Benthic macrofaunal bioturbation activities from shelf to deep basin in spring to summer transition in the Arctic Ocean

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Abstract :

The aim of this study was to assess bioturbation rates in relation to macrozoobenthos and environmental variables in the Svalbard fjords, Barents Sea and Nansen Basin during spring to summer transition. The results showed differences in benthic community structure across sampled area in relation to sediment type and phytopigment content. Fjords, Barents Sea and the shallow parts of Nansen Basin (<400 m) were characterized by high functional groups diversity, and by biodiffusive and non-local rates ranging from 0.05 to 1.75 cm−2 y−1 and from 0.2 to 3.2 y−1, respectively. The deeper parts of Nansen Basin, dominated by conveyors species, showed only non-local transport rates (0.1−1 y−1). Both coefficients intensity varied with benthic biomass. Non-local transport increased with species richness and density and at stations with mud enriched by fresh phytopigments, whereas biodiffusion varied with sediment type and organic matter quantity. This study quantified for the first time the two modes of sediment mixing in the Arctic, each of which being driven by different environmental and biological situations.

Highlights

► This is the first complex report on bioturbation in spring to summer transition conducted over a large depth gradient in the Arctic Ocean. ► Benthic community structure and related biodiffusion and non-local transport varied in Svalbard fjords, Barents Sea and Nansen Basin. ► Changes in environmental conditions, and related changes in quality and quantity of available organic matter, had impact on benthic communities and bioturbation. ► Large inputs of fresh OM to the seabed can trigger bioturbation activities.

Keywords : non-local transport, biodiffusive transport, macrozoobenthos, spring season, sea ice cover, Arctic Ocean

1. Introduction

The structure and functioning of benthic communities depend on the quality and quantity of organic matter (OM) export fluxes to the sea floor and this dependence increases with increasing depth. Shallow Arctic shelves benthos is often fueled by high OM fluxes to the sea floor due to tight pelagic-benthic coupling (e.g. Grebmeier et al., 2006; Tamelander et al., 2008), while deep-sea communities become food-limited due to low amount of OM reaching

51 sea floor (Maiti et al., 2010). The seasons strongly shape the OM fluxes to the sea floor in the

52 Arctic marine ecosystems. Phytoplankton and ice algae are two principal sources of primary

53 production (PP) in the Arctic Ocean with ice algae being the first food source available after

54 polar night (Søreide et al., 2006, 2008; Leu et al., 2010). Although phytoplankton is

55 quantitatively dominant, ice algal blooms tend to occur earlier in the seasonally ice-covered

56 Arctic seas and may contribute up to 50–60% of total PP (Gosselin et al., 1997; McMinn et

57 al., 2010; Fernandez-Mendez et al., 2015; Van Leeuwe et al., 2018). During the spring, PP is

58 typically greater than zooplankton consumption and thus highest vertical carbon fluxes are

59 recorded (Andreassen and Wassmann, 1998; Tamelander et al., 2006). Later in the season, the

60 zooplankton grazing reduces the OM flux but also adds to it by producing fecal pellets, which

61 helps phytoplankton sink rapidly to the sea bottom (Olli et al., 2002). In fjords and on the

62 shelf, benthic communities can also be fueled by terrestrial OM carried by rivers and/or

63 glaciers, mainly during summer (Bourgeois et al., 2016). Benthic organisms act as temporal

64 couplers in the seasonal systems, since they can consume variable carbon sources over the

65 different seasons (McMeans et al., 2015), therefore benthic communities reflect rather long

66 term (months to years) water column production, while the benthic activities reflect short term

67 (days to weeks) environmental conditions (Morata and Renaud, 2008).

68   Bioturbation occurs when an organism moves through the sediment, constructs and

69 maintains burrows, and ingests and defecates. This process results in mixing of particles and

70 solutes within the substratum (Kristensen et al., 2012), and alters sediment structure (e.g.,

71 grain size distribution; Montserrat et al., 2009), and production, mineralization and

72 redistribution of OM (Kure and Forbes, 1997). Life habit, motility, and manner of feeding of

73 infaunal species induce either random particle movement over a short distance (biodiffusion

74 (Db) hereafter) (Gérino et al., 2007; Meysman et al., 2003) or biologically induced

75 discontinuous particle transfer between the sediment surface and deeper sediment layers, for

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76 example via burrowing or feeding behavior (non-local transport (r) hereafter) (Boudreau,

77 1986; Meysman et al., 2003; Duport et al., 2007; Gogina et al., 2017). According to the mode

78 of particle mixing, benthic organisms can be classified into five functional groups of sediment

79 reworking which may include biodiffusion and/or non-local transport: biodiffusors, gallery-

80 diffusors, upward- and downward-conveyors, and regenerators (François et al., 1997). The

81 presence and intensity of these bioturbation modes are therefore mediated by fauna

82 characteristics like biomass, density, burrowing depth or feeding behavior (François et al.,

83 1999; Gérino et al., 1998; Sandnes et al., 2000; Gilbert et al., 2007; Michaud et al., 2005,

84 2006; Duport et al., 2007; Aschenbroich et al., 2017). In turn, species composition, nature and

85 intensity of their effects on sediment mixing depends on temperature (Ouelette et al., 2004;

86 Duport et al., 2007; Maire et al., 2007), food inputs (Nogaro et al., 2008) and sediment

87 characteristics (Needham et al., 2011). Changes in species composition and activities, and

88 therefore in bioturbation mode and/or intensity, are expected to influence biochemical

89 processes near the sediment-water interface, including carbon cycling. Bioturbation rate can

90 therefore be influenced by seasonal changes in PP in the above water column and deposited

91 OM in the seafloor (food bank; Morata et al., 2015).

92   Only a few studies of bioturbation exist in the Arctic Ocean. Teal et al. (2008) created

93 the database with global bioturbation intensity coefficient (Db) and layer depth (L), where

94 they showed that the Arctic, Central Pacific and most tropical regions are missing bioturbation

95 data. In polar regions, it has been shown that sediment mixing rates were higher through

96 biological transports in the shallow sediments directly impacted by the OM input along the

97 marginal ice covered area of the Barents Sea (Maiti et al., 2010) and in the Svalbard fjords

98 (Konovalov et al., 2010). On the contrary, the deep sediments of the Arctic Ocean were

99 marked by lower sediment mixing rates in relation to a lower benthic biomass correlated with

100 lower OM inputs (Clough et al., 1997). Soltwedel et al. (2019), however, did not confirm a

101 higher bioturbation activity in the high productive Marginal Ice Zone (MIZ) in Fram Strait

102 compared to the less productive ice zone. Seasonal aspects of bioturbation in the Arctic were

103 preliminarily studied by Morata et al. (2015), whose experiments showed that the bioturbation

104 activity was positively correlated with fresh food input during the polar night. McClintic et al.

105 (2008) found no seasonal variation in bioturbation intensity during June and October in West

106 Antarctic continental shelf which suggests that deposit feeders are able to access food

107 particles accumulated during high PP periods. Still, our knowledge on benthic communities

108 responsible for bioturbation processes and their relation to OM inputs in the Arctic Ocean and

109 adjacent shelves remains limited, particularly during the spring bloom.

110   The main aim of this study was to understand the impacts of differences in

111 environmental conditions on benthic communities and their bioturbation function during the

112 spring to summer transition. We focused on the Svalbard area where fjords, shelf and deep

113 Nansen Basin differ considerably in terms of physical forcing affecting the quality and

114 quantity of the OM inputs to the seafloor. Sediment reworking rates were quantified in

115 relation to taxonomic and functional composition of the benthic macrofaunal communities,

116 and in relation to the environmental variables. This work is the first study on bioturbation

117 processes conducted in the Arctic Ocean during spring to summer transition time over a large

118 depth gradient. It will contribute to our understanding of response of macrofauna and their

119 activity to the quality and quantity of OM in the Arctic seabed.

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121 **2. Material and methods**

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123 *2.1. Study area*

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125   Sampling was conducted in the Svalbard Archipelago, the Barents Sea and deep Nansen

126   Basin north of Svalbard (Fig. 1, Table 1). This area is highly influenced by cold Arctic Water

127   coming from the north and warm Atlantic Waters coming from the south, and the relative

128   influence of those two water masses varies largely in the study area.

