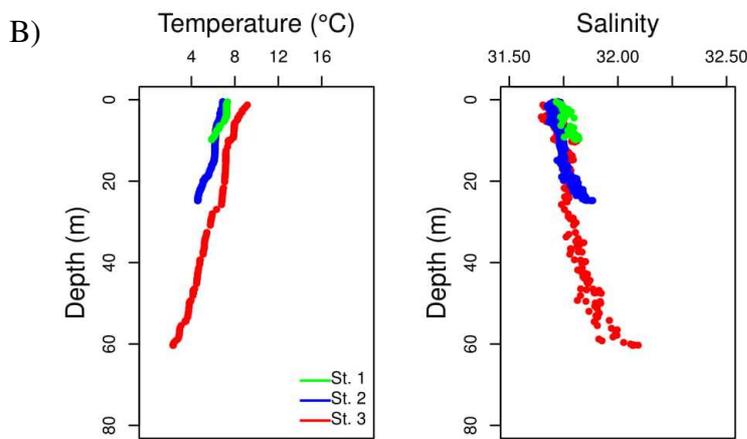
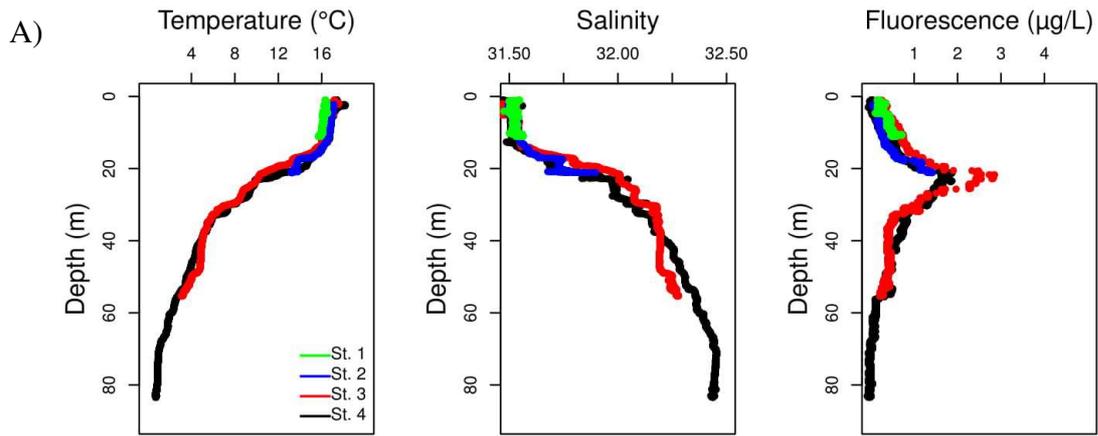
303 respectively. Station effects on SOM stable isotope signatures during the High Stratification  
304 Period and station-depth effects influencing stable isotope signatures from sand dollars were  
305 also tested by one-way and two-ways PERMANOVAs, respectively.

306 Finally, one Principal Component Analysis (PCA) was computed on the entire POM fatty  
307 acid data set to identify POM seasonal variation. In addition, two others PCAs were realized  
308 separately on POM fatty acid profiles from High and Low Stratification Periods in order to  
309 highlight spatial and depth variations. The PCA procedure used a Hellinger similarity matrix  
310 in order to reduce the influence of rare fatty acids in the ordination (Legendre and Gallagher  
311 2001).

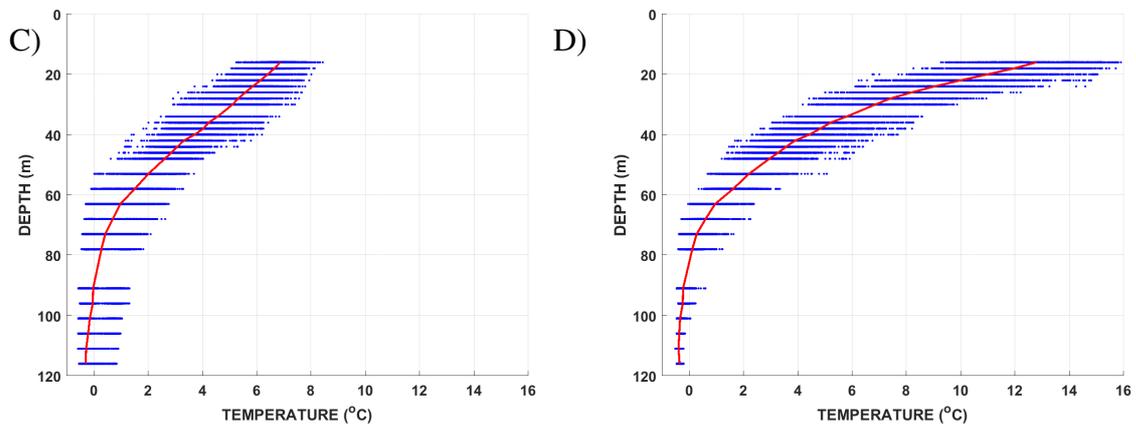
### 312 **3. RESULTS**

#### 313 **3.1 Environmental measurements**

314 During the High Stratification Period, CTD profiles showed pronounced water column  
315 stratification characterized by temperatures above 16 °C in surface waters and below 4°C in  
316 bottom waters (i.e. below 50 m, Figure 2A). The thermocline occurred at around 15 – 25 m,  
317 where temperature decreases from 15°C to 9°C. This zone also exhibits a peak in fluorescence  
318 (Figure 2A). During the Low Stratification Period, datasets showed more gradual declines in  
319 temperature. These decreased continuously from about 10 °C or less at the surface to 4 °C at  
320 the bottom (Figure 2B). Figure 2 shows averaged temperature profiles for the first week of  
321 July and the last week of August 2017 (Fig. 2C and 2D, respectively). These profiles show a  
322 clear increase in stratification in which the temperature gradient increases from about 5°C to  
323 10°C between 15 and 60 m. This shift matches that observed in CTD profiles taken during  
324 Low and High Stratification Periods. Consistency across sampled years (2017-2018) suggests  
325 that inter-annual variation is negligible compared to seasonal variation in terms of their  
326 relative influence on water column stratification.



