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### Food source diversity, trophic plasticity, and omnivory enhance the stability of a shallow benthic food web from a high-Arctic fjord exposed to freshwater inputs

Guillaume Bridier <sup>(1)</sup>, <sup>1\*</sup> Frédéric Olivier, <sup>2</sup> Laurent Chauvaud, <sup>1</sup> Mikael K. Sejr, <sup>3,4</sup> Jacques Grall<sup>1,5</sup>

<sup>1</sup>Laboratoire des Sciences de l'Environnement Marin (LEMAR) UMR 6539 UBO/CNRS/IRD/Ifremer, Plouzane, France <sup>2</sup>Biologie des Organismes et Écosystèmes Aquatiques (BOREA) UMR 7208 MNHN/SU/UNICAEN/UA/CNRS/IRD, Paris, France

<sup>3</sup>Arctic Research Centre, Aarhus University, Aarhus, Denmark

<sup>4</sup>Department of BioScience, Aarhus University, Silkeborg, Denmark

<sup>5</sup>Observatoire Marin, UMS 3113, Institut Universitaire Européen de la Mer, Plouzané, France

#### Abstract

Under climate change, many Arctic coastal ecosystems receive increasing amounts of freshwater, with ecological consequences that remain poorly understood. In this study, we investigated how freshwater inputs may affect the small-scale structure of benthic food webs in a low-production high-Arctic fjord (Young Sound, NE Greenland). We seasonally sampled benthic invertebrates from two stations receiving contrasting freshwater inputs: an inner station exposed to turbid and nutrient-depleted freshwater flows and an outer station exposed to lower terrestrial influences. Benthic food web structure was described using a stable isotope approach ( $\delta^{13}$ C and  $\delta^{15}$ N), Bayesian models, and community-wide metrics. The results revealed the spatially and temporally homogeneous structure of the benthic food web, characterized by high trophic diversity (i.e., a wide community isotopic niche). Such temporal stability and spatial homogeneity mirrors the high degree of trophic plasticity and omnivory of benthic consumers that allows the maintenance of several carbon pathways through the food web despite different food availability. Furthermore, potential large inputs of shelf organic matter together with local benthic primary production (i.e., macroalgae and presumably microphytobenthos) may considerably increase the stability of the benthic food web by providing alternative food sources to locally runoff-impacted pelagic primary production. Future studies should assess beyond which threshold limit a larger increase in freshwater inputs might cancel out these stability factors and lead to marked changes in Arctic benthic ecosystems.

35 Arctic ecosystems are experiencing strong modifications of 36 abiotic conditions under climate change, including increasing 37 water temperatures and decreasing sea-ice coverage <sup>38</sup> (AMAP 2017). In addition, freshwater inputs to the coastal 39 domain are currently increasing in most locations along the 40 Arctic coastline (Haine et al. 2015; Sejr et al. 2017). The 41 impacts of such inputs on marine systems can be complex 42 and influenced by numerous factors such as the freshwater 43 origin (e.g., marine- vs. land-terminating glacier) and local 44topography (e.g., absence/presence of a sill in fjords; Hopwood 45 et al. 2020). Consequences of increased freshwater on the 46 pelagic compartment include modifications of primary pro-47 duction, water column stratification, turbidity, and nutrient 48 concentrations, but also of organic matter quality (Meire 49

et al. 2017; Paulsen et al. 2017; Bridier et al. 2019), with subseguent impact on food webs (Middelbo et al. 2018). 90

Surprisingly, impacts on benthic ecosystems have received 91 less attention, with studies mainly focusing on the distur-92 bance generated by high sedimentation close to marine gla-93 94 ciers (e.g., sediment instabilities, bivalve gill clogging, etc.) 95 that may impoverish the specific and functional richness of 96 benthic communities (Sejr et al. 2010; Włodarska-Kowalczuk 97 et al. 2019). Some food-web studies have revealed significant 98 contributions of terrestrial organic matter to the diet of ben-99 thic organisms, but they have mainly concerned large hydro-100 logical systems (e.g., Mackenzie River) over very large spatial 101 scales (i.e., >100 s of km; Bell et al. 2016). By contrast, fjords 102 and coastal subtidal habitats have been less investigated, 103 although they should be the first to be affected by freshwater 104 inputs (i.e., fiords' water masses are more confined and sur-105 rounded by land than are shelf water masses). Because benthic 106 organisms are essential for the functioning of marine ecosys-107 tems (e.g., through carbon and nutrient cycling, and benthic-108

<sup>50</sup> 51

<sup>52 \*</sup>Correspondence: guillaume.bridier@univ-brest.fr

 $<sup>^{53}</sup>$  Additional Supporting Information may be found in the online version of  $^{54}$  this article.

pelagic coupling; Griffiths et al. 2017) and are key resources
 for several marine mammal and seabird species
 (e.g., Grebmeier et al. 2006), understanding the consequences
 of environmental changes for benthic food webs should be
 improved to enable accurate predictions of marine ecosystem
 responses to climate change.

7 In this study, we aimed to understand the effects of local <sup>8</sup> freshwater inputs on the functioning of a high-Arctic fjord by <sup>9</sup> investigating carbon pathways through the benthic food web. 10 For this purpose, we compared stable isotope signatures from <sup>11</sup> benthic organisms and organic matter sources, using  $\delta^{13}$ C and <sup>12</sup>  $\delta^{15}$ N measurements from two stations distributed along a gra-<sup>13</sup> dient of freshwater inputs (controlling other environmental <sup>14</sup> factors, e.g., turbidity, nutrient depletion, and organic matter <sup>15</sup> ouality: Meire et al. 2017; Paulsen et al. 2017; Bridier <sup>16</sup> et al. 2019). Ecological studies using stable isotopes have been <sup>17</sup> widely used to trace transfers of organic matter within benthic <sup>18</sup> communities (e.g., Abrantes et al. 2014). Numerous studies <sup>19</sup> have shown the ability of stable isotope mixing models and <sup>20</sup> trophic position models to quantify the relative importance of 21 production originating from various origin and to better <sup>22</sup> understand feeding strategies of benthic invertebrates <sup>23</sup> (e.g., McTigue and Dunton 2017; Michel et al. 2019). In addi-<sup>24</sup> tion, several authors recently suggested that the bivariate  $\delta^{13}$ C  $^{25}$  –  $\delta^{15}$ N isotope space ( $\delta$ -space) filled by a community accurately <sup>26</sup> depicts its isotopic niche (Layman et al. 2007; Jackson, <sup>27</sup> et al. 2011). Several metrics describing such isotopic niches  $^{28}$  (e.g., area, dimensions, and shape of the  $\delta$ -space) were then <sup>29</sup> developed to assess food-web complexity/stability and to <sup>30</sup> determine the diversity of organic matter sources fueling a <sup>31</sup> community (Layman et al. 2007; Jackson et al. 2011; Reid <sup>32</sup> et al. 2016).