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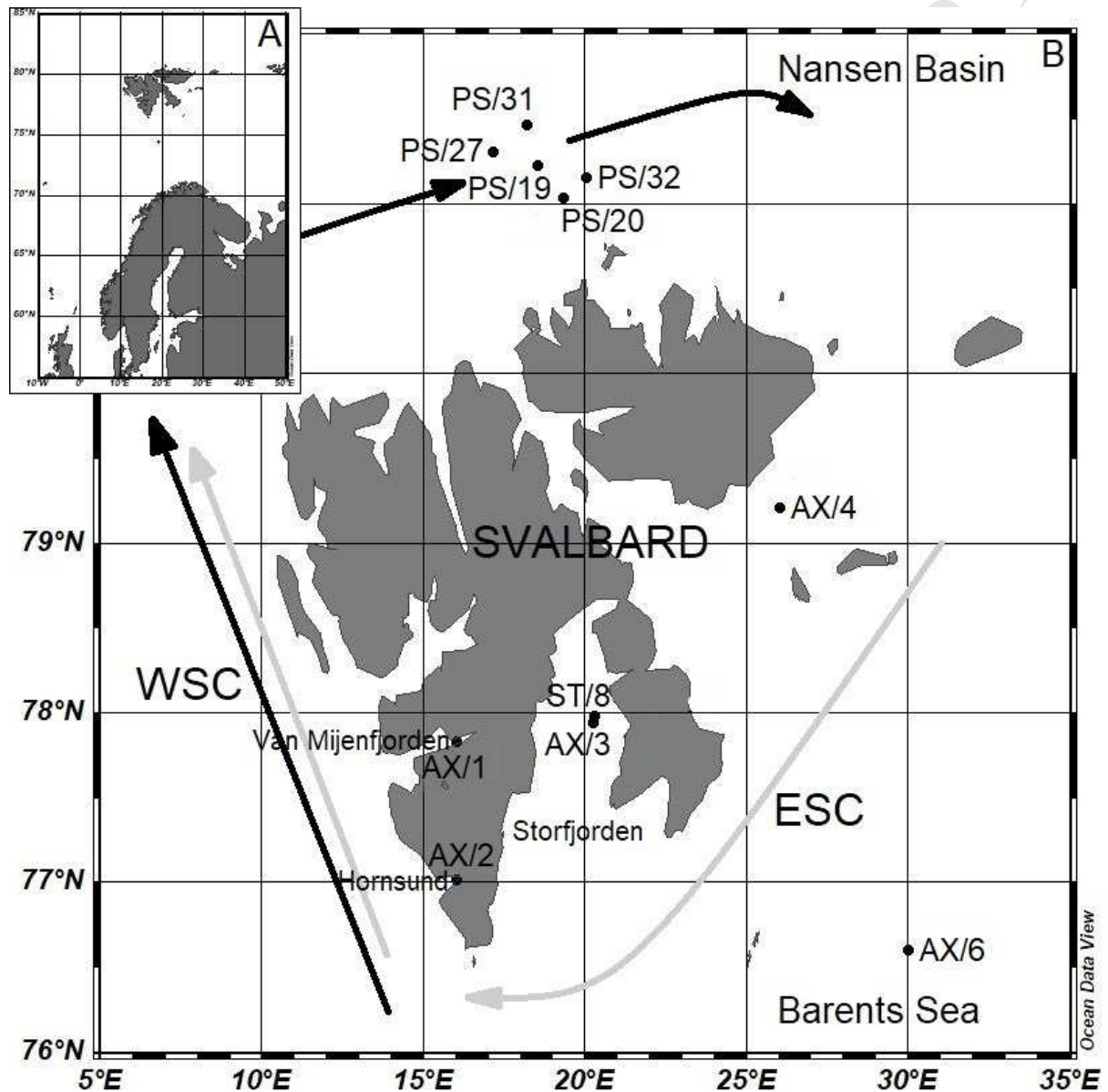
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131   Fig. 1. Geographical location of the study region (A) and (B) sampling locations during two

132   cruises (AX – ARCEx, PS – TRANSSIZ) with two major currents surrounding Svalbard:

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133   WSC - West Spitsbergen Current, warm Atlantic waters (black) and the ESC – East

134   Spitsbergen Current, cold Arctic waters (gray) (after Svendsen et al., 2002).

135   Table 1. Main characteristics of the sampling stations.

Station	Date	Cruise name	No of cores	Area	Latitude (°N)	Longitude (°E)	Main current	Depth [m]	Bottom Water Salinity	Bottom Water Temperature (°C)
AX/1	19.05.2016	ARCEx	5	Van Mijenfjorden	77.83°	16.47°	ESC	59	34.5	-0.8
AX/2	20.05.2016	ARCEx	5	Hornsund	77.02°	16.45°	ESC	121	34.5	-0.8
AX/3	21.05.2016	ARCEx	5	Storfjorden	77.94°	20.22°	ESC	96	34.5	-0.8
ST/8	15.07.2016	SteP	4	Storfjorden	77.98°	20.28°	ESC	99	34.1	4.5
AX/4	24.05.2016	ARCEx	5	Erik Eriksen Strait	79.21°	26.00°	ESC	217	34.7	0.5
AX/6	25.05.2016	ARCEx	5	Southern Barents Sea	76.60°	30.01°	ESC	278	35.0	2.5
PS/20	30.05.2015	TRANSSIZ	3	Northern Barents Sea	81.04°	19.32°	WSC	170	34.9	0.9
PS/32	06.06.2015	TRANSSIZ	4	Northern Barents Sea	81.16°	20.01°	WSC	312	34.9	2.1
PS/19	29.05.2015	TRANSSIZ	5	Northern Barents Sea	81.23°	18.51°	WSC	471	35.1	1.4
PS/27	01.06.2015	TRANSSIZ	5	Northern Barents Sea	81.31°	17.15°	WSC	842	34.9	0.2
PS/31	04.06.2015	TRANSSIZ	5	Nansen Basin	81.47°	18.17°	WSC	1656	34.9	2.5

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140   Van Mijenfjorden and Hornsund are located on the west coast of Spitsbergen,

141   Svalbard. Van Mijenfjorden is a small fjord, nearly closed by an island at its mouth. It is

142   separated into two basins: the outer (115 m depth) and inner (74 m depth), and by 45 m deep

143   sill that restricts exchange of water between the fjord and the coastal waters (Skarđhamar and

144   Svendsen, 2010). Hornsund is a large open glacial fjord with eight major tidal glaciers located

145   in the central and inner parts and large terrestrial inflow (Błaszczyk et al., 2013; Drewnik et

146   al., 2016). The average depth is 90 m with a maximum of 260 m (Kędra et al., 2013). Strong

147   gradients in sedimentation, PP and benthic fauna occur along the increasing distance to the

148   glaciers (Włodarska-Kowalczuk et al., 2013). These high latitude fjords are productive

149   systems, where PP starts in early spring and continue to late autumn (Fetzer et al., 2002). The

150   annual PP reaches up to 216 g C m^{-2} y^{-1} in Hornsund (Smoła et al., 2017). The Barents Sea is

151   a shelf sea with water depths ranging from 35 m in the Svalbard Bank to up to 400 m or more

152   in deep depressions and proximal canyon boundaries (Cochrane et al., 2012). The southern

153   part of the Barents Sea is relatively warm and ice free while its northern parts are seasonally

154   ice covered, with maximum ice coverage from March to April and minimum ice coverage

155   generally occurring in September (Vinje, 2009; Ozhigin et al., 2011; Jørgensen et al., 2015). It

156   is one of the most productive areas in the Arctic Ocean with average PP about 100 g C m^{-2} y^{-1}

157   and maximum PP reaching over 300 g C m^{-2} y^{-1} on shallow banks (Sakshaug, 2004).

158   Storfjorden is located east of Spitsbergen and has a maximum depth of 190 m (Skogseth et al.,

159   2005). A polynya appears regularly in Storfjorden. It is a very productive area of the Barents

160   Sea, and its productivity is correlated with the duration of the seasonal sea cover

161   (Winkelmann and Knies, 2005). In Storfjorden the production of marine organic carbon may

162   exceed 300 mg C cm^{-2} kyr^{-1}, while the production of total organic carbon (TOC) may exceed

163   500 mg C cm^{-2} kyr^{-1} (Pathirana et al., 2013; Rasmussen and Thomsen, 2014). Nansen Basin,

164   with a maximum depth of 4000 m, is part of the Eurasian basin of the Arctic Ocean. In

165   general, annual gross PP is within the range of 5–30 g C m^{-2} (Codispoti et al., 2013).

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167   *2.2. Sampling*

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169   Benthic sampling was conducted during spring cruises of R/V Polarstern PS92 –

170   TRANSSIZ in May and June 2015, and R/V Helmer Hanssen – ARCEx in May 2016 (Table

171   1). Samples were collected at 10 stations located along the depth gradient, from Svalbard

172   fjord (depth: 59 – 121 m), through the Barents shelf and slope (from 170 to 842 m) to the

173   deep Nansen Basin (max. depth: 1656 m) (Fig. 1). Almost all stations north of Svalbard (P32,

174   PS/19, PS/27 and PS/31) were sea ice covered during sampling, except PS/20 station. One

175   station in Storfjorden (AX/3) was revisited in July 2016 during the cruise of R/V L'Atalante –

176   STeP 2016 (ST/8).

177   At each station the bottom water temperature and salinity were determined by the

178   shipboard Conductivity Temperature Density (CTD) rosette. Bottom-water samples were

179   collected using Niskin bottles attached to a CTD and were filtered on pre-combusted

180   Whatman GF/F glass microfiber filters in triplicate and frozen at -20 °C for later analyses of

181   bottom water organic carbon (BW C$_{org}$), total nitrogen (BW N$_{tot}$), δ^{13}C (BW δ^{13}C), δ^{15}N (BW

182   δ^{15}N), and C/N ratio (BW C/N).