327



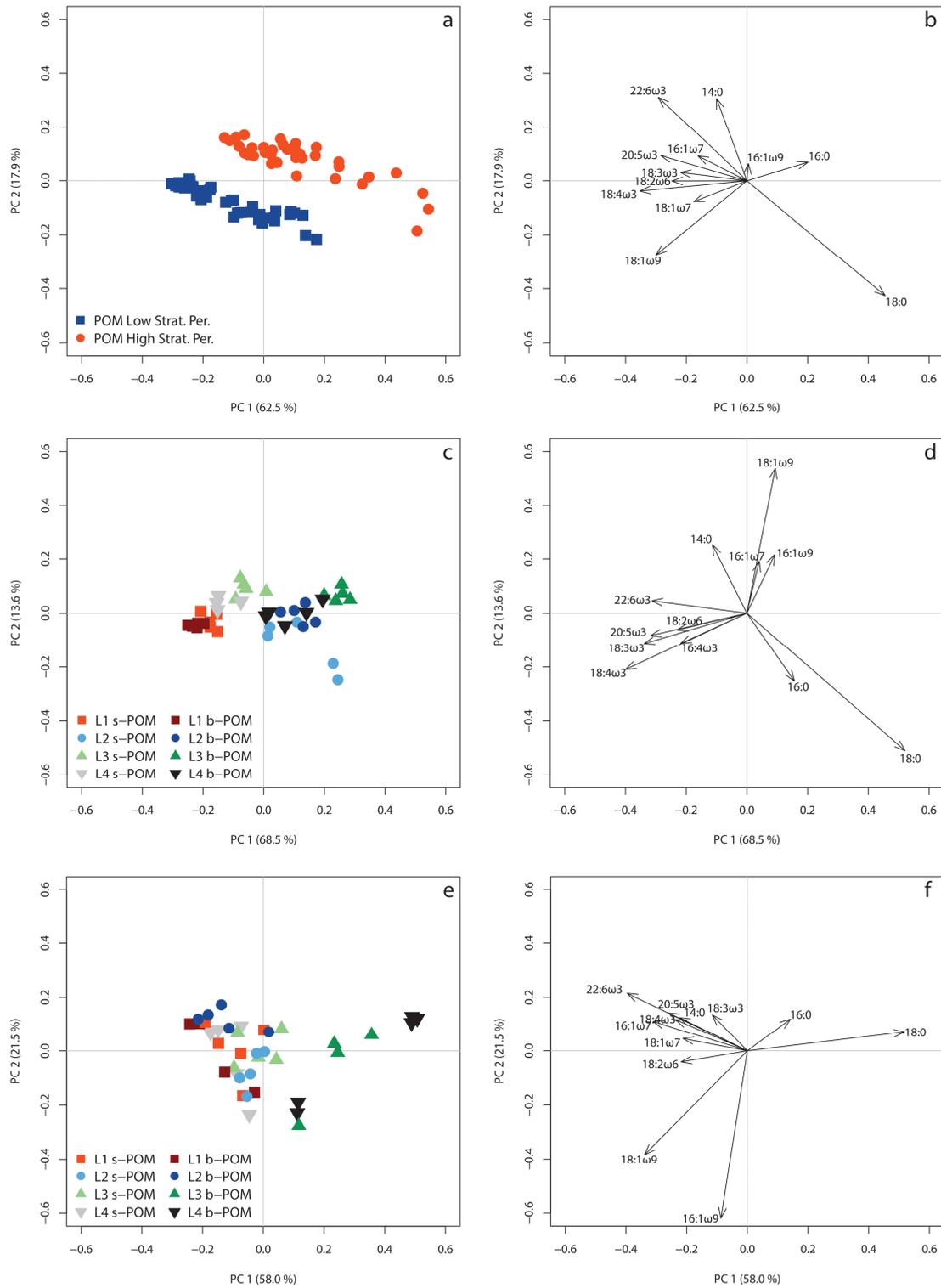
328

329 *Figure 2: Temperature (°C), Salinity and Fluorescence (µg.l-1) depth profiles at sample*  
 330 *stations in either August 2017 (L1 to L4, A) or July 2018 (L1 to L3, B). Averaged (red lines)*  
 331 *and raw temperatures (blue dots) at station F3B14 from 1 to 7th July 2017 (C) and from 25th*  
 332 *to 31th August 2017 (D).*

## 333 **3.2 Fatty acids profiles of POM and SOM samples**

### 334 3.2.1 Particulate Organic Matter

335 Sixty fatty acids were identified in POM and SOM samples (51 and 52 fatty acids during  
336 High and Low Stratification Periods, respectively). Only fatty acids with a relative abundance  
337 higher than 0.2 % in all samples were represented in Table S1 (Supplementary material).  
338 POM fatty acid profiles varied considerably between High and Low Stratification Periods ( $p$   
339  $< 0.001$ , Table S1). Seasonal differences in POM composition were mainly observed for  
340 PUFAs. Relative to those collected during the High Stratification Period, samples collected  
341 during the Low Stratification Period contained higher levels of PUFAs, especially 18:2 $\omega$ 6,  
342 18:3 $\omega$ 3, 18:4 $\omega$ 3 and 20:5 $\omega$ 3 (Figure 3a, b,  $\Sigma$  PUFA range = 5.3 – 36.7 % and 3.0 – 19.7 % for  
343 Low and High Stratification Periods, respectively). Samples collected during the High  
344 Stratification Period contained larger levels of saturated Fatty Acids (SFA) relative to those  
345 collected during the Low Stratification Period ( $\Sigma$  SFA range = 53.7 – 80.6 % and 38.2 – 61.5  
346 % for High and Low Stratification Periods, respectively). POM quantity showed strong  
347 temporal variation with four-fold higher concentrations of total suspended solids (TSS) during  
348 the Low Stratification Period (mean [TSS] =  $4.0 \pm 1.0$  mg l<sup>-1</sup>) compared to the High  
349 Stratification Period (mean [TSS] =  $1.5 \pm 1.1$  mg l<sup>-1</sup>). TSS samples exhibited similar fatty  
350 acid concentrations for both seasons (mean [FA] =  $4.4 \pm 2.8$   $\mu$ g mg<sup>-1</sup> TSS for High  
351 Stratification vs  $5.0 \pm 4.0$   $\mu$ g mg<sup>-1</sup> TSS for Low Stratification Period).