33 Such advanced approaches have widely shown their ability <sup>34</sup> to describe the functioning of benthic ecosystems exposed to <sup>35</sup> high environmental pressures (e.g., flood events; Abrantes <sup>36</sup> et al. 2014) by tracking changes in organic matter pathways <sup>37</sup> within communities over time and space. However, these <sup>38</sup> methods are still rarely used in polar areas (but see Włodarska-<sup>39</sup> Kowalczuk et al. 2019). Using community-wide trophic niche <sup>40</sup> metrics and stable isotope mixing/trophic position models, we 41 investigated the small-scale variability (i.e., inner vs. outer <sup>42</sup> fjord communities) of benthic food-web structures from a <sup>43</sup> high-Arctic fjord exposed to freshwater inputs. Through this <sup>44</sup> comparison, our goal is to better understand the effects of <sup>45</sup> freshwater inputs on Arctic benthic food webs and to identify <sup>46</sup> the drivers of community resilience and stability in the face of 47 ongoing climate change.

#### 50 Materials and methods

#### 51 Study site and sampling stations

We conducted our study in Young Sound, a high-Arcticfjord of NE Greenland (Fig. 1). This fjord ranks among the 54

least-productive coastal ecosystems in the world (pelagic pri- 55 mary production ~ 10 g C m<sup>2</sup> yr<sup>-1</sup>; Rysgaard et al. 1999) due 56 to prolonged sea-ice cover (9-10 months per year; Rysgaard 57 et al. 1999) and seasonal stratification generated by strong riv- 58 erine inputs (Holding et al. 2019). This low production is 59 partly compensated by high benthic primary production in its 60 shallow coastal areas (i.e., < 30 m) which exceed from 2 to 61 7 times local phytoplankton production and accounts for 62 20-40% of the whole outer fjord primary production (Glud 63 et al. 2002; Krause-Jensen et al. 2007; Attard et al. 2016). On 64 the other hand, ice-algae contribute only marginally 65 (i.e., <1%) to the overall Young Sound primary production, 66 mainly as a result of high snow cover and low seawater salin- 67 ity directly under sea-ice (Glud et al. 2002; Limoges 68 et al. 2018). 69

Two shallow stations (i.e., depth range = 10-30 m) were 70 prospected: (1) an inner station (74°24'36"N-20°19'48"W, sur- 71 veved in May 2017 and August 2018). close to the Zackenberg 72 River (river discharge =  $0.15-0.25 \text{ km}^3 \text{ yr}-1$ ; Citterio 73 et al. 2017), and (2) an outer station (74°12'36"N-20°6'36"W, 74 surveyed in May and August 2018), situated at the fjord 75 mouth. These two localities were selected because of contra- 76 sted exposure to freshwater inputs associated to an inner/outer 77 fjord gradient in physical and chemical conditions. Consider-78 able freshwater inputs in Young Sound innermost areas (rang-79 ing from 0.9 to 1.4 km<sup>-3</sup> yr<sup>-1</sup>; Bendtsen et al. 2014) generate 80 strong spatial variations in surficial water salinity, ranging 81 from 8 in the innermost part of the fjord to 30 in the outer- 82 most part (Rysgaard et al. 2003; Bendtsen et al. 2014). More- 83 over, the inner station is located at the direct vicinity 84 (i.e., ~ 500-750 m) of several small deltas and it receives addi- 85 tional inputs in freshwater and sediment while no deltas were 86 reported close to the outer station (Kroon et al. 2017). These 87 contrasted exposure of inner and outer stations to freshwater 88 inputs and inert particles explain the observed differences in 89 sediment grain-size distributions between both sites. Propor- 90 tion of pelites (particles  $< 63 \mu m$ ) in the sediment is three-fold 91 higher at the inner (i.e., 69.2%) than the outer station 92 (i.e., 21.7%, see Fig. S1, Supplementary Information), 93 reflecting very contrasting loadings of terrestrial material 94 between these two coastal areas. 95

This freshwater input gradient leads to contrasting environ-96 mental conditions between inner and outer stations. Stronger 97 stratification at the inner station reduces the size of phyto-98 plankton cells (Holding et al. 2019), with potential subsequent 99 impact on marine primary consumers (Middelbo et al. 2018). 100 Higher input of terrestrial material and nutrient depletion at 101 the inner station (Paulsen et al. 2017) is also reported to lessen 102 the quality of the organic matter (Bridier et al. 2019). Finally, 103 a two-fold lower pelagic primary production has been 104 recorded at the inner station compared to the outer station 105 because of the negative impacts of freshwater inputs on inner 106 fjord turbidity and nutrient concentrations (Meire et al. 2017). 107 108

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Fig. 1. Map representing the two study locations (white circles), the CTD transect (red line) and the three main rivers (white squares) in the study area are from Bendtsen et al. (2014).