183   Sediment samples were collected with a box corer of 0.25 m^2 sampling area. The

184   overlying water from box corer was gently removed from sediment surface and push-cores

185   samples (12 cm Ø and 20 cm deep, 113.0940 cm^2 surface layer) were collected. The top 2 cm

186   sediment of the core was sampled for biogeochemical variables (grain size, chlorophyll *a* (Chl

187   *a*) and phaeopigments (Phaeo), organic matter (SOM), organic carbon (Sed C$_{org}$) and total

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188 nitrogen (Sed N_{tot})). Samples were frozen in -20 °C and transported to the laboratory for

189 analysis.

190   Additional sediment cores were taken from the box corer for bioturbation experiments

191 following procedures described by Morata et al. (2015). Sediment cores (3 to 5 per station,

192 Table 1) were kept in dark cold room on board (i.e., temperature at 2 °C, the average between

193 -0.8°C and 4.5°C being the range of temperatures observed in the bottom waters, Table 1).

194   Fluorescent luminophores (5 g; 90–120 μm diameter) were homogeneously added to

195 the overlying water and gradually spread on the sediment surface of each core without

196 disturbing the resident infauna. Cores were then filled with bottom water and aerated by

197 bubbling to keep the overlying water saturated with oxygen. Overlying water was renewed

198 every four days. Sediment cores were incubated in those conditions for 10 days which is the

199 minimum time to enable the characterization of the different transport modes. Incubation time

200 that exceeds 15 days increases the probability of complete homogenization of the sedimentary

201 column, and may thus prevent the differentiation of transport modes (François et al., 1997).

202 This choice of 10 days for duration of experiment was a compromise between the response

203 that we were expecting from the benthic communities and the available time on board to

204 process the experiments.

205   After this time of incubation in stable conditions the surface water was carefully

206 removed and cores were sliced horizontally in 0.5 cm layers from 0 to 2 cm depth, and in 1

207 cm layers between 2 and 10 cm depth. In total, 12 samples were taken, and each sediment

208 layer was homogenized. A subsample of each sediment layer was directly frozen (-20 °C) and

209 used for bioturbation analyses. The remaining sediment of each core samples were sieved

210 onboard through 0.5 mm sieve for benthic community structure analysis, and fixed with 10 %

211 buffered formaldehyde.

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213 *2.3. Biogeochemical environmental analyses*

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215   Sediments for grain size analysis were freeze-dried at -70 °C, homogenized and dry

216 sieved into coarse-grained fractions (>0.250 mm) and fine-grained (<0.250 mm). For the fine

217 fraction, analyses were performed using a Malvern Mastersizer 2000 laser particle analyzer

218 and presented as volume percent. Mean grain size parameters were calculated using the

219 geometric method of moments in the program GRADISTAT 8.0 (Blott and Pye, 2001).

220   Pigment concentrations were analyzed fluorometrically following methods described

221 in Holm-Hansen et al. (1965) to determine Chl *a* and Phaeo concentrations. About 1 g of dried

222 sediment was extracted with 10 ml of 90 % acetone at 4 °C in the dark. After 24 h, sediment

223 was then centrifuged (3000 rpm for 2 min), and analysed using a Turner Designs AU-10

224 fluorometer before and after acidification with 100 µl 0.3 M HCl.

225   For sediment and bottom water biogeochemical parameters analyses, sediments and

226 filters were dried, homogenized and weighed into silver capsules. For sediment and bottom

227 water $\delta^{13}C$ and $\delta^{15}N$, C_{org} and N_{tot} analyses, samples were acidified with 2 M HCl to remove

228 inorganic carbon and dried at 60 °C for 24 h. The analyses were performed on an Elemental

229 Analyzer Flash EA 1112 Series combined with an Isotopic Ratio Mass Spectrometer IRMS

230 Delta V Advantage (Thermo Electron Corp., Germany). SOM content was measured as loss

231 on ignition at 450°C for 4 h (Zaborska et al., 2006). Sed C_{org} content was measured following

232 the method of Kennedy et al. (2005). About 10 mg of dried sediment was acidified with 50 µl

233 of 1 N HCl three times. Analyses were run on a Thermo Quest Flash EA 1112 CHN analyzer.

234

235 *2.4. Benthic community analysis*

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237   In the laboratory, macrofaunal organisms were picked from sediments under a binocular

238   microscope and identified to the lowest possible taxonomic level. Each taxon was counted,

239   weighed (g wet weight) and transferred to 70 % ethanol. Mobility and feeding (WoRMS

240   Editorial Board, 2019), and burrowing behavior (for references see Table 4) were attributed to

241   each taxon. Benthic fauna was classified into five bioturbation functional groups based on the

242   type of the sediment mixing: biodiffusors, gallery-diffusors, upward- or downward-conveyors,

243   and regenerators. Biodiffusors move particles in a random manner in short distances (Gérino,

244   1992). Gallery-diffusors transport material from the surface sediment layer to deeper by

245   constructing tubes or tunnels system (François et al., 2002). Upward-conveyors transport

246   material from depth to the sediment surface and downward-conveyors transport sediment non-

247   locally to deeper layers (Fisher et al., 1980; Knaust and Bromley, 2012). Regenerators create a

248   biodiffusion-like process, with large amounts of sediment transported out of the reworked

249   zone with a strong input to the overlying water column, as well as passive downward

250   transport of surface sediment to the bottom of the burrow after burrow abandonment (Gardner

251   et al., 1987; Knaust and Bromley, 2012). Organism density and biomass were evaluated per

252   taxon, trophic and bioturbation functional group, and in total for each sediment core, and

253   subsequently converted per 1 m^{-2} (area) in order to provide relevant surface values. The

254   biomass to density (B/D) ratio was calculated per core as a proxy of the mean organism size.

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256   *2.5. Bioturbation analyses*

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258   After the sediment cores were sliced, part of the sediment from each sediment layer

259   was freeze-dried at -70 °C, and homogenized with a mortar and pestle. Three replicates of 0.2

260   g sediment from each layer were taken and placed on a black box (9.5 cm x 7 cm) under a

261   constant UV light source (350 ± 370 nm, Tube UV BLB G5T5 6 W). Images were taken with

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262 a digital camera (Nikon digital captor 2.342.016 pixels) with 28 µm per pixel resolution from

263 a constant 12 cm from the sediment sample to assure identical acquisition conditions for all

264 images (aperture time 1 s; diaphragm aperture f/13, ISO 200). Images were saved in red-

265 green-blue (RGB) colour in jpeg format. The images were analysed using an image

266 processing toolbox (@mathworks) in order to differentiate luminophores from the background

267 sediment by using an appropriate set of RGB threshold levels (Michaud, 2006). Finally, the

268 particle size appropriate for each luminophore was selected (6 pixels × 6 pixels for the

269 smallest luminophores), and the pictures were corrected (cleaned) by removing the particle

270 sizes smaller and larger than the actual size of the specific luminophore (90–120 µm). The

271 sum of areas (in pixels) of the remaining objects and the number of objects (i.e.,

272 luminophores) were calculated for each picture and averaged between the three pictures from

273 each sediment layer. Finally, with these abundances for all sediment depths for each core, the

274 results were computed as the percentage of detected pixels per depth according to the total

275 number of pixels detected per core thus representing the luminophores distribution over depth

276 for each sediment core.

277 The reaction diffusion type model used in this paper to describe luminophore

278 redistribution following macrofaunal reworking is based on the general diagenetic equation

279 (Berner,1980):

280 $$\frac{\partial Q}{\partial t} = \frac{\partial}{\partial z}\left(Db\frac{\partial Q}{\partial z}\right) + r\left(Q\right) \qquad (1)$$

281 where Q is the quantity of the tracer (e.g., luminophores), t is the time, z is the depth, Db is

282 the apparent biodiffusion coefficient, and r(Q) is the non-continuous displacement of tracer.

283 The term r(Q) is defined as follows:

284 $$r\left(Q(z,t)\right) = \begin{cases} \frac{r}{z_2 - z_1}\int_0^{x1} Q(x,t)dx \; if \; z \in [z_1; z_2] \\ -rQ(z,t) \; if \; z \in [0; z_1[\\ 0 \; if \; z > z_2 \end{cases} \qquad (2a\text{-}c)$$

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285   where z_1 and z_2 define the upper and lower limits of the tracer redistribution, x and z are

286   depth variables and r is the biotransport coefficient that is the percentage of tracer that left the

287     $[0; x_1]$ deposit and was redistributed in the $[z_1; z_2]$ layer. The redistribution of tracer between

288   z_1 and z_2 and the disappearance of tracer from the 0-z_1 layer are, respectively, described by

289   Eqs. (2a) and (2b). Eq. (2c) indicates that no tracer movement occurs below z_2.

290   This displacement term was originally exemplified in a model describing gallery-

291   diffusion of macrofaunal reworking (François et al., 2002). This biological reworking process

292   describes the diffusive-like mixing of particles in the region of intense burrowing activity and

293   the rapid transport of organic and inorganic material from the upper sediment layers to the

294   lower regions of reworking (i.e. 'biotransport' or "non-local transport").