352

353 *Figure 3: Principal Component Analyses (PCA) based on Hellinger-transformed POM fatty*

354 *acid percentages from both High and Low Stratification Periods (a, b) as well as from*

355 *separate Low (c, d) and High (e, f) Stratification Periods. Individual factor maps are*

356 *represented in left plots (a, c, e) while variables factor maps are showed and right plots,*  
357 *respectively (b, d, f). Variable factor maps include only the 12 most discriminant fatty acids.*

358 During the Low Stratification Period, all stations showed statistically distinctive POM fatty  
359 acid profiles ( $p < 0.05$ ). Spatial variation was particularly pronounced between L1 and the  
360 other stations sampled since both s-POM and b-POM samples from L1 displayed the highest  
361 relative contributions of PUFAs (especially 18:2 $\omega$ 6, 18:3 $\omega$ 3, 18:4 $\omega$ 3 and 20:5 $\omega$ 3; Figure 3 c,  
362 d). Samples collected during the High Stratification Period showed high spatial variation in b-  
363 POM fatty acid profiles (Appendix, Table S3). The High Stratification b-POM samples also  
364 varied considerably between L1-L2 and L3-L4 stations ( $p < 0.01$ ; Appendix, Table S3). This  
365 variation appeared primarily as higher relative contributions of PUFAs (especially 18:2 $\omega$ 6,  
366 18:4 $\omega$ 3, 20:5 $\omega$ 3 and 22:6 $\omega$ 3) at L1-L2 relative to those measured from L3-L4 (Figure 3e, f).

### 367 3.2.2 Sedimentary Organic Matter

368 Table 3 and Figure S2 show seasonal differences in SOM fatty acid profiles between High  
369 and Low Stratification Periods. SOM samples from the Low Stratification Period displayed  
370 higher levels of PUFAs (especially for 18:4 $\omega$ 3 and 20:5 $\omega$ 3) compared with samples collected  
371 during the High Stratification Period ( $\Sigma$  PUFA = 12.9 % vs 5.7 % for Low and High  
372 Stratification Periods, respectively). By contrast, SFA (16:0 and 18:0 in particular)  
373 contributions were lower in samples from the Low Stratification Period relative to those  
374 collected during the High Stratification Period ( $\Sigma$  SFA = 39 % vs 77.4 %). MonoUnsaturated  
375 Fatty Acid (MUFA) contributions differed significantly between both seasons ( $\Sigma$  MUFA = 9.3  
376 vs 44.8 % for High and Low Stratification Periods, respectively), especially for 16:1 $\omega$ 7 (3.4 vs  
377 23.8 %) and 18:1 $\omega$ 9 (1.6 vs 9.4 %). However, no spatial variations were observed between L1  
378 and L2 stations during the High Stratification Period ( $p > 0.05$ ).

379

380 *Table 3: Fatty acid (FA) composition from sand dollar and Sedimentary Organic Matter*  
381 *(SOM) samples collected in August 2017 and July 2018. Values correspond to mean*  
382 *percentages from 3-9 samples with standard deviation in brackets. SFA, MUFA, PUFA, BrFA*  
383 *and EFA refer to Saturated, MonoUnsaturated, PolyUnsaturated, Branched and Essential*  
384 *fatty acids, respectively. EPA: Eicopensaconoic acid (i.e. 20:5 $\omega$ 3); DHA: Docohexaconoic*  
385 *acid (i.e. 22:6 $\omega$ 3), nd: not detected. Fatty acid percentages < 2 % in all samples are not*