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#### 33 Sampling

Benthic consumers were sampled using a triangular dredge 34 35 (1 mm mesh size, August 2018) or a suction dredge (1 mm 36 mesh size) operated by scuba divers (May 2017 and 2018). All 37 entire individuals were collected for stable isotope analyses in 38 order to meet species diversity requirements for isotopic diver-39 sitv indices (i.e., n > 20 species; Brind'Amour and 40 Dubois 2013). Number of replicates varied from 1 to 9 individuals per benthic species. Three potential food sources were 41 42 sampled in our study: particulate organic matter (POM), sedi-43 mentary organic matter (SOM) and terrestrial organic matter 44 (TOM). Bottom POM samples were collected on each site at 45 1 m above the seabed by using a 10 liter Niskin bottle (May 46 2017 and August 2018). Scuba divers collected SOM samples 47 by aspirating the first 1-5 mm of the sediment surface del-48 imited in a 25  $\times$  25 cm (i.e., 625 cm<sup>2</sup>) quadrat with a 450 ml 49 syringe (August 2016). Finally, TOM samples were taken in 50 August 2018 upstream of the Zackenberg River delta 51 (74°28'14.3"N, 20°34'47.4"W, salinity = 0.38) using 10 liter 52 bottles. Sampling replication varied from 3 to 6 samples per 53 food source. Water and sedimentary samples were then fil-54 tered on precombusted (5 h at 400°C) GF/F filters (pore size =  $0.07 \ \mu$ m) until clogging (for further details, see Bridier 87 et al. 2019). In addition, we used the stable isotope signatures 88 of *Fucus* sp. and *Saccharina latissima* measured by De Cesare 89 et al. (2017). All samples were stored at – 80°C before labora-90 tory analyses. Finally, surficial waters salinity (i.e., 0–30 m) 91 was measured in August 2018 through a set of CTD profiles 92 conducted along the fjord to assess the spatial extent of the 93 freshwater plume (Fig. 1). We also performed two additional 94 CTD profiles at the studied inner and outer stations to record 95 local 0–10 m seawater salinity. Additional information on 96 sampling dates and sample replications are available in the 97 Supplementary Information (Tables S1 & S2). 98

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#### Laboratory analyses

Stable isotope analyses ( $\delta^{13}$ C and  $\delta^{15}$ N) were performed on 101 either one or a pool of complete individuals (guts apart) and 102 muscle tissues from large species (e.g., shrimp, fish; Supple-103 mentary Information, Table S1). Animal tissues were freeze-104 dried for at least 48 h at – 50°C and ground to a fine powder 105 in a ball mill (cycles of 10 min at 30 Hz). Half of the 106 carbonate-rich tissues were acidified with hydrochloric acid 107 (10% HCl) for carbon isotope analyses to prevent the bias 108

1 induced by inorganic carbon in  $\delta^{13}$ C signatures while the 2 other half remained untreated for nitrogen isotope analyses to 3 avoid acidification bias in  $\delta^{15}$ N values (Jacob et al. 2005). Sam-4 ples were not lipid-extracted, due to the usually low lipid con-5 tent in Arctic benthic invertebrates (Clarke and Peck 1991) 6 and to avoid potential bias in  $\delta^{15}$ N values (Post et al. 2007). 7 No mathematical lipid corrections were done because the large 8 variability of  $\delta^{13}$ C lipid bulk signatures among Arctic species 9 makes questionable the use of generalized mathematical equa-10 tions based on a constant lipid  $\delta^{13}$ C value (Mohan 11 et al. 2016).

All stable isotope analyses were performed at the University 12 13 of California. Davis (UC Davis Stable Isotope Facility. Depart-14 ment of Plant Sciences, CA). Stable isotope measurements 15 were realized with a PDZ Europa ANCA-GSL elemental ana-16 lyzer interfaced to a PDZ Europa 20-20 isotope ratio mass 17 spectrometer (Sercon, UK). Sample stable isotope ratios were 18 expressed in relation to stable isotope ratios from Vienna Pee 19 Dee Belemnite ( $\delta^{13}$ C) and atmospheric nitrogen (N<sub>2</sub>,  $\delta^{15}$ N), 20 based on following the equation:  $\delta X = [(R_{sample})/(R_{sample})$  $R_{\text{standard}}$  – 1] × 1000; where X is the  $\delta^{13}$ C or  $\delta^{15}$ N value of the 21 22 analyzed sample and R the corresponding <sup>13</sup>C/<sup>12</sup>C or <sup>15</sup>N/<sup>14</sup>N 23 molar ratio (Peterson and Fry 1987). Standard deviations of 24 stable isotope measurements were estimated to  $\pm$  0.2 for  $\delta^{13}$ C 25 and  $\pm$  0.3 for  $\delta^{15}$ N, based on replicated measurements of inter-26 national standards (run every 15<sup>th</sup> sample) from the Interna-27 tional Atomic Energy Agency (IAEA600) and the United States Geological Survey (USGS40, USGS41, USGS62, and USGS65). 28 29

#### 30 Data analyses

Community convex hulls (areas compassing all the data) 31 32 and standard ellipses (95% confidence ellipses compassing 33 40% of the data) were plotted in a  $\delta$ -space to visualize isotopic 34 niches. Potential shifts on the  $\delta^{13}$ C or  $\delta^{15}$ N axis between 35 community isotopic niches were investigated by computing 36 the overlap between inner and outer standard ellipses 37 (i.e., the percentage shared by two communities in relation to 38 the smallest ellipse). Community trophic niche widths were 39 assessed by calculating the standard ellipse area and mean distance to centroid (i.e., the mean distance of each species to 40 the  $\delta^{13}C - \delta^{15}N$  centroid) metrics (Layman et al. 2007; Jackson 41 42 et al. 2011). Standard ellipses' eccentricities were also calculated 43 to compare the shapes of isotopic niches (e.g., a lower eccen-44 tricity would highlight a narrower community ellipse range 45 on the  $\delta^{13}$ C axis; Reid et al. 2016).