295   According to the experimental conditions, the following initial conditions were used:

296     $$Q\,(z, O) = \begin{cases} Q_0 \; if \; z \in [x_1; x_2[\\ O \; else \end{cases} \tag{3}$$

297   where $[x_1; x_2]$ is the tracer deposit layer. Finally, a zero-flux Neuman boundary condition was

298   considered:

299     $$\frac{\partial Q}{\partial z}(0, t) = \lim_{z \to \infty} \frac{\partial Q}{\partial z}(z, t) = 0 \tag{4}$$

300   The application of this bioturbation model to tracer redistributions, initially started by

301   François et al. (1997, 2001) and later revised by Duport al., (2007), allowed the quantification

302   of two particle mixing coefficients: an apparent biodiffusion coefficient Db and a biotransport

303   coefficient r. The biodiffusion coefficient Db takes into account the diffusion-like transport

304   due to the activity of the organisms. We assume that the actual concentration dependent

305   diffusion of tracers is negligible. The biotransport coefficient (r) represents a non-local mixing

306   pattern associated with a biologically induced transfer of particles from one place to another

307   in a discontinuous pattern (i.e. a non-continuous transport; Boudreau, 1986; Meysman et al.,

308   2003). Estimates of the parameters Db and r were finally obtained by minimizing a weighted

309   sum of squared differences between observed and calculated tracer concentrations (François

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310   et al., 1999, 2002). For each core, many adjustments between the observed and modelled

311   profiles are necessary in order to find the minimum weighted sum of squared differences.

312   This model was used with MatLab (@mathworks), thus it gives qualitative data (i.e.,

313   kind of sediment mixing) and quantitative data (intensity of the sediment mixing) on the

314   sediment mixing function for the entire benthic community at the sediment-water interface.

315

316   *2.6. Statistical analysis*

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318   Bray-Curtis similarity matrix, based on square-root transformed data was used for the

319   multivariate analysis of the macrobenthic community. Principal coordinate analysis (PCO)

320   was conducted to explore multivariate variability among different sampling stations based on

321   the (B/D) ratio community composition data matrix. Pearson rank correlation (>0.5) vectors

322   of species B/D with axes were overlaid on the PCO plots to visualize the relationships

323   between ordination axes and the directions and degrees of variability in the biological

324   variables. Differences in species composition in samples among the groups of stations were

325   explored using non-parametric multivariate methods applied to Bray-Curtis dissimilarity

326   matrix calculated from biomass/density ratio (B/D) (one-way PERMANOVA). Whenever the

327   significant effect of factor was detected by the main PERMANOVA test, pair-wise tests for

328   differences between levels of each significant factor was performed. SIMPER procedure

329   (similarity percentage species contribution) was used to discriminate species responsible for

330   the differences between sites. In all models, a forward-selection procedure was used to

331   determine the best combination of predictor variables for explaining the variations in

332   macrofauna assemblages. The selection criteria chosen for the best-fitting relationship were

333   based on R^2 values (Anderson et al. 2008). A distance-based linear model (DistLM) was used

334   to analyse and model the relationships between the macrofaunal community structure and the

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335   environmental factors. A distance-based redundancy analysis (dbRDA) was used to visualize

336   the variability along the two axes that best discriminated groups of samples defined by a priori

337   assigned groups. Superimposed vectors corresponded to Pearson's correlations (>0.5) of

338   environmental factors with the dbRDA axes. Calculations of the pseudo-F and p values were

339   based on 999 permutations of the residuals under a reduced model. The significance level for

340   all the statistical tests was $p = 0.05$.

341   The normality of environmental factors and biological factors (non-local and biodiffusion

342   coefficients, benthic density and biomass) was verified with use of Shapiro-Wilk test

343   ($p<0.05$). Since data did not have a normal distribution, Spearman correlations were

344   calculated to estimate the relationships between faunal community characteristics (Table 8)

345   and environment (Appendix 1). Differences in benthic density, biomass, non-local and

346   biodiffusion coefficient were evaluated with the use of the nonparametric Kruskal-Wallis test,

347   and the Dunn's post-hoc multiple comparison test was applied to identify the differences

348   among stations groups. Station ST/8, sampled in July, was excluded from those analyses due

349   to lack of environmental information and because it was sampled during a different season

350   than the other stations. Additionally, a non-parametric pairwise Mann-Whitney U-test was

351   performed to compare differences between the spring and summer season in Storfjorden

352   (AX/3 vs ST/8). All analyses were performed using the PRIMER package v. 7 Clarke and

353   Gorley, 2006; Anderson et al., 2008) and the Statsoft software STATISTICA v. 9.

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355   **3. Results**

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357   *3.1. Environmental patterns*

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359   Bottom water salinity ranged from 34.5 to 35.1 and bottom water temperature ranged

360   from -0.8 °C to 2.5 °C   during our sampling. The lowest BW C_{org} concentrations were

361   measured in Erik Eriksen Strait (AX/4; 0.1 ± 0.1 %) and the highest in Storfjorden (AX/3; 0.6

362   ± 0.0 %). The BW δ^{13}C values ranged from -27.7‰ on the slope north of Svalbard (PS/32) to

363   -22.2 ‰ in Storfjorden. The lowest BW C/N ratio values were found at the deepest station

364   (PS/31: 6.1 ± 0.0) and the highest values were measured in the southern Barents Sea (AX/6:

365   10.3 ± 1.2) (Table 2). Sandy and muddy sediments dominated in the study area. The lowest

366   SOM concentrations were measured at station PS/32, on slope (2.6% ± 0.1) and the highest in

367   Storfjorden (AX/3; 6.5% ± 0.3). The most depleted sediment δ^{13}C values occurred in fjords

368   (AX/1: -24.2‰ and AX/2: -25.4‰) while the most enriched values were found on southern

369   Barents Sea shelf (AX/6: -22.2‰). The lowest Sed C/N ratio values were found in deep basin

370   (PS/27: 7.8 ± 0.4) and the highest value occurred in Van Mijenfjorden (AX/1: 18.7 ± 0.5)

371   (Table 3).

372   Table 2. Bottom water (BW) characteristics for each sampling station: C_{org}, N_{tot}, $\delta^{13}C$, $\delta^{15}N$ (in %) and C/N values (mean ± SD, n=3).

Station	BW C_{org} (%)	BW N_{tot} (%)	BW $\delta^{13}C$ (‰)	BW $\delta^{15}N$ (‰)	BW C/N
AX/1	0.204±0.017	0.023±0.002	-24.7±0.1	5.7±0.7	10.3±1.1
AX/2	0.187±0.005	0.024±0.001	-24.0±0.1	3.9±0.5	8.9±0.2
AX/3	0.630±0.037	0.097±0.005	-22.2±0.2	4.8±0.3	7.6±0.2
ST/8	-	-	-	-	-
AX/4	0.137±0.047	0.015±0.003	-24.0±0.1	5.1±0.2	10.2±1.7
AX/6	0.268±0.013	0.031±0.005	-24.5±0.9	5.9±1.7	10.3±1.2
PS/20	0.354±0.017	0.063±0.001	-23.5±0.0	1.4±0.0	6.6±0.2
PS/32	0.180±0.002	0.030±0.001	-27.7±0.1	1.9±0.6	7.0±0.2
PS/19	0.188±0.014	0.032±0.001	-24.6±0.2	2.1±0.2	6.8±0.2
PS/27	0.226±0.007	0.040±0.001	-22.9±0.2	2.0±0.7	6.6±0.1
PS/31	0.258±0.013	0.050±0.002	-23.8±0.1	2.3±0.7	6.1±0.0

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381 Table 3. Sediment variables for each sampling station: sediment type, C_{org}, N_{tot}, $\delta^{13}C$, $\delta^{15}N$, OM (in %), C/N, Chl a (μg DW g^{-1}) and Chl a/Phaeo

382 values (mean $\pm$ SD, n=no of cores).

Station	No of cores	Sediment type	Gravel (%)	Sand (%)	Mud (%)	Sed C_{org} (%)	Sed N_{tot} (%)	Sed $\delta^{13}C$ (‰)	Sed $\delta^{15}N$ (‰)	Sed C/N	SOM (%)	Chl a (μg/g)	Chl a/ Phaeo
AX/1	3	Sand	0.0	78.1	21.9	1.9 ± 0.0	0.1 ± 0.0	-24.2	4.0	18.7 ± 0.5	5.1 ± 0.4	2.3 ± 0.2	0.5 ± 0.1
AX/2	3	Sand	1.3	86.8	12.0	1.8 ± 0.0	0.1 ± 0.0	-25.4	4.8	18.1 ± 0.2	4.4 ±0.3	1.4 ±0.1	0.4 ±0.0
AX/3	3	Mud	0.0	40.8	59.2	2.1 ±0.0	0.2 ±0.0	-22.9	3.6	10.8 ±0.1	6.5 ±0.3	19.4 ±2.6	1.9 ±0.4
ST/8	2	-	-	-	-	2.1 ±0.0	0.2 ±0.0	-	-	11.0 ±0.4	7.3 ±0.6	21.8 ±1.3	51.8 ±34.2
AX/4	3	Sand	2.3	66.4	31.2	1.0 ±0.0	0.1 ±0.0	-23.6	5.3	8.2 ±0.2	5.1 ±0.6	2.2 ±0.3	0.3 ±0.0
AX/6	3	Mud	1.3	42.6	56.1	2.1 ±0.0	0.3 ±0.0	-22.2	4.6	9.9 ±0.2	5.7 ±0.6	2.6 ±0.5	0.4 ±0.0
PS/20	2	Sand	7.5	51.3	41.2	0.9 ±0.0	0.1 ±0.0	-22.8	2.8	8.5 ±0.1	4.6 ±0.3	7.6 ±1.7	1.1 ±0.2
PS/32	2	Sand	1.9	76.6	21.5	0.5 ±0.1	0.1 ±0.0	-22.8	4.0	8.1 ±0.2	2.6 ± 0.1	12.8 ± 1.6	1.9 ± 0.4
PS/19	3	Sand	0.1	74.5	25.3	1.6 ±0.0	0.2 ±0.0	-22.7	4.6	9.5 ±0.3	8.3 ±0.8	2.9 ±0.5	0.4 ±0.0
PS/27	3	Sand	6.3	62.3	31.5	0.8 ±0.0	0.1 ±0.0	-22.9	3.0	7.8 ±0.4	3.7 ±0.3	2.6 ±0.5	0.5 ±0.0
PS/31	3	Sand	30.1	46.0	23.9	0.8 ±0.1	0.1 ±0.0	-23.0	3.9	16.7 ±3.8	4.4 ±0.1	1.1 ±0.4	0.3 ±0.0