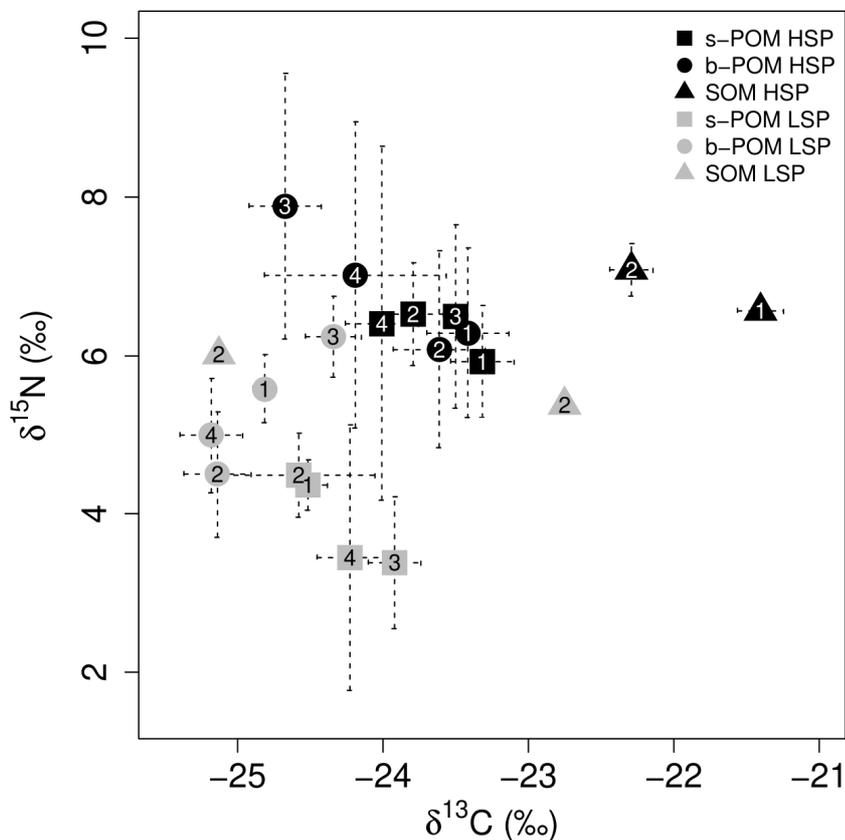
	High Stratification Period (August 2017)				Low Stratification Period (July 2018)			
	<i>Echinarachnius parma</i>			SOM	<i>Echinarachnius parma</i>			SOM
	Station 1 N = 3	Station 2 N = 3	Station 4 N = 4	Stations 1 & 2 N = 7	Station 1 N = 6	Station 2 N = 5	Station 3 N = 9	Station 2 N = 2
14:0	5.2 (1.2)	4.8 (0.4)	4.9 (0.6)	6.7 (1.3)	4.8 (1.2)	5 (0.4)	4.9 (0.7)	6 (0.6)
15:0	0.9 (0.2)	0.9 (0.2)	0.8 (0.1)	2.6 (0.5)	0.8 (0.1)	0.9 (0.3)	0.7 (0.1)	2.2 (0.2)
16:0	9.8 (2.3)	10.8 (1.2)	7.2 (0.8)	43.7 (4.1)	9.6 (1.8)	10.8 (1.4)	8.2 (1.0)	23.5 (1.0)
18:0	5.6 (0.9)	5.2 (0.7)	3.9 (0.3)	17.7 (3.8)	5.3 (1.1)	5.2 (0.8)	4.9 (0.7)	4.7 (0.1)
$\Sigma$ SFA	23.0 (4.1)	23.4 (2.8)	18.0 (1.2)	77.4 (8.2)	22.1 (3)	23.1 (2.2)	20 (1.4)	39 (0.2)
16:1 $\omega$ 7	7.7 (2.9)	8.1 (0.4)	12.5 (2.5)	3.4 (3.5)	8 (3)	10.9 (3.5)	9.7 (2.4)	23.8 (1.5)
16:1 $\omega$ 9	tr	0.2 (0.0)	0.3 (0.0)	0.5 (0.2)	0.2 (0.1)	0.4 (0.5)	0.2 (0.1)	4.6 (2.2)
18:1 $\omega$ 7	2.5 (0.2)	3.1 (0.6)	3.0 (0.2)	1.2 (1.1)	2.6 (0.3)	2.8 (0.4)	3.2 (0.2)	2.5 (0.1)
18:1 $\omega$ 9	1.9 (0.9)	2.3 (0.3)	1.8 (0.3)	1.6 (1.4)	5.1 (2.3)	4.7 (1.6)	4.2 (1.9)	9.4 (2.2)
20:1 $\omega$ 7	2.6 (0.4)	2.4 (0.1)	2.4 (0.5)	0.4 (0.2)	2.6 (0.4)	2.4 (0.1)	2.4 (0.5)	0.3 (0.0)
20:1 $\omega$ 9	1.2 (0.1)	1.3 (0.1)	1.2 (0.3)	0.3 (0.2)	2.4 (0.9)	1.9 (0.2)	2.3 (0.5)	0.3 (0.0)
20:1 $\omega$ 15	8.8 (2.0)	6.5 (1.5)	5.9 (1.7)	nd	7.4 (1.5)	5.2 (1.2)	6.8 (1.0)	nd
21:1 $\omega$ 9	2.3 (0.6)	1.6 (0.4)	1.5 (0.2)	0.5 (0.5)	2.3 (0.6)	1.6 (0.4)	1.5 (0.2)	nd
$\Sigma$ MUFA	29.4 (1.2)	27.9 (1.6)	31.2 (1.1)	9.3 (6.7)	30.4 (1.5)	29.9 (1.3)	30.8 (1.3)	44.8 (1.4)
16:4 $\omega$ 1	1.4 (0.7)	1.3 (0.3)	2.2 (0.5)	nd	1.6 (1)	1.9 (1)	1.7 (0.7)	0.6 (0.0)
18:4 $\omega$ 3	2.1 (0.1)	2.5 (0.5)	2.7 (0.2)	0.4 (0.2)	2.5 (0.5)	2.9 (0.3)	3.2 (0.5)	1.4 (0.4)
20:2 $\Delta$ 5, 13	2.2 (0.5)	2.0 (0.1)	2.0 (0.5)	nd	1.8 (0.5)	2 (0.5)	2.2 (0.3)	nd
20:2 $\Delta$ 5, 11	5.1 (1.3)	4.1 (0.3)	3.6 (0.8)	nd	4.5 (1.5)	3.5 (0.8)	3.7 (0.5)	nd
20:4 $\omega$ 6	1.8 (0.4)	2.0 (0.2)	2.9 (0.8)	0.4 (0.3)	1.3 (0.4)	1.8 (0.6)	1.6 (0.2)	0.5 (0.0)
20:5 $\omega$ 3	28.5 (4.0)	26.7 (2.2)	28.5 (1.1)	1.3 (1.0)	29.2 (3.4)	26.9 (2.2)	28.7 (2.2)	4.2 (0.5)
22:6 $\omega$ 3	1.7 (0.0)	4.1 (1.8)	2.3 (0.3)	0.4 (0.2)	1.4 (0.3)	1.8 (0.2)	2.1 (0.1)	0.5 (0.1)
$\Sigma$ PUFA	47.1 (5.4)	47.8 (4.2)	49.8 (2.3)	5.7 (1.7)	47 (3.3)	46 (2.3)	48.3 (2.3)	12.9 (1.0)
$\Sigma$ BrFA	0.5 (0.1)	0.9 (0.0)	1.0 (0.1)	6.7 (0.7)	0.6 (0.1)	0.9 (0.1)	0.9 (0.2)	3.3 (0.2)
$\Sigma$ EFA	32.1 (4.3)	32.8 (3.7)	33.8 (2.0)	2.2 (1.3)	32 (3.5)	30.6 (1.9)	32.4 (2.2)	5.2 (0.7)
$\Sigma$ PUFA/ $\Sigma$ SFA	2.1 (0.6)	2.1 (0.4)	2.8 (0.3)	0.1 (0.0)	2.2 (0.4)	2 (0.3)	2.4 (0.3)	0.3 (0.0)
EPA/DHA	16.9 (2.6)	7.1 (2.4)	12.7 (1.6)	2.9 (1.7)	20.8 (3.2)	15 (1.3)	13.9 (1)	8.3 (1.3)
[FA] (mg/g)	31.7 (23.0)	22.8 (19.7)	52.5 (38.5)	0.2 (0.1)	78.0 (43.0)	63.9 (33.7)	90.3 (23.1)	1.8 (1.1)

386 *shown. The entire table is provided in the appendix (see Table S2).*

387

388 **3.3 Stable isotopes signatures of POM and SOM samples**

389 POM samples showed a general decrease in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values from High to Low  
390 Stratification Periods ( $p < 0.001$ , Figure 3). Two-way PERMANOVA detected significant  
391 station, depth and station-depth interaction effects on POM's  $\delta^{13}\text{C}$  values ( $p < 0.01$ ) but not  
392  $\delta^{15}\text{N}$  values ( $p > 0.05$ ) during the High Stratification Period. During the Low Stratification  
393 Period, station and depth factors exerted influence on POM  $\delta^{13}\text{C}$  values ( $p < 0.01$ ), while only  
394 depth factors and station-depth interactions exerted effects on  $\delta^{15}\text{N}$  values ( $p < 0.05$ ).  
395 Supplementary materials list pairwise PERMANOVA results (Table S3).