The horizontal structure of benthic food webs was 46 47 described using Bayesian stable isotope mixing models per-48 formed on primary consumer stable isotope signatures to 49 assess the diversity and importance of organic matter sources 50 fueling benthic invertebrates (Parnell et al. 2013). Mixing 51 models were calculated using the simmr package 52 (Parnell 2019) to include the variability of consumer and 53 endmember stable isotope signatures as well as the uncer-54 tainty in trophic enrichment factors (TEFs) for diet estimates Food-web structure of a Greenland fjord

(Parnell et al. 2013). Although  $\delta^{13}$ C TEFs are considered to be 55 between primary consumers and carnivores 56 similar (Post 2002; McCutchan et al. 2003), they are known to be 57 highly variable (e.g., ranging from  $\sim 0$  to 4%) among species 58 from a same guild, depending on animal physiology and/or 59 food source quality (e.g., Caut et al. 2009). In order to integer 60 such variability, we used an intermediate  $\delta^{13}$ C TEF with a high 61 level of uncertainty (i.e.,  $2 \pm 2\%$ ) which considers that  $\delta^{13}$ C 62 fractionation can potentially be very low (e.g., 0‰) or very 63 high (e.g., 4‰) for some species. Mixing models used Post's 64 TEF for  $\delta^{15}$ N signatures (i.e.,  $3.4 \pm 1.0\%$ ). Stable isotope signa- 65 tures of POM and SOM sources as well as those of Fucus 66 sp. and S. latissima were combined a posteriori into two 67 unique sources (i.e., "POM/SOM" and "Benthic sources", 68 respectively) because of their close isotopic compositions 69 (Phillips et al. 2014). 70

Vertical structure was studied using a trophic position 71 model (Quezada-Romegialli et al. 2018) to assess the degree of 72 omnivory in food webs by comparing the trophic positions of 73 consumers in relation to their putative food sources. Trophic 74 positions were calculated using two-baseline (i.e., POM/SOM 75 and macroalgae (i.e., *Fucus* sp. and *S. latissima*]) Bayesian 76 models from the *tRophicPosition* package (Quezada-Romegialli et al. 2019) based on the following equations from Quezada-Romegialli et al. (2018): 79

$$\delta^{15} N_{C} = \Delta N (TP + \lambda) + \alpha (\delta^{15} N_{b1} + \delta^{15} N_{b2}) - \delta^{15} N_{b2}$$

and

$$\alpha = \begin{pmatrix} \frac{\delta^{13}C_{b2} - (\delta^{13}C_{c} + \Delta C)}{\frac{TP - \lambda}{\delta^{13}C_{b2} + \delta^{13}C_{b1}} \end{pmatrix}$$
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where  $\delta^{15}N$ ,  $\delta^{15}N_{b1}$ , and  $\delta^{15}N_{b2}$  refer to the  $\delta^{15}N$  values of consumers, first and second baselines, respectively;  $\delta^{13}C_c$ ,  $\delta^{13}C_{b1}$ , and 90  $\delta^{13}C_{b2}$  are the  $\delta^{13}C$  values of consumers, first and second baselines, 91 respectively;  $\Delta N$  refer to the TEF for nitrogen (i.e.,  $3.4 \pm 1$ );  $\Delta C$  is 92 the TEF for carbon (i.e.,  $2 \pm 2$ ); TP is the consumer's trophic position and  $\lambda$  is the baseline's trophic position. 94

Standard ellipse area credibility intervals were calculated on 95 species mean isotope signatures through a Bayesian approach 96 using 200,000 posterior iterations. Standard Ellipses Areas 97 without overlap of their 95% credibility intervals were consid- 98 ered significantly different. Unfortunately, this Bayesian 99 approach could not be applied to estimate mean distance to 100 centroid and ellipse eccentricity credibility intervals because 101 calculations these are based on both intra-group 102 (i.e., dispersion between replicates of a single species) and 103 inter-group (i.e., dispersion among species; Jackson 104 et al. 2011) variability and several species had no replicates. 105 Bayesian mixing and trophic position models were performed 106 only on August samples as replication for May samples was 107 too low. Stable isotope signatures of the main abundant 108

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consumers from the inner and outer stations were then pooled 2 to meet replication requirements for the calculation of the 3 residual error term (i.e., n > 4; Parnell et al. 2010). Bayesian 4 mixing and trophic position models were based on 200,000 5 iterations, 100,000 burn-ins, 500 thinned samples, and three 6 chains. Gelman-Rubin convergence statistics were computed to determine if the mixing model had a properly run with a 7 8 suitable number of iterations (i.e.. Gelman-Rubin 9 diagnostics > 1.1 indicates unsatisfactory runs; Gelman 10 et al. 2004). All Gelman-Rubin statistics were below 1.03 and 11 indicated thus satisfactory runs. Each mixing model was built 12 when the range of consumer isotope signatures inside the 13 mixing polygon. Distribution of posterior predictive values 14 were plotted to ensure that the produced model fitted with 15 the original data. All data analyses were performed with R 16 (R Core Team 2019) using scripts provided by N. D. McTigue 17 (from Harris et al. 2018) and L. N. Michel (from Michel 18 et al. 2019).

#### 20 Results

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#### 21 Spatial variations in summer surface seawater salinity 2.2

Seawater salinity in surface waters was highly variable along the fjord transect (Fig. 2). Terrestrial inputs generated a shallow low salinity surface layer ( $\approx 5$  m) ranging from 0 to 15 (Fig. 2) in Young Sound's innermost areas. Salinity then 26 steadily increasing as the plume flowed toward the shelf. Fjord areas in the vicinity of the inner station showed intermediate 28 sea surface salinity ( $\approx 15-20$ ) and halocline depth ( $\approx 2-3$  m). 29 On the other hand, highest salinities were measured around 30 the outer station (i.e., 20-25). These salinities were however more variable at small-spatial scale because of the 32

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simultaneous exposition of the outer fjord area to both 55 inflowing shelf waters, outflowing fjord waters and southward 56 coastal currents. Salinity profiles conducted at the exact stud- 57 ied station locations also showed strong differences between 58 sites as illustrated by the averaged (0-10 m) surface salinity 59 measured at 21.0 and 28.7, in the inner and outer stations, 60 respectively (see Table S3, Supplementary Information). 61