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389   *3.2. Macrobenthic community structure*

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391   In total, 186 taxa were identified. The number of taxa per station ranged from 9 (AX/2)

392   to 68 (PS/32) (Table 4). Four burrowing and four sediment-mixing types were recorded. Sub-

393   surface burrowing, Cirratulidae (biodiffusor) and *Lumbrineris* sp. (gallery diffusor) dominated

394   in Svalbard fjords in biomass and density, and in Storfjorden in density. The deep burrowing

395   *Yoldia hyperborea* (conveyor) dominated in biomass at AX/3. Two biodiffusors, the tube

396   building polychaete *Myriochele heeri* and the deep burrowing bivalve *Astarte borealis*

397   dominated in Erik Eriksen station (AX/4) in density and biomass respectively. The tube

398   building *Spiochaetopterus typicus* (conveyor) dominated in terms of density and was second

399   dominant in biomass in the Southern Barents Sea (AX/6). The sea star *Ctenodiscus* sp.

400   dominated in biomass at this station. The tube building polychaete, *Maldane glebifex*,

401   dominated in both density and biomass at the shelf station PS/20. Deep burrowing bivalves

402   (*Yoldiella lenticula, Yoldia hyperborea*) dominated in density at PS/32 while the tube building

403   polychaete *Galathowenia oculata* dominated in biomass. Burrow-building taxa were mostly

404   biodiffusors and dominated at all shallow stations. Deep burrowing and tube building taxa

405   were mostly conveyor bioturbators and dominated at deeper stations (Table 4). Fourteen

406   mobility-feeding groups were recorded, and sessile and mobile macrofauna dominated at all

407   stations except from the deepest one (PS/31) where discretely mobile fauna dominated. The

408   lowest number of functional groups was found in Hornsund (AX/2) where 4 groups (sessile

409   surface feeders, discretely subsurface feeders, mobile omnivore and mobile subsurface

410   feeders) occurred. Sessile subsurface feeders dominated at PS/20 (30%) and PS/27 (33%).

411   Sessile surface feeders were predominant in fjords (AX/1: 52% ; AX/2: 80%), Storfjorden

412   (AX/3: 35%), in the southern Barents Sea (AX/6: 45%) and on slope (PS/19: 18%). The share

413   of discretely mobile fauna increased with depth, and discretely mobile surface feeders

414   dominated in the Nansen Basin (PS/31: 44%). The highest number of mobile subsurface

415   feeders was found on the shelf (PS/32: 23%). The number of mobile taxa was similar for all

416   stations. The mobile surface fauna dominated in Erik Eriksen Strait (AX/4: 25%) (Fig. 2).

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441 Table 4. Functional traits, relative density and biomass of the three dominant taxa for each sampling station. Class: P – Polychaeta, B – Bivalvia,

442 An – Anthozoa, As – Asteroidea, O – Ophiuroidea, S – Sipunculidea. Mobility and feeding groups (M/F) are marked by codes: mobility type (D -

443 Discretely mobile, M – Mobile, S – Sessile) and feeding type (car - carnivore, omn - omnivore, sub - subsurface feeder, sur - surface feeder, sus -

444 suspension feeder). Burrowing depth (BT): 1 – surface burrowing, 2 – subsurface burrowing, 3 – deep burrowing. Tubes (T): "+" – I-shaped

445 tube, "-" – no tube. Sediment mixing types (SMix): biodiffusor (B), upward conveyor (UC), gallery diffusor (GD), downward conveyor (DC).

Station	No of taxa	Taxa	Class	M/F	BT	T	SMix	Density %	Taxa	Class	M/F	BT	T	SMix	Biomass %
AX/1	20	Cirratulidae [2]	P	Ssur	2	-	B	41.4	Lumbrineris sp. [6]	P	Momn	2	-	GD	72.1
		Polycirrus arcticus [4,5]	P	Ssur	3	+	DC	7.1	Polycirrus arcticus [4,5]	P	Ssur	3	+	DC	11.5
		Lumbrineris sp. [6]	P	Momn	2	-	GD	6.4	Aglaophamus malmgreni [4]	P	Mcar	2	-	B	10.6
AX/2	9	Cirratulidae [2]	P	Ssur	2	-	B	66.7	Cirratulidae [2]	P	Ssur	2	-	B	49.3
		Polycirrus arcticus [4,5]	P	Ssur	3	+	DC	13.1	Polycirrus arcticus [4,5]	P	Ssur	3	+	DC	36.6
		Lumbrineris sp. [6]	P	Momn	2	-	GD	8.3	Lumbrineris sp. [6]	P	Momn	2	-	GD	8.7
AX/3	34	Cirratulidae [2]	P	Ssur	2	-	B	31.2	Yoldia hyperborea [7]	B	Msub	3	-	C	57.4
		Lumbrineris sp. [6]	P	Momn	2	-	GD	14.1	Maldane sarsi [8]	P	Ssub	3	+	C	12
		Yoldia hyperborea [7]	B	Msub	3	-	C	6.3	Nuculana radiata [4]	B	Msub	3	-	B	11.5
ST/8	29	Lumbrineris sp. [6]	P	Momn	2	-	GD	18.3	Yoldia hyperborea [7]	B	Msub	3	-	C	30.5
		Cirratulidae [2]	P	Ssur	2	-	B	11	Nuculana radiata [4]	B	Msub	3	-	B	27.8
		Eteone longa [9, 10]	P	Msub	1	-	GD	7.3	Macoma calcarea [11]	B	Ssur	3	-	B	13.7
AX/4	63	Myriochele heeri [17]	P	Msur	3	+	B	12.1	Astarte borealis [4]	B	Msus	3	-	B	90

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Station	N	Species							Species						
		Macoma sp.[1,11]	B	Ssur	3	-	B	11.6	Actinaria[4]	An	Scar	1	-	B	1.8
		Maldane sarsi[8]	P	Ssub	3	+	C	8.2	*Yoldiella lenticula*[7]	B	Msur	3	-	C	1.5
AX/6	36	*Spiochaetopterus typicus*[8]	P	Ssur	3	+	C	34.9	*Ctenodiscus* sp.[20]	As	Msur	1	-	B	47.3
		Macoma sp.[1,11]	B	Ssur	3	-	B	6.4	*Spiochaetopterus typicus*[8]	P	Ssur	3	+	C	27.3
		Heteromastus sp.[12,13,14]	P	Msub	3	-	C	6.4	*Aglaophamus malmgreni*[4]	P	Mcar	2	-	B	6.4
PS/20	58	*Maldane glebifex*[8]	P	Ssub	3	+	C	22.4	*Maldane glebifex*[8]	P	Ssub	3	+	C	24.5
		Yoldiella lenticula[7]	B	Msur	3	-	C	8.7	*Chirimia biceps*[8]	P	Ssub	3	+	C	9.4
		Macoma calcarea[11]	B	Ssur	3	-	B	7.1	*Nicomache lumbricalis*[8]	P	Ssub	3	+	C	9.4
PS/32	68	*Yoldiella lenticula*[7]	B	Msur	3	-	C	13.8	*Galathowenia oculata*[3]	P	Msur	2	+	C	7.7
		Yoldia hyperborea[7]	B	Msub	3	-	C	8.7	*Ctenodiscus* sp.[20]	As	Msur	1	-	B	7.5
		Axinopsida orbiculata[15]	B	Dsub	3	-	C	5.9	*Yoldiella lenticula*[7]	B	Msur	3	-	C	6.3
PS/19	38	Cirratulidae[2]	P	Ssur	2	-	B	12	*Amphiura sundevalli*[4]	O	Msus	1	-	B	25.5
		Notoproctus oculatus[8]	P	Ssub	3	+	C	10.1	Lumbrineridae[6]	P	Somn	2	-	GD	9.3
		Yoldia hyperborea[7]	B	Msub	3	-	C	8.9	Nemertea[4]	N	Momn	1	-	B	7.1
PS/27	35	*Prionospio cirrifera*[16]	P	Dsur	2	+	C	13.2	*Streblosoma intestinale*[4]	P	Dsur	3	+	C	43
		Notoproctus oculatus[8]	P	Ssub	3	+	C	13.2	*Chone fauveli*[3]	P	Ssur	2	+	C	32.6
		Lumbriclymene minor[8]	P	Ssub	3	+	C	8.8	*Notoproctus oculatus*[8]	P	Ssub	3	+	C	4.2
PS/31	19	*Levinsenia gracilis*[18]	P	Dsur	2	-	C	33.6	*Nephasoma lilljeborgi*[19]	S	Dsur	3	-	C	28
		Paraonidae[2]	P	Msub	2	-	B	19.3	*Levinsenia gracilis*[18]	P	Dsur	2	-	C	14.2
		Cirrophorus sp.[2]	P	Dsub	2	-	B	16.8	Paraonidae[2]	P	Msub	2	-	B	11