396

397 *Figure 3: Mean ( $\pm$ SD) stable isotope signatures ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) of surface and bottom*  
398 *Particulate Organic Matter (s-POM and b-POM, respectively) and Sedimentary Organic*  
399 *Matter (SOM) samples collected during High Stratification (August 2017, black symbols) and*  
400 *Low Stratification (July 2018, grey symbols) periods. Numbers within symbols refer to*  
401 *sampled stations.*

402 The SOM samples collected during the Low Stratification Period showed more depleted  $\delta^{13}\text{C}$   
403 and  $\delta^{15}\text{N}$  values than samples collected during the High Stratification Period ( $\approx$  depletion of -  
404 1.6 and - 1.4 ‰ for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , respectively). During the High Stratification Period, SOM  
405 from L2 displayed significantly higher  $\delta^{15}\text{N}$  and lower  $\delta^{13}\text{C}$  values than L1 ( $p < 0.05$ ).

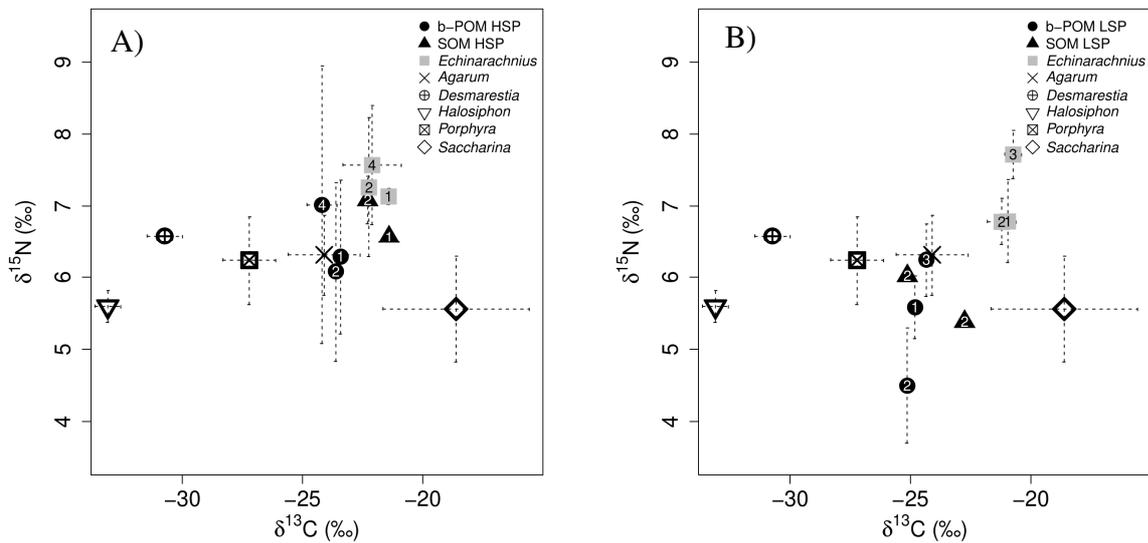
#### 406 **3.4 Fatty acids profiles and stable isotopes signatures from sand dollars**

407 Overall, fatty acid profiles from *E. parma* stomachs showed relatively low variation between  
408 years and stations. All samples contained relatively high proportions of PUFAs (range = 46 –  
409 49.8 %), especially 20:5 $\omega$ 3 (range = 26.7 – 29.2 %). Presence of 16:4 $\omega$ 1, 18:4 $\omega$ 3, 20:4 $\omega$ 6 and  
410 22:6 $\omega$ 3 were also noticed in fatty acid profiles (Table 3). Samples contained lower  
411 proportions of SFAs ( $\Sigma$  SFA range = 18 - 23.4 %), which consisted primarily of 14:0, 16:0  
412 and 18:0. Proportions of MUFAs ranged between 27.9 and 31.2 % and were dominated by  
413 16:1 $\omega$ 7 (range = 7.7 – 12.5 %) and 20:1 $\omega$ 15 (range = 5.2 – 8.8 %).

414 Although *E. parma* samples showed significant different fatty acid profiles between High and  
415 Low Stratification Periods ( $p < 0.01$ ), lipid profiles from these two years were highly similar  
416 (83.14 % of similarity, Table 3). *E. parma* fatty acid profiles showed significant differences  
417 among stations during the High Stratification Period ( $p < 0.01$ ) but not during the Low  
418 Stratification Period ( $p > 0.05$ ).

419

420 The *E. parma* samples collected during the Low Stratification Period gave slightly enriched  
 421 carbon isotopic values relative to those collected during the High Stratification Period ( $p <$   
 422  $0.01$ , Figure 4a, b). *E. parma* samples collected from different stations did not show  
 423 significant differences in carbon isotopic values ( $p > 0.05$ ). Nitrogen isotopic values from *E.*  
 424 *parma* samples differed between L3 and L1-L2 stations ( $p < 0.01$ ) but not between seasons ( $p$   
 425  $> 0.05$ ). During the High Stratification Period, *E. parma* and SOM samples gave similar  
 426 respective  $\delta^{13}\text{C}$  values of  $-21.4 \pm 0.1\text{‰}$  vs  $-21.4 \pm 0.2\text{‰}$  for L1 and  $-22.2 \pm 0.3\text{‰}$  vs  $-22.3 \pm$   
 427  $0.1\text{‰}$  for L2 (Figure 4a).