#### Isotopic niches of outer and inner communities

64 Isotopic niches of the inner and outer communities were highly similar in both seasons as reflected by their high over-66 lap (74.8% and 77.5% during winter and summer, respectively; Fig. 3a,b). Such seasonal stability and spatial 67 homogeneity of Young Sound food webs is confirmed by the 69 absence of significant differences in standard ellipse areas 70 between both stations and seasons (p > 0.05, see credibility 71 interval overlaps in Supplementary Information, Fig. S2). 72 Although no statistical analyses could be performed on the 73 Layman metrics (mean distance to centroid and eccentricity) 74 due to the absence of replication for several species 75 (i.e., n < 5), the absence of strong variations between seasons 76 and stations suggests no major seasonal or spatial differences of food web structures occurred (Table 1). 78

#### Benthic food web horizontal structure

Outputs from our mixing models highlighted а low/insignificant contribution of TOM for all primary consumers, except perhaps for the isopod Arcturus baffini, Ascidiacea and Pectinaria hyperborea which were characterized by large variation in its credibility intervals (Fig. 4). The contribution of other organic matter sources was variable among



Fig. 2. Contour plot representing salinity variation in the upper 30 m of the water column along an inner/outer fjord transect (see Fig. 1). Black dashed lines indicate the position of the inner and outer stations. 108

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**Fig. 3.** Standard ellipses (solid lines) and convex hulls (dashed lines) of the inner and outer communities during winter (**a**) and summer (**b**) seasons, respectively. Isotopic niche overlap is defined as the percentage of  $\delta$ -space shared between inner and outer communities in relation to the surface of the smallest ellipse. Food sources are represented by black symbols. POM: particulate organic matter, SOM: sedimentary organic matter, Out.: Outer station, In.: Inner station.

Table 1. Standard ellipse area (‰<sup>2</sup>), mean distance to centroid
 (‰) and standard ellipse eccentricity from the inner and outer
 communities sampled in winter and summer.

5	Wir	nter	Sum	mer
7	Outer	Inner	Outer	Inner
Standard ellipse area	8.45	10.29	9.07	11.30
Mean distance to centroid	2.12	2.34	2.34	2.53
Eccentricity	0.77	0.66	0.80	0.64
)				

33 primary consumers. Several species considered here as suspen-34 sion (i.e., A. baffini, Astarte moerchi, Astarte elliptica, Balanus 35 sp., Hiatella arctica) or deposit (i.e., Margarites coastalis, 36 P. hyperborea) feeders appeared to feed in significant propor-37 tion on benthic sources (from 18.9% for Balanus sp. to 47.4% 38 for A. moerchi, modes of the posterior probability distribu-39 tions), while for other species its contribution remained low 40 (10.4-14.0%, Fig. 4). Aggregated POM and SOM sources 41 showed large contributions for all species (from 43.3% for 42 A. elliptica to 85.4% for Ophiocten sericeum, modes of the poste-43 rior probability distributions). 44

#### 46 Benthic food web vertical structure

47 Consumer trophic positions calculated using two-baseline 48 Bayesian models (based on POM and SOM baselines, 49 according to mixing model outputs) were highly variable among species (Fig. 5). The mean trophic position of primary 51 consumers (i.e., suspension and deposit feeders) ranged from 52 1.7 for *Atylus carinatus* and *Balanus* sp. to 2.6 for *P. hyperborea*, 53 while for predatory/scavenging consumers (combined 54 together as "carnivores") it ranged from 2.3 for *Metopa glacialis*  to 3.8 for *Argis dentata* (Fig. 5). Credibility intervals varied overall over large ranges, exceeding in some cases the extent of one trophic level (e.g., *Colus* sp., *Icelus bicornis*, *P. hyperborea*, Fig. 5).

80 The modal trophic positions of all primary consumers, 81 except for the crustaceans A. carinatus and Balanus sp., were 82 higher than 2, with significant values for A. baffini, Ascidiacea, 83 and O. sericeum only (Fig. 5). The modal trophic positions of 84 four taxa initially considered as primary consumers 85 (A. elliptica, Ascidiacea, A. baffini, P. hyperborea) were higher 86 than the lowest value of a secondary consumer (M. glacialis). 87 In contrast, modal trophic positions of five other species ini-88 tially considered as secondary consumers (Colus sp., 89 M. glacialis, Nereis sp., Nymphon hirtipes, Ophiura robusta) were 90 lower than 3 (Fig. 5). Finally, all primary consumers' credibil-91 ity intervals overlapped with those of one or several secondary 92 consumers, except for A. carinatus (Fig. 5). 93

#### Discussion

#### Temporal and spatial variability of the benthic food web

Although Young Sound experiences an extreme seasonality 97 (Rysgaard et al. 1999; Rysgaard and Nielsen 2006) and strong spatial gradients associated to freshwater inputs (Fig. 2; Meire 99 et al. 2017; Paulsen et al. 2017; Holding et al. 2019), in the present study we did not observe any spatiotemporal varia-101 tions in the benthic food-web structures. Such similarity 102 between inner and outer standard ellipse areas and positions 103 on the  $\delta^{13}$ C axis (reflected by high standard ellipse area over-104 laps) suggests that both communities are based mostly on the 105 same organic matter sources. Moreover, high mean distance to 106 centroid and eccentricity values in the inner and outer com-107 munities indicate that both trophic webs are based on several 108

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Fig. 4. Boxplots representing relative contributions of benthic sources (left); combined particulate organic matter and sedimentary organic matter sources (middle); and terrestrial organic matter (right) to the diet of main primary consumers. The center line, boxes, and error bars represent the modes and 50% and 95% credibility intervals based on posterior probability distributions, respectively. Outliers were omitted for clarity. POM: particulate organic matter; SOM: sedimentary organic matter. 



ဆိုးဖုဒ္ pla အို သူတိုး ဆိုပါ သူ၊ Fig. 5. Modal trophic positions of main primary (blue circles) and secondary/tertiary consumers (red circles) with their associated 95% credibility inter-vals based on posterior probability distributions. 

1 organic matter sources (Layman et al. 2007). Although these 2 metrics might be highly sensitive to sampling effort, all stan-3 dard ellipse areas had a sample size sufficient to avoid such 4 potential bias (i.e., n > 20, Brind'Amour and Dubois 2013).