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447 References in superscripts: [1] Gilbert at al. (2007); [2] Gérino at al. (1992, 2007); [3] Fauchald and Jumars (1979); [4] Queirós at al. (2013); [5] Gingras et

448 al. (2008); [6] Petch (1986); [7] Stead and Thompson (2006); [8] Smith and Shafer (1984); [9] Mazik and Elliott (2000); [10] Mermillod-Blondin et al.

449 (2003); [11] Michaud et al. (2006); [12] D'Andrea et al. (2004); [13] Mulsow et al. (2002); [14] Quintana et al. (2007); [15] Zanzerl and Dufour (2017); [16]

450 Bouchet et al. (2009); [17] Duchêne and Rosenberg (2001); [18] Venturini et al. (2011); [19] Shields and Kędra (2009); [20] Shick (1976).

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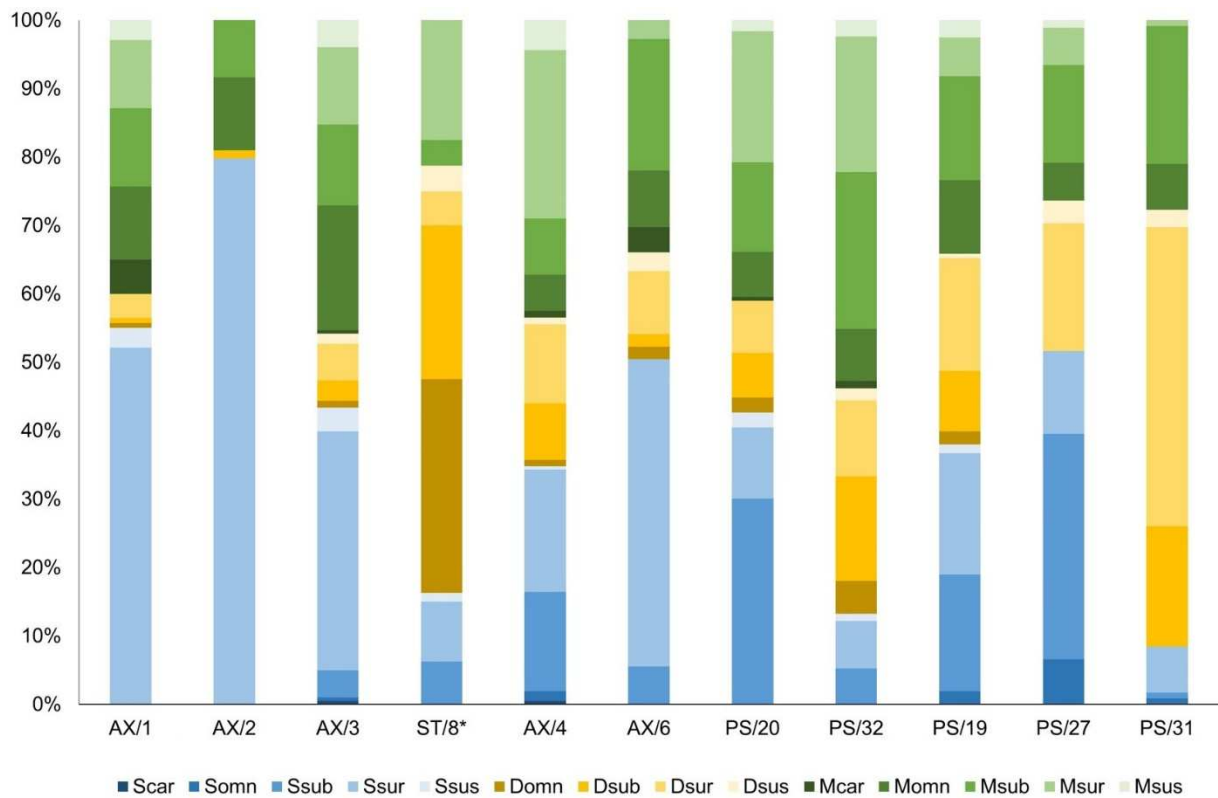
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Fig. 2. Percentages of mobility and feeding groups at different sampling stations. Station ST/8 marked with * was sampled in summer season. Functional traits codes: mobility type (D - Discretely mobile (yellow), M – Mobile (green), S – Sessile (blue)) and feeding type (car - carnivore, omn - omnivore, sub - subsurface feeder, sur - surface feeder, sus - suspension feeder).

Stations were separated into 4 groups, based on the PCO analysis: A - fjords (Van Mijenfjorden: AX/1, Hornsund: AX/2), B - Storfjorden (AX/3), C - Barents Sea shelf (Erik Eriksen Strait: AX/4, southern Barents Sea: AX/6, and northern Barents Sea: PS/20, PS/32), D - northern Barents Sea, stations deeper than 400m on continental stock: PS/19, PS/27 and Nansen Basin: PS/31. PCO explained 22.5% of the variability among sampling stations: the first axis explained 13.6% and the second axis 8.9% (Fig. 3). Fjords' communities were correlated with presence of polychaete *Polycirrus arcticus* and cumacean *Diastylis lucifera* while benthic patterns in Storfjorden were correlated with presence of polychaetes *Maldane*

sarsi and *Apistobranchus tullbergi*, and bivalves *Musculus discors, Ennucula tenuis* and *Yoldia hyperborea.* Those correlations were negative for deeper stations where benthic communities were mainly correlated with presence of polychaetes *Notoproctus oculatus* and *Prionospio cirrifera.* The shelf stations varied the most with less clear patterns for benthic communities.
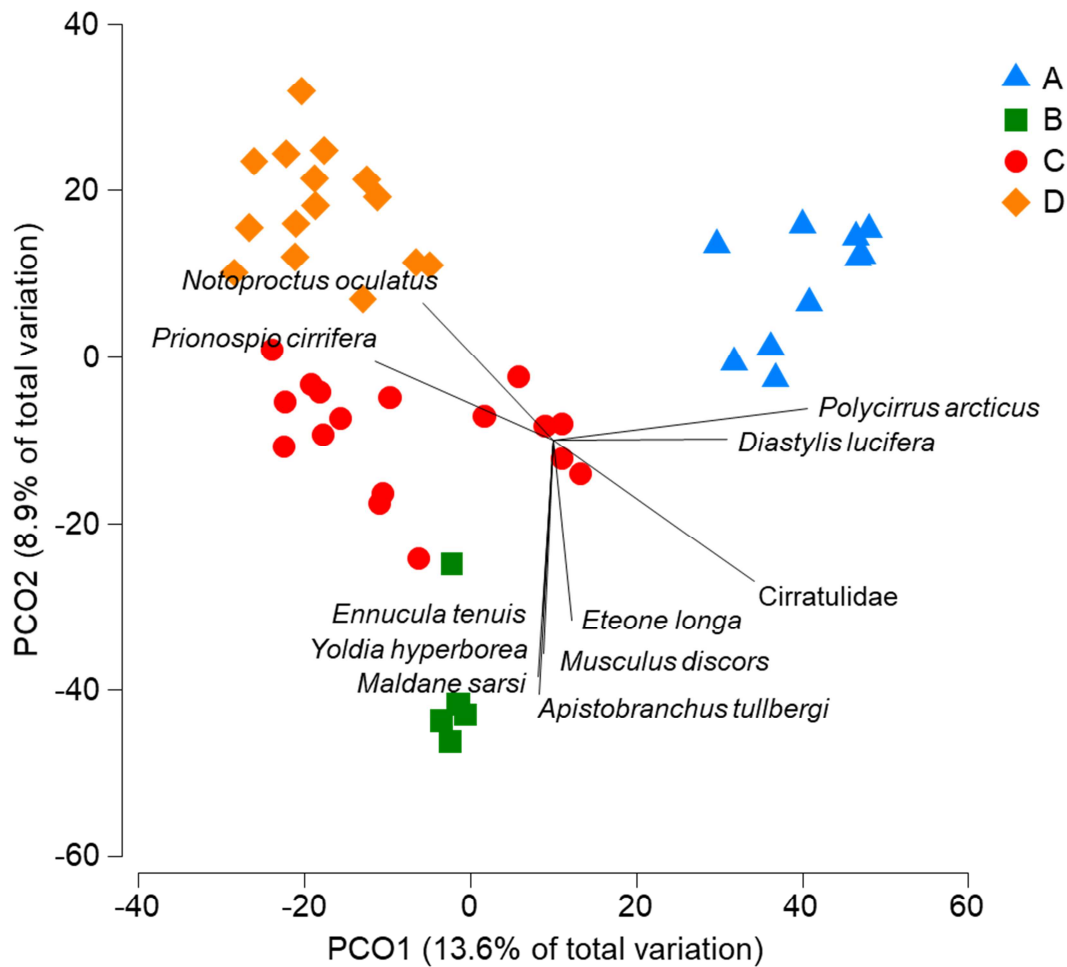
Fig. 3. PCO analysis for macrobenthic communities based on species biomass to density ratio, and the Bray-Curtis similarity among four sampling areas: A (Hornsund, Van Mijenfjorden); B (Storfjorden); C (Barents Sea shelf); D (northern Barents Sea and Nansen Basin). Significantly correlated species with the PCO coordinates (r>0. 5) are shown on the plot.