428  
 429 *Figure 4: Mean ( $\pm$  SD) stable isotope signatures ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) measured from*  
 430 *Echinarachnius parma* *stomachs and the organism's potential food sources during High*  
 431 *Stratification (August 2017, A) and Low Stratification (July 2018, B) periods. b-POM: bottom*  
 432 *Particulate Organic Matter; SOM: Sedimentary Organic Matter. Numbers within symbols*  
 433 *indicate stations.*

## 434 4. DISCUSSION

### 435 4.1 Spatiotemporal variations in POM sources

436 During both seasons, microalgal fatty acids represented significant proportions of POM fatty  
437 acid profiles. Dinoflagellate (22:6 $\omega$ 3, 18:4 $\omega$ 3) and diatom markers (20:5 $\omega$ 3, 16:1 $\omega$ 7) were  
438 notably present (Figure 3, Table S1). Macroalgae also made significantly apparent  
439 contributions to the organic matter pool as indicated by the presence of 18:2 $\omega$ 6 and 18:3 $\omega$ 3  
440 PUFAs (range  $\Sigma$  (18:2 $\omega$ 6 + 18:3 $\omega$ 3) = 1.4 – 13.5 %, Table S1). Stable isotope signatures were  
441 consistent with a contribution from the macroalgae *A. clathratum* and possibly several other  
442 mixed species (e.g. *D. aculeata* and *S. latissima*). Higher relative percentages of 18:2 $\omega$ 6 and  
443 18:3 $\omega$ 3 indicated that macroalgal contributions to POM were much higher during the Low  
444 Stratification Period relative to the High Stratification Period conditions. On the whole, the  
445 Low Stratification Period was characterized by fresh and high quality organic matter as  
446 indicated by high levels of EFAs (Essential Fatty Acids) and PUFAs (especially 18:2 $\omega$ 6,  
447 18:4 $\omega$ 3, 20:5 $\omega$ 3). Higher TSS concentrations observed during this season may also indicate  
448 higher food availability compared to that available during the High Stratification Period  
449 (Table S1).

450 Our results revealed also major variations along the cross-shore transect. Strong spatial  
451 variations were observed in both surface and bottom waters during the Low Stratification  
452 Period due to a predominance of macroalgal sources for POM collected from near shore  
453 environments while POM from more distal environments (i.e. depth > 20 m) appeared to  
454 originate from a mixture of microalgal and macroalgal sources. In contrast, POM sources and  
455 quality were homogenous in surface waters during the High Stratification Period. Bottom  
456 water samples showed however higher organic matter quality in shallow areas (depth < 30 m)  
457 due to higher contributions of microalgal material to POM (fatty acid markers 16:1 $\omega$ 7,  
458 18:4 $\omega$ 3, 20:5 $\omega$ 3, 22:6 $\omega$ 3).

## 459 **4.2 Influence of stratification on POM quality and pelagic-benthic coupling**

460 Differences in pelagic trophic conditions may arise from seasonal drivers of water column  
461 stratification and vertical mixing. Seawater surface temperatures at SPM rise in March and  
462 increase steadily until mid-September when water column stratification reaches its maximum  
463 (Lazure et al. 2018, Poitevin et al. 2018). Nutrient profiles from SPM waters show a typical  
464 vertical distribution with depleted nutrient concentrations at the surface (especially for nitrates  
465 and silicates) and nutrient-rich bottom waters (C. Jauzein pers. com.) during the stratified  
466 period. Extremely high-water column stratification during the High Stratification Period may  
467 then act as a barrier to nutrient exchange between surface and sub-surface waters. Limitation  
468 in nutrient vertical fluxes during the High Stratification Period and the absence of significant  
469 horizontal nutrient input to this oligotrophic environment by rivers (Doré et al. 2020) likely  
470 limit primary production compared to the Low Stratification Period. The much lower TSS  
471 concentrations recorded during the High Stratification Period ( $[TSS] = 1.5 \pm 1.1$  vs  $4.0 \pm 1.0$   
472  $\text{mg l}^{-1}$  for the High and Low Stratification periods, respectively) support this interpretation.

473 Spatial variation in POM fatty acid profiles during the High Stratification Period also seems  
474 to reflect the influence of stratification on pelagic-benthic coupling and b-POM freshness.  
475 Numerous studies have shown that nutrient limitations under increased stratification lead to  
476 shifts in the size distributions of phytoplankton communities from a predominance of larger to  
477 smaller cells (Kiørboe 1993, Falkowski & Oliver 2007, Finkel et al. 2010). Tighter coupling  
478 between smaller phytoplankton cells and heterotrophic bacteria promotes more efficient  
479 recycling of organic matter in surface waters (through regenerated primary production) and  
480 limits vertical export to sediment (Legendre & Le Fèvre 1995, Bopp et al. 2005, Turner et al.  
481 2015). Warmer surface temperatures during the High Stratification Period may also enhance  
482 POM degradation by stimulating heterotrophic microbial activity (Piontek et al. 2009,  
483 Wohlers et al. 2009, Turner et al. 2015). Moreover, slower sedimentation rates of smaller cells

484 usually increase the residence time of phytoplankton within the water column extending thus  
485 exposure to oxidation and microbial degradation (Turner et al. 2002, Guidi et al. 2009,  
486 Marañón 2015). Together, these processes reduce the quantity and freshness of the organic  
487 matter reaching the seabed (Budge and Parrish 1998, Parrish et al. 2005, Guidi et al. 2009,  
488 Turner et al. 2015). On both deep stations, extremely low PUFA levels were observed in  
489 bottom compared to surface waters that could reflect effects of stratification on phytoplankton  
490 size structure, microbial degradation and pelagic-benthic coupling strength. The higher  
491 relative levels of PUFAs measured in near shore bottom water samples (< 30 m depth) may  
492 derive from autotrophic production of organic matter around the pycnocline supported by  
493 (small) local nutrient pulses from subsurface waters. Such subsurface autotrophic production  
494 has been widely reported in sub-Arctic/Arctic oligotrophic and highly-stratified surface  
495 waters. It is usually the result of a compromise between the low nutrient concentrations at the  
496 surface and low light availability in deep waters (Martin et al. 2010, Tremblay et al. 2015).  
497 Part of the subsurface fluorescence peak observed in this study may also reflect higher  
498 photosynthetic pigment concentrations in shade-adapted phytoplankton species growing in  
499 subsurface waters (Fennel and Boss 2003, Tremblay et al. 2015). Spatial variation in POM  
500 during the Low Stratification Period indicates a more efficient pelagic-benthic coupling under  
501 condition of continuous water column stratification. Smaller shifts in PUFA levels between  
502 surface and bottom waters during this period support this interpretation (Table S1).

503 Lower food availability and lower organic matter quality during the High Stratification Period  
504 conditions may also reflect the influence of sharp stratification on internal waves. Pronounced  
505 water column stratification caused by higher sea surface temperatures can result in more  
506 stable internal waves (Nielsen et al. 2004, Woodson 2018) and prevent their breakage (and  
507 their action on turbulence and nutrient mixing). This may have especially affected near shore  
508 stations (i.e. L1 and L2) during the High Stratification Period. Amplitudes of internal waves

509 are usually dampened by water column stratification (Walter et al. 2014, Woodson 2018).  
510 Weaker vertical oscillation of the thermocline during the High Stratification Period may thus  
511 limit deep water nutrient inputs to surface waters.