The absence of temporal variability in the benthic food 5 6 webs despite strong seasonal variation of POM and SOM base-7 lines (Fig. 3a,b) and changes in food source availability 8 (Bridier et al. 2019) may appear surprising. Indeed, several 9 works on Arctic food webs previously highlighted similar tem-10 poral stabilities that authors partly explained by the moderate 11 seasonality of systems that were characterized by multiple 12 pulses of fresh organic matter per year (e.g., Renaud 13 et al. 2011). Considering the extreme seasonality of primary 14 production in Young Sound (i.e., limited to 2-4 months per 15 year; Rysgaard et al. 1999; Holding et al. 2019), there is no evi-16 dence for regular input of fresh organic matter in this fjord. 17 We rather hypothesize that the temporal stability reflects the 18 low tissue-turnover rates (expected to range from 8 months to 19 more than 1 year) observed in Arctic benthic invertebrates, 20 which display long lifespan and slow growth (Kaufman 21 et al. 2008; Weems et al. 2012; McMeans et al. 2015). As a 22 consequence, isotope signatures of benthic invertebrates 23 would reflect environmental conditions over the year rather 24 than during one particular season.

Despite strong environmental gradients, which vary at a 25 26 seasonal scale, we also did not detect any spatial variation in 27 the benthic food webs in Young Sound. Although the sampled stations in this study cover only a part of the fjord's length, 28 significant gradients of salinity (Paulsen et al. 2017; Sejr 29 30 et al. 2017), organic matter quality (Bridier et al. 2019), and primary production (Meire et al. 2017) have been reported 31 32 between the same stations. In a similar spatial and salinity gra-33 dient of Hornsund (Svalbard), Włodarska-Kowalczuk 34 et al. (2019) highlighted a clear  $\delta^{13}$ C shift between benthic 35 food webs of inner and outer fjords, which they attributed to 36 different relative contributions of various organic matter sources. The absence of such a trend in Young Sound may sig-37 38 nify that the organic matter pool fueling inner and outer communities is minimally affected by environmental gradients. 39 40 Considering that the inner and outer communities displayed similar general functioning, we consider that their related con-41 42 sumers should be in fact part of a single benthic food web. We 43 will discuss below the potential origins of this spatial homoge-44 neity that exists despite strong gradients in freshwater inputs. 45

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## 47 Importance of the diversity of food sources on benthic48 food web stability

Based on the horizontal structure of the benthic food web (which extends over 7‰ on the  $\delta$ 13C axis) and the high standard ellipse area values coupled to low eccentricity metrics, we conclude that primary consumers feed on several organic matter sources (Layman et al. 2007; Reid et al. 2016). We then hypothesize that some of these food sources may support the resilience of benthic food webs in shallow habitats facing high 55 freshwater inputs and low pelagic primary production. 56

Contrary to several food-web studies conducted in shallow 57 Arctic areas (e.g., Harris et al. 2018), we did not detect signifi- 58 cant contributions of TOM to the diet of primary consumers 59 in the Young Sound fjord. Although stable isotope signatures 60 of terrestrial material may be modified by bacteria,  $\delta^{15}$ N signa-61 tures of TOM (– 2.2‰) appear too depleted to reach the  $\delta^{15}$ N 62 signatures of marine POM and SOM, even after bacterial deg- 63 radation (Lehmann et al. 2002). Several hypotheses can be 64 proposed to explain such opposite results. The first and sim- 65 plest would be that we have failed to collect species feeding 66 massively on TOM. However, while the highest reliance on 67 terrestrial material is usually shown by sub-surface deposit 68 feeders (e.g., Orbinidae, Maldanidae; Harris et al. 2018; 69 McGovern et al. 2020), these species exhibited relatively 70 enriched  $\delta^{13}$ C signatures in the present study (Supplementary 71) Information, Table S1) leading us to reject this hypothesis. 72 Second, both the outer and inner sampling stations could be 73 located too far out of the zone of influence of the Zackenberg 74 River delta to receive significant contributions of TOM. But 75 that is not the case for the inner station, located ~ 5 km from 76 the delta, where Bridier et al. (2019) detected a significant 77 influence of terrestrial material inputs. Therefore, we hypothe-78 size that such opposite results might reflect differences in the 79 quality and quantity of TOM inputs across Arctic regions. 80 Indeed, soils from Scandinavia, Siberia or Canada/Alaska con-81 tain much more organic carbon than soils from Greenland 82 (i.e., 100–260 vs.  $< 30 \text{ kg m}^{-2}$ , respectively; Parmentier 83 et al. 2017). Moreover, Siberian and Alaskan rivers usually flow 84 through permafrost areas covered with abundant vegetation 85 (Walker et al. 2005) while most of the Young Sound river 86 inputs are from glacial meltwater flowing on rocky sediment 87 basin bare from any vegetation (Bendtsen et al. 2014; Paulsen 88 et al. 2017). These geographical features are likely to reduce 89 the quantity and quality of TOM inputs in Young Sound and 90 may thus explain the poor assimilation of this food source in 91 the benthic food web. Contrary to previous shallow food-web 92 studies (e.g., Harris et al. 2018), this negligible contribution of 93 TOM to the benthic food web implies that the negative 94 impact of freshwater inputs on the Young Sound POM quality 95 and availability cannot be balanced by local additional contri-96 bution from terrestrial materials. 97

In contrast, benthic primary consumers fed substantially 98 on the POM/SOM pool. Although carbon stable isotope signa-99 tures usually provide a powerful tool to discriminate organic 100 matter sources in marine ecosystems, POM and SOM sources 101 measured in this study were weakly discriminated which pre-102 cluded the evaluation of their respective contribution to the 103 benthic food web. Such stable isotope signatures overlap prob-104 ably reflects strong resuspension of sedimentary materials 105 toward the overlying bottom waters (i.e., 1 m above the sea- 106 bed). The relatively low degradation of settled particles in 107 polar ecosystems usually leads to the accumulation of a 108

1 persistent sediment food bank of labile detritus (Smith 2 et al. 2006; Mincks et al. 2008). The re-suspension of these 3 labile detritus (through bottom currents or bioturbation) has a 4 considerable importance for arctic benthic food webs facing 5 periods of low food availability by providing an alternative 6 food source for suspension feeders (Smith et al. 2006; 7 Włodarska-Kowalczuk et al. 2019). We hypothesize that such 8 resuspension events in Young Sound might thus partly 9 increase the temporal stability and spatial homogeneity of the 10 benthic food web in the face of strong spatiotemporal varia-11 tions in primary production and organic matter quality (Meire 12 et al. 2017; Bridier et al. 2019).