477   Polychaeta dominated at all stations. There were significant differences in density

478   (Kruskal-Wallis test; $p<0.05$; significant differences (post hoc test) between group A:B, A:C

479   and C:D) (Fig. 4A). Benthic density ranged from 1485.5 ind./m^2 ± 168.7 standard error (SE)

480   (station AX/2) to 2475.8 ind./m^2 ± 369.9 SE (station AX/1) in group A. In group B benthic

481   density was 3625.3 ind./m^2 ± 83.9 SE (station AX/3). In group C density ranged from 1927.6

482   ind./m^2 ± 196.5 SE (station AX/6) to 6388.5 ind./m^2 ± 399.3 SE (station PS/32). In group D

483   density ranged from 1609.3 ind./m^2 ± 295.1 SE (station PS/27) to 2794.1 ind./m^2 ± 404.8 SE

484   (station PS/19). There were significant differences in biomass among areas (Kruskal-Wallis

485   test; $p<0.05$; significant differences (post hoc test) between group A:B, B:D and C:D) (Fig.

486   4B). Benthic biomass ranged from 2.6 g wet weight/m^2 ± 0.5 SE (station AX/2) to 37 g wet

487   weight/m^2 ± 18.4 SE (station AX/1) in group A. In group B benthic biomass was 172.3 g wet

488   weight/m^2 ± 37.3 SE (station AX/3). In group C biomass ranged from 7.8 g wet weight/m^2 ±

489   1.1 SE (station PS/32) to 112.9 g wet weight/m^2 ± 61.3 SE (station AX/4). In group D biomass

490   ranged from 2.2 g wet weight/m^2 ± 0.5 SE (station PS/31) to 11.2 g wet weight/m^2 ± 5.7 SE

491   (station PS/27).
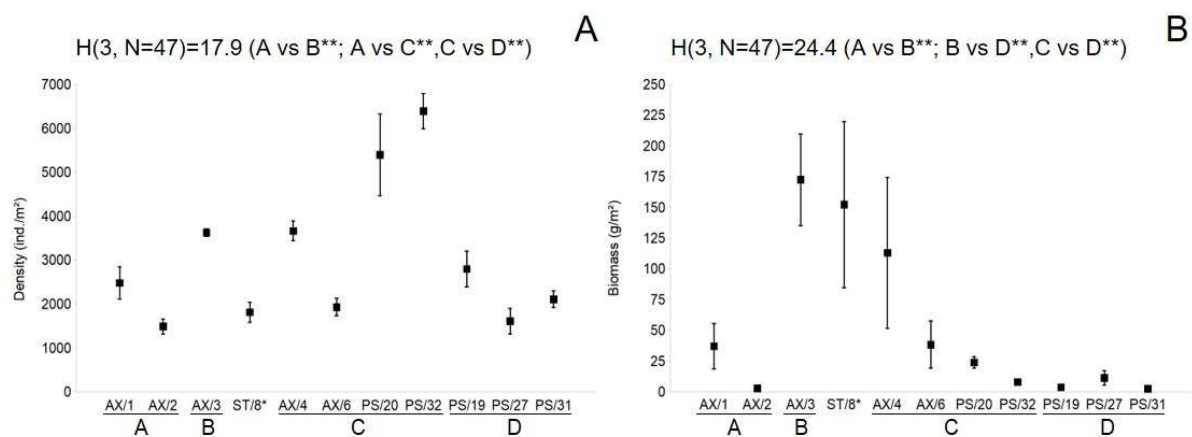
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493   Fig. 4. Mean density (ind./m^{-2}) (A) and biomass (g/m^{-2}) (B); ± SE, n= no of cores (Table 1) at

494   stations sampled in Van Mijenfjorden, Hornsund (group A); Storfjorden (group B); Barents

495   Sea shelf (group C); northern Barents Sea and Nansen Basin (group D). Station ST/8 marked

496 with * was sampled in summer season. Kruskal – Wallis results for differences between

497 sampling sites are given; significant test results are marked with ** (p<0.05).

498   There were significant differences in the benthic communities structure

499 (biomass/density ratio) among different locations (PERMANOVA test Pseudo-F : 5.07,

500 p=0.001). Significant differences were found for each group (significant pairwise

501 comparisons p=0.001); see Table 5 for details.

502

503 Table 5. PERMANOVA results for the multivariate descriptors of benthic communities with

504 significant pair-wise comparisons results for different groups.

Benthic parameter	Source of variation	Df	MS	Pseudo-F	P (perm)
Biomass/Density ratio	Gr	3	16606.0	5.07	0.001
	Res	43	3272.8		
	Total	46			

Benthic parameter	Regime	Site	t	Df	P(MC)	P (perm)
Biomass/Density ratio	Groups	A:B	2.886	13	0.001	0.001
		A:C	2.469	25	0.001	0.001
		A:D	2.715	23	0.001	0.001
		B:C	1.874	20	0.001	0.001
		B:D	2.151	18	0.001	0.001
		C:D	1.852	30	0.001	0.001

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506

507   Benthic taxa that contributed mostly to the groups similarities were: *Polycirrus*

508 *arcticus* (44.7 %) in fjords (A), *Yoldia hyperborea* (31.7 %) in Storfjorden (B),

509 *Spiochaetopterus typicus* (16.8 %) in the Barents Sea shelf (C) and *Nephasoma diaphanes*

510 *diaphanes* (16 %) in the northern Barents Sea and Nansen Basin (D) as revealed by SIMPER

511 analysis (Table 6).

512

513 Table 6. SIMPER analysis results based on B/D ratio. Species that contributed more than 5%

514 of the average similarity for different sampling stations groups are listed.

Group	Average similarity	Species	Contribution %
A	39.7	*Polycirrus arcticus*	44.7
		Cirratulidae	28.5
		Lumbrineris sp.	18.7
B	35.9	*Yoldia hyperborea*	31.7
		Maldane sarsi	31
		Nuculana radiata	9
		Lumbrineris sp.	8.1
		Cirratulidae	5.8
C	12	*Spiochaetopterus typicus*	16.8
		Lumbrineris sp.	10.7
		Yoldiella lenticula	7.3
		Maldane sarsi	5.6
D	14.8	*Nephasoma diaphanes diaphanes*	16
		Maldane glebifex	11.7
		Prionospio cirrifera	10.1
		Notoproctus oculatus	9.8
		Nemertea	9.5
		Lumbrineris sp.	6.3
		Byblis minuticornis	5.9

515

516   The results of DistLM analyses showed that salinity explained 10.1% of the variation

517   observed in the macrofauna community while Sed δ^{13}C (10%) and Sed C/N (9.3%) were next

518   main contributors. Nine variables were included by the DistLM procedure to construct the

519   best fitting model, together explaining 46.8% of total variation. However, one of the variables

520   was not statistically significant (gravel) (Table 7). The most important parameter contributing

521   to the first axis of the dbRDA plot was Sed C/N and explained 17.2% of fitted variation. It

522   also positively correlated with fjords' group (A). The most important parameter contributing

523   to the second axis was sediment Chl *a* and explained 25.7% of fitted flux variation. It was

524   positively correlated with Storfjords group (B) and most stations in group C (shelf) (Fig. 5).