512 Longer sedimentation rates during the High Stratification Period imply that POM is probably  
513 more subjected to horizontal advection during settling. This means that b-POM deposited at a  
514 given location may not originate from the same location at the surface. This effect introduces  
515 the possibility that seasonal variation in organic matter composition and quantity reflects  
516 POM advection rather than differences in stratification. Pronounced differences between  
517 surface and bottom currents (i.e.  $\sim 10 \text{ cm s}^{-1}$ ) and a low sedimentation rate (e.g.  $5 \text{ m d}^{-1}$ , i.e.  
518 16 days of sedimentation between the surface and 80 m depth, Turner et al. 2015) would place  
519 POM sampled at 80 m depth during the High Stratification Period  $\sim 130 \text{ km}$  from surface  
520 waters where it originated. However, primary production and stratification are generally  
521 homogeneous around the Newfoundland Shelf (Craig and Colbourne 2002, Cyr and Larouche  
522 2015, Pepin et al. 2017). Therefore, although b-POM may have undergone some advection  
523 during the High Stratification Period, this would not influence POM quality and quantity  
524 since the impact of stratification on primary production and vertical sedimentation rates are  
525 likely homogeneous across the Newfoundland Shelf.

### 526 **4.3 Additional contribution of macroalgae to POM**

527 The high levels of  $18:2\omega6$  and  $18:3\omega3$  (Figure 3, Table S1) reported here suggest that  
528 macroalgae represent a major source of POM around SPM, especially during the Low  
529 Stratification Period. An additional fatty acid, the  $20:4\omega6$  marker, displays high levels in  
530 macroalgae samples but low relative abundance in POM samples (Appendix, Table S4). This  
531 may arise from the lower relative chemical stability of certain macroalgal fatty acids. Also,  
532 microalgal fatty acids detected in POM derive primarily from living cells whereas macroalgal  
533 fatty acids mostly derive from thalli detritus subjected to more intensive degradational

534 processes. The 18:2 $\omega$ 6 and 18:3 $\omega$ 3 may also derive from seagrass or terrestrial organic matter  
535 (Kelly and Scheibling 2012, Mathieu-Resuge et al. 2019). The distinctive  $\delta^{13}\text{C}$  values  
536 measured from POM relative to known ranges for seagrass ( $\delta^{13}\text{C} > -12 \text{‰}$ ) and terrestrial  
537 organic matter ( $\delta^{13}\text{C} < -28 \text{‰}$ ) however argue against a contribution from these sources (see  
538 Peterson 1999).

539 Field observation also support the interpretation of a significant autochthonous macroalgal  
540 contribution to POM. Scuba diving surveys conducted near the sampling area have found that  
541 shallow areas are populated by the two macroalgal species *A. clathratum* and *S. latissima* (P.  
542 Poitevin pers. obs.). Kelp forests can constitute major sources of dissolved and particulate  
543 organic matter in marine coastal ecosystems via exudation and fragmentation processes (e.g.  
544 blade erosion, thalli dislodgment, blade shedding, Krumhansl & Scheibling 2011, Krumhansl  
545 & Scheibling 2012, Leclerc et al. 2013, Pessarrodona et al. 2018). Fragmentation processes  
546 depend on several factors (i.e. grazing, variations of temperature, hydrodynamics) that vary  
547 with time and season (Krumhansl & Scheibling 2011, Krumhansl & Scheibling 2012,  
548 Simonson et al. 2015). Although variation in macroalgal input between Low and High  
549 Stratification Periods should depend on such factors, their specific roles are difficult to assess.  
550 Larger proportions of macroalgal detritus in the shallowest area likely reflect autochthonous  
551 inputs (Krumhansl & Scheibling 2011, Krumhansl & Scheibling 2012), whereas lower  
552 macroalgae contributions in deeper areas should either reflect different degrees of thalli  
553 fragmentation or transport from shallow areas (Krumhansl & Scheibling 2012, Renaud et al.  
554 2015, Filbee-Dexter et al. 2018).

555 Differentiating macroalgal input from the effects of stratification on the quality and  
556 composition of POM is complex. The higher proportions of  $\Sigma$  PUFA found in L2, L3 and L4  
557 POM samples during the Low Stratification Period (e.g. s-POM = 13.7 – 25.8 %) relative to  
558 those measured from the High Stratification Period (s-POM = 9.5 – 14.4 %) along with

559 similar concentrations of macroalgal markers (e.g. 18:2 $\omega$ 6, 18:3 $\omega$ 3) suggest that organic  
560 matter quality reflects the absence of sharp vertical stratification rather than macroalgal input.  
561 By contrast, strong seasonal variation in the macroalgal markers from the L1 POM samples  
562 coincided with relatively little variation in microalgal markers (e.g. 16:1 $\omega$ 7, 22:6 $\omega$ 3). This  
563 suggests that POM seasonality for most near shore stations reflected macroalgal pulses.  
564 Assessing the effects of stratification on the export and sedimentation of macroalgal detritus  
565 into deep water areas was not feasible in this study. Other studies have described the salient  
566 roles of temperature (Simonson et al. 2015), grazing (Wernberg & Filbee-Dexter 2018) or  
567 wave exposure (Krumhansl & Scheibling 2011) on these transfers, but none have yet  
568 investigated how stratification may limit such transport and deposition. Detection of fatty acid  
569 macroalgae markers in s-POM samples from offshore stations along with their absence from  
570 b-POM samples (e.g. 18:2 $\omega$ 6 and 18:3 $\omega$ 3, station L3 and L4, Figure 3, Table S1) suggest that  
571 stratification may limit sedimentation of macroalgal detritus. Given the future increases of  
572 stratification expected from rising sea surface temperatures, future research should seek to  
573 constrain these processes.