13 Finally, benthic sources (i.e., Fucus sp. and S. latissima) 14 appear to constitute an additional major source of organic dominating primary 15 matter for biomass consumers 16 (e.g., A. elliptica, H. arctica, M. coastalis). Such contribution is 17 in line with in situ measurements of seabed primary 18 production that revealed substantial production of benthic 19 micro- and macroalgae (2-7 times higher compared with 20 phytoplankton production above 30 m; Glud et al. 2002; 21 Krause-Jensen et al. 2007; Attard et al. 2016). Macroalgae 22 account for the main part of the benthic primary production (Glud et al. 2002; Rysgaard & Glud 2007), mainly through the 676 24 production of three species (i.e., Desmarestia aculeata, Fucus 25 sp. and S. latissima) together representing more than 90% of 26 the overall macroalgal production (Glud et al. 2002; Krause-27 Jensen et al. 2007). However, it appears that Desmarestia 28 aculeata is unlikely to be a major source of organic matter for 29 the benthic food web because of its poor palatability for ben-30 thic invertebrates (e.g., Wessels et al. 2006). In contrast, 31 numerous studies showed that both Fucus sp. and S. latissima 32 productions are able to provide a considerable part of food 33 web carbon requirements of arctic shallow benthic ecosystems 34 (Renaud et al. 2015; Gaillard et al. 2017). These two macro-35 algae might thus offer essential alternative food sources to the 36 Young Sound benthic food web in a context of low pelagic 37 primary production.

Benthic microalgae represent also a non-negligible part of 38 39 the benthic primary production in Young Sound (i.e., 16% of 40 the overall outer fjord primary production; Glud et al. 2002). These benthic microalgae are often far neglected in arctic food 41 42 webs studies, notably because of the great difficulties to obtain 43 accurate isotopic signature in arctic for these primary pro-44 ducers (McTigue and Dunton 2017). Both benthic micro- and 45 macroalgae isotope signatures are known to be <sup>13</sup>C-enriched 46 compared to those from pelagic organic matter sources (France 1995). In the case of Young Sound, we cannot exclude 47 48 that a part of the enriched <sup>13</sup>C signal in several benthic inver-49 tebrates (e.g., A. elliptica, M. coastalis, H. arctica) could also 50 reflect the assimilation of such benthic microalgae as a food source. While enriched- $\delta^{13}$ C ice algae would also theoretically 51 52 constitute an additional potential food source, their extremely 53 low production in Young Sound (i.e., 0.0% of the overall outer 54 fjord primary production; Glud et al. 2002) seems obviously

too weak to drive such  $\delta^{13}$ C enrichment in several biomass- 55 dominant consumers (e.g., *A. moerchi, H. arctica*; Sejr 56 et al. 2000). 57

Overall, the horizontal structure of the food web suggests a 58 significant contribution of carbon of benthic origin to the diet 59 of primary consumers (i.e., species from Fig. 4 fed in average 60 at 25.2% on benthic sources), in accord with what has been 61 reported from other Arctic locations (e.g., Dunton and 62 Schell 1987; Renaud et al. 2015). This finding is also consis-63 tent with two annual carbon budgets showing that Young 64 Sound is a net heterotrophic fjord (Rysgaard and Nielsen 2006; 65 Glud and Rysgaard 2007). In this ecosystem, local pelagic pri- 66 mary production provides a minor part of food-web carbon 67 requirements, which are balanced by additional supplies of 68 local benthic primary production and allochthonous inputs 69 from the shelf (both providing ~ 3 times more organic carbon 70 than local primary production; Glud and Rysgaard 2007). 71 Although this study is not able to distinguish relative contri-72 butions from local (i.e., fjord) and shelf primary production to 73 the POM pools, these results suggest that a major part of 74 POM/SOM contributions in primary consumers would actu-75 ally be related to an assimilation of shelf primary production. 76 Such dominant contributions of both benthic primary produc-77 tion and allochthonous organic matter to the benthic food 78 web would actually signify that both food sources are less 79 impacted by freshwater inputs than are the phytoplankton. 80

For instance, benthic primary production is not as directly 81 impacted by inputs of turbid and nutrient-depleted freshwa-82 ters as pelagic primary production. Benthic primary producers 83 are usually more adapted to nutrient depletion because of the 84 direct access of benthic microalgae to the nutrients released 85 from sediments (MacIntyre et al. 1996) and the relatively low 86 nutrient requirements of perennial macroalgae (Pedersen and 87 Borum 1996). Such adaptations are reflected by the balance of 88 pelagic and benthic primary production by nutrient regimes 89 of shallow coastal ecosystems. Oligotrophic systems generally 90 promote benthic primary production over pelagic primary 91 production, while eutrophic settings favor the dominance of 92 phytoplankton at the expense of benthic micro- and macro-93 algae (Duarte 1995; Glud et al. 2009). Therefore, we believe 94 that nutrient depletion could affect benthic primary producers 95 to a lesser degree than pelagic producers, which would in turn 96 display homogeneous production along our spatial gradient. 97

Whereas it may be argued that freshwater inputs impact 98 pelagic and benthic primary production through increased 99 turbidity and sedimentation, several studies have shown that 100 pelagic and benthic primary producers are both well adapted 101 to low-light conditions in Young Sound (Glud et al. 2002; 102 Krause-Jensen et al. 2007; Holding et al. 2019). Similarly, 103 although strong sedimentation may inhibit the settlement of 104 macroalgae (Filbee-Dexter et al. 2019), benthic micro- and 105 macroalgae tolerate moderate sedimentation rates (Wulff 106 et al. 1997; Ronowicz et al. 2020). For these reasons, we 107 believe that nutrient concentration rather than turbidity is 108

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1 the main factor controlling primary production in the Young 2 Sound fjord.

Moreover, although turbid and nutrient-depleted freshwa-3 4 ter inputs strongly impact primary production toward the 5 fjord head, production on the adjacent shelf remains relatively 6 unaffected due to higher light and nutrient availability (Meire et al. 2017; Holding et al. 2019). Large inflows of shelf water 7 8 masses into the fjord generated by the seasonal estuarine cir-9 culation (Bendtsen et al. 2014) permit the supply of high-10 quality allochthonous organic matter to the benthic food web 11 (Rysgaard and Nielsen 2006; Glud and Rysgaard 2007). Higher 12 resilience of benthic primary producers and lower exposure of 13 offshore phytoplankton to freshwater inputs may thus explain 14 why these two components make such large contributions to 15 the benthic food web. Therefore, although local pelagic pro-16 duction shows strong spatial variation (Meire et al. 2017), its 17 contribution to the diet of primary consumers is not sufficient 18 to mirror the gradient in the benthic food-web structure.

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#### 20 Potential role of omnivory on benthic food-web stability

The absence of spatial variation in the benthic food web may also result from large trophic adaptations of the commuanity to local carbon availability. According to the benthic food-web structure, the fact that numerous consumers seem to feed on several food sources or several trophic levels could be interpreted as a means to cope with variable resource availability in the ecosystem. We hypothesize that such flexible foraging behavior of benthic invertebrates may enhance the food web's stability in a context of strong seasonal and spatial variations of food availability and quality.

31 Several species confirmed our trophic assignments and 32 showed modal trophic positions consistent with their putative 33 trophic levels (e.g., H. arctica or Musculus discors primary con-34 sumer, A. dentata predator). One the other hand, the trophic 35 positions of some taxa usually considered suspension or 36 deposit feeders (Ascidiacea, A. baffini, O. sericeum) were signifi-37 cantly above those of the strict primary consumers. Also, 38 numerous species considered carnivores were actually below of strict 39 the trophic levels secondary consumers 40 (e.g., M. glacialis, Nereis sp., N. hirtipes, O. robusta). Such observed trophic positions could reflect a wide trophic plastic-41 42 ity of primary consumers but also high levels of omnivory in 43 secondary/tertiary consumers. Indeed, when confronted with 44 conditions of low food availability, primary consumers may 45 broaden their forage base by feeding on various  $\delta^{15}$ N-enriched 46 animal/(macro)algal detritus (Mincks et al. 2008). In addition, 47 secondary consumers may also expand their diet to several 48 trophic levels in summer by feeding on both nutritive prey 49 and abundant primary producers (McMeans et al. 2015). These 50 two feeding strategies (i.e., trophic plasticity and omnivory) may thus considerably increase the stability of benthic com-51 52 munities by sustaining large carbon fluxes through the food 53 web throughout the year despite strong freshwater input gra-54 dients and extreme seasonality.

High levels of omnivory highlighted by the trophic posi- 55 tion models may also be a result of the TEFs used in this study. 56 For instance, the low modal trophic positions of A. carinatus 57 and Balanus sp. primary consumers (significantly below 2) 58 may indicate that Post's fractionation factors are actually too 59 high for aquatic consumers (McCutchan et al. 2003). How- 60 ever, neither Post's nor McCutchan's fractionation factors 61 seemed appropriate for our trophic position estimates (see 62 McCutchan's equivalent to Fig. 5 in Supplementary Informa-63 tion, Fig. S3). The high overlap (not dependent on the applied 64 TEFs) between primary and secondary consumers shows in 65 any case that either trophic plasticity or omnivory is a key fea- 66 ture of the benthic food web. A lower fractionation factor would only imply that more primary consumers would exhibit 68 high trophic plasticity by feeding on  $\delta^{15}$ N-enriched detritus, 69 while fewer secondary consumers would be omnivorous. 70

#### Perspectives

Our study reveals that contributions of alternative food 73 sources (i.e., benthic production and allochthonous inputs of 74 organic matter) and trophic adaptations of benthic consumers 75 (i.e., omnivory, trophic plasticity) are key to the stability of 76 benthic food webs exposed to freshwater inputs. However, 77 future research might assess whether these factors will be able 78 to maintain such stability as these freshwater inputs continue 79 to increase.

For instance, deep communities (i.e., below the euphotic 81 zone) probably have less access to benthic micro- and macro-82 algae as they rely on the export of benthic production from 83 shallow coastal habitats (Krumhansl and Scheibling 2012). 84 Considering the negative impact of freshwater inputs on phy-85 toplankton productivity (Meire et al. 2017), further studies 86 might thus investigate whether deeper habitats will be more sensitive to forthcoming increases in terrestrial inputs than 88 shallower communities, as their food webs might be less able 89 to adjust their energy requirements to benthic primary 90 production. 91

In addition, it might be interesting to examine how 92 increasing freshwater inputs would alter supplies of benthic 93 primary production and allochthonous organic matter in ben-94 thic food webs. Benthic primary producers will not necessary 95 be adapted to increased sedimentation under a climate change 96 scenario. Although benthic primary producers can cope with 97 moderate sedimentation (Wulff et al. 1997; Ronowicz 98 et al. 2020), abrupt and extreme sedimentation events may 99 exceed their tolerance threshold, leading to a considerable 100 decline in their productivity (Sahade et al. 2015). On the other 101 hand, increasing freshwater inputs may at the same time 102 enhance the fjord's estuarine circulation (i.e., surface outflows 103 of turbid freshwater plumes and subsurface inflows of shelf 104 water masses), increasing in turn inputs of allochthonous 105 organic matter to the fjord (Rysgaard et al. 2003; Glud and 106 Rysgaard 2007). The balance between these two scenarios 107 deserves further interest in forthcoming studies, in order to 108

1 better assess the sensitivity of the benthic food web, as well as 2 the whole system's functioning, to such changes.

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