#### 574 **4.4 Organic matter transfers and spatiotemporal variations in SOM sources**

575 Significant seasonal differences observed in SOM fatty acid profiles reflect different organic  
576 matter quality and origins between High and Low Stratification Periods (Table 3). Large  
577 levels of SFAs observed during the High Stratification Period (14:0, 16:0 and 18:0,  
578 especially) reveal a high degradation state of the organic matter (Table 2). Sources  
579 contributing to SOM during the High Stratification Period were limited and consisted of  
580 minor inputs from microphytobenthos ( $\Sigma$  of 20:5 $\omega$ 3 and 16:1 $\omega$ 7 < 5%) and macroalgae ( $\Sigma$  of  
581 18:2 $\omega$ 6 and 18:3 $\omega$ 3 < 1%). SOM samples from the Low Stratification Period contained higher  
582 concentrations of PUFAs and EFAs ( $\Sigma$  PUFA = 12.9 and  $\Sigma$  EFA = 5.2 for Low Stratification  
583 vs  $\Sigma$  PUFA = 5.7 % and  $\Sigma$  EFA = 2.2 % for High Stratification) including diatom markers

584 (16:1 $\omega$ 7, 20:5 $\omega$ 3 and 16:4 $\omega$ 1). These high temporal variations of SOM sources and quality  
585 result likely from the microphytobenthos dynamics, with a major bloom during the Low  
586 Stratification Period (illustrated by much higher contributions of 16:1 $\omega$ 7, 20:5 $\omega$ 3 and 16:4 $\omega$ 1)  
587 turning toward degraded OM during the High Stratification Period (reflected by high levels of  
588  $\Sigma$  SFA). Such a pattern is consistent with the typical dynamics of microphytobenthos which  
589 usually includes one single massive bloom per year (e.g. occurring in April in the Gulf of  
590 Mexico and in the Bay of Brest, Pinckney & Lee 2008, Chatterjee et al. 2013; in July in the  
591 Seto Inland Sea, Yamaguchi et al. 2007). Although POM samples collected during the Low  
592 Stratification Period contained higher relative contributions of macroalgal fatty acids, these  
593 markers appeared in low concentrations in SOM profiles ( $\Sigma$  18:2 $\omega$ 6, 18:3 $\omega$ 3, 18:4 $\omega$ 3 and  
594 22:6 $\omega$ 3 < 1.6 %) demonstrating that they represent only a minor source for the SOM pool.  
595 Low macroalgal and high microphytobenthic contributions in SOM samples may reflect a  
596 strong microbial degradation of macroalgal detritus by benthic heterotrophic bacteria and an  
597 effective recycling of nutrients released through this microbial loop by benthic microalgae  
598 (e.g. Hardison et al. 2010).

599 Several authors questioned about the trophic ecology of *E. parma*, especially if this species  
600 feed either on the sediment or on suspended particles from the water column (e.g. Seilacher  
601 1979, Ellers & Telford 1984, Miller et al. 1992). Some studies have suggested that vertical  
602 orientations observed among several sand dollar species (e.g. *Dendraster excentritus*, *Encope*  
603 *melchioni*, *Heliophora orbiculus*, *Rotula augusti*, Merrill & Hobson 1970, Lawrence et al.  
604 2004 and references therein) may indicate filter-feeding (Timko 1976, O'Neill 1978) while  
605 others (Seilacher 1979, Ellers & Telford 1984, Miller et al. 1992) suggest that deposit-feeding  
606 occurs by using podia from both oral and aboral sides to select and transport food particles  
607 toward the mouth. Our study supports this latter hypothesis. Since carbon isotopic  
608 fractionation between primary and secondary producers is usually relatively low or

609 nonexistent in high-turnover tissue (e.g. digestive glands, Gaillard et al. 2017, De Cesare et al.  
610 2017, Bridier et al. 2019), similar  $\delta^{13}\text{C}$  values for both SOM and sand dollar samples indicates  
611 a diet dominated by SOM. Such hypothesis is also confirmed by fatty acids profiles results: a  
612 dominant suspension feeding activity should have implied a high spatial variability of sand  
613 dollars' fatty acids profiles reflecting the high spatial variability of b-POM. Our almost  
614 identical sand dollars' fatty acids profiles from 10 to 80 m suggest thus a homogenous SOM  
615 pool along stations (although we were not able to collect SOM samples in the deepest areas).  
616 Previous studies have reported similar findings of homogenous SOM composition between  
617 near shore and offshore environments noting that SOM represents long-term accumulation  
618 from the water column (Chouvelon et al. 2015, Schaal et al. 2016).

619 Spatial homogeneity in fatty acid profiles from SOM and sand dollar samples contrasts the  
620 above interpretations that stratification diminishes both POM quality and pelagic-benthic  
621 coupling. However, the predominance of the 16:1 $\omega$ 7, 16:4 $\omega$ 1 and 20:5 $\omega$ 3 diatom markers  
622 indicates that microphytobenthos dominate the SOM pools. This dominance may explain the  
623 decoupling of POM and SOM pools. Homogenous benthic production along the bathymetric  
624 gradient could reflect the adaptation of microphytobenthos to both low light availabilities and  
625 nutrient depletion (by using nutrients released from the sediment, MacIntyre et al. 1996,  
626 Leynaert et al. 2009). A major and homogenous contribution of this food source to the diet of  
627 *Echinarachnius parma* with depth could thus counterbalance the impact of stratification on  
628 POM quality and pelagic-benthic coupling strength.

#### 629 **4.5 Conclusion**

630 Characterization of organic matter sources and quality revealed multiple negative effects of  
631 highly stratified water column on the organic matter sources and quality from a sub-Arctic  
632 Archipelago. This study detected weaker pelagic-benthic coupling, lower food availability  
633 and more degraded organic matter delivered to benthic compartment during the High

634 Stratification Period. Such observations may be explained by the strong water column  
635 stratification that would abate vertical organic matter transfer and limit nutrient replenishment  
636 of surface waters by reducing surface/sub-surface nutrient exchanges. By contrast,  
637 pronounced water column stratification would allow more efficient pelagic-benthic coupling  
638 and nutrient exchanges around the pycnocline and may facilitate nutrient upwelling through  
639 internal waves. Macroalgal material represents a major source of high organic matter quality  
640 in shallower areas. Considering complex processes of thalli fragmentation that includes  
641 numerous, interrelated environmental and biological factors, the intensity and seasonality of  
642 the pulses of macroalgal detritus could however vary significantly in time. In the context of  
643 ongoing climate change, our results suggest that intensified water column stratification  
644 associated with rising sea surface temperatures may strongly modify pelagic-benthic coupling  
645 as well as future quality and composition of POM pools from North-West Atlantic shelf  
646 ecosystems. Conversely, shallow areas may be more resilient to changes in water conditions  
647 due to local contribution of high-quality organic matter from benthic primary producers.

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