525

526   Table 7. Results of DistLM procedure for fitting environmental variables to the macofauna

527   community data. %Var - percentage of explained variance; %Cum - cumulative percentage

528   explained by the added variable. Significance level $p < 0.05$. Environmental factors: D –

529   depth, S – salinity, T – temperature, types of sediment (mud, sand, gravel), BW C_{org} – bottom

530   water C_{org}, BW N_{tot} – bottom water N_{tot}, BW δ^{13}C – bottom water δ^{13}C BW, BW δ^{15}N –

531   bottom water δ^{15}N, BW C/N – bottom water C/N, Sed C_{org} – C_{org} concentration in sediment,

532   Sed N_{tot} – sediment N_{tot}, Sed δ^{13}C – sediment δ^{13}C, Sed δ^{15}N – sediment δ^{15}N, Sed C/N –

533   sediment C/N, SOM – sediment organic matter, Chl *a* – sediment Chlorophyll *a* and Chl
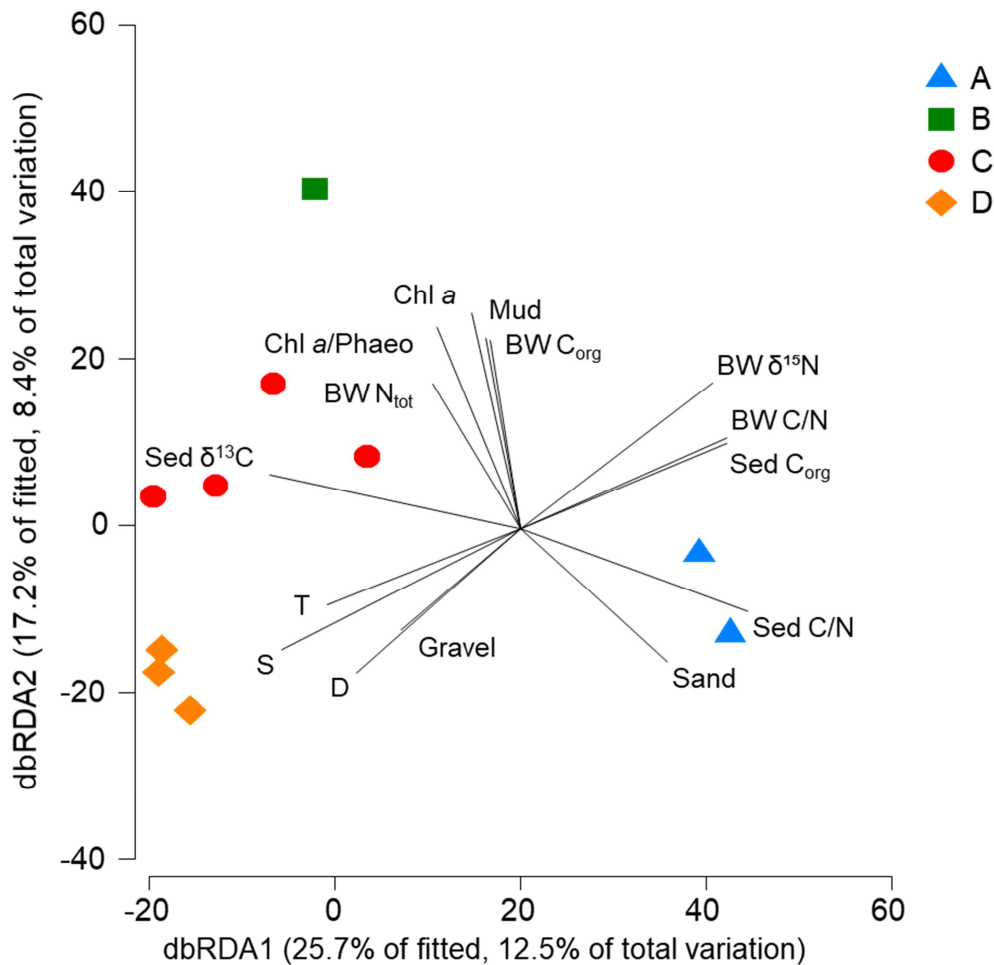
534   *a*/Phaeo – sediment Phaeopigments.

MARGINAL TESTS			
Variable	Pseudo-F	Var%	P
S	5.06	10.1	0.001
Sed δ^{13}C	5.01	10.0	0.001
Sed C/N	4.59	9.3	0.001
BW C/N	4.31	8.7	0.001
BW δ^{15}N	4.25	8.6	0.001
Sed C_{org}	4.11	8.4	0.001
D	3.99	8.1	0.001
T	3.96	8.1	0.001
Chl *a*	3.66	7.5	0.001
Sand	3.62	7.4	0.001
Mud	3.46	7.1	0.001
Chl *a*/ Phaeo	3.34	6.9	0.001
BW C_{org}	3.26	6.8	0.001
BW N_{tot}	3.16	6.6	0.002
Gravel	3.11	6.5	0.001
Sed N_{tot}	2.43	5.1	0.001
Sed δ^{15}N	2.09	4.4	0.004
BW δ^{13}C	2.04	4.3	0.001
SOM	1.56	3.4	0.032

SEQUENTIAL TESTS					
Variable	R²	Pseudo-F	Var%	Cum%	P
D	0.08	3.99	8.1	8.1	0.001
S	0.16	3.98	7.6	15.7	0.001
Sand	0.30	4.06	7.0	22.7	0.001
BW δ^{15}N	0.44	3.71	5.5	28.2	0.001
BW C/N	0.49	3.70	5.1	33.3	0.001
BW δ^{13}C	0.38	3.06	4.9	38.1	0.001
T	0.20	2.44	4.5	42.7	0.001
Mud	0.33	2.26	3.8	46.4	0.001
Gravel	0.23	1.29	2.4	48.8	0.127

535

Fig. 5. Distance-based Redundancy Analysis (dbRDA) plot of the DistLM model visualizing the relationships between the environmental parameters and the biomass/density ratio of species between four sampling areas: A (Hornsund, Van Mijenfjorden); B (Storfjorden); C (Barents Sea shelf); D (northern Barents Sea and Nansen Basin). Environmental variables with Pearson rank correlations with dbRDA axes > 0.5 are shown. Environmental factors: D – depth, S – salinity, T – temperature, types of sediment (mud, sand, gravel), BW C_{org} – bottom water C_{org}, BW N_{tot} – bottom water N_{tot}, BW $\delta^{15}N$ – bottom water $\delta^{15}N$, BW C/N – bottom water C/N, Sed C_{org} – C_{org} concentration in sediment, Sed $\delta^{13}C$ – sediment $\delta^{13}C$, Sed C/N – sediment C/N, Chl a – sediment Chlorophyll a and Chl a/Phaeo – sediment Phaeopigments.
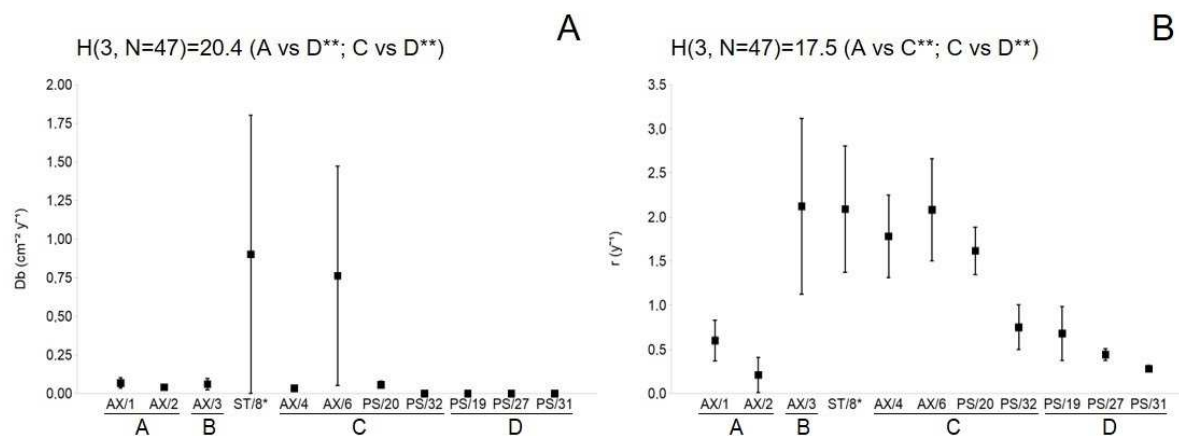
3.3.Bioturbation

548

549   After 10 days, almost all luminophores (~95%) remained on sediment core surface at all

550   sampling stations meaning that about 5% of luminophores were transported into sediments.

551   The fastest decrease was noted at the B group (Storfjorden : AX/3 and ST/8), and at the C

552   group (Southern Barents Sea station (AX/6) ; Nansen Basin < 400 m (PS/20, PS/32)) where

553   ~15 to 25% of surface luminophores were buried. While luminophores were still present all

554   along the sedimentary column in the Storfjorden station, some subsurface peaks of

555   luminophores were clearly measured below 3 cm in the C group. The lowest decrease of the

556   luminophores over depth was noted in the A group (Svalbard Fjords AX1/1, AX/2) and in the

557   D group at deepest station (PS/31) in the Nansen Basin where 92 to 98% of luminophores

558   remained at surface with slight subsurface peaks of tracers (about: only 0.91 %) between 1 to

559   3 cm deep .

560   Biodiffusion rates ranged from 0.04 cm^{-2} y^{-1} ± 0.01 standard error (SE) (station AX/2)

561   to 0.07 cm^{-2} y^{-1} ± 0.03 SE (station AX/1) in group A. In group B biodiffusion rates was 0.06

562   cm^{-2} y^{-1} ± 0.04 SE (station AX/3). In group C biodiffusion ranged from 0 (station PS/32) to

563   0.76 cm^{-2} y^{-1} ± 0.71 SE (station AX/6). There was no biodiffusive transport in group D. There

564   were significant differences in biodiffusion among areas (Kruskal-Wallis test; $p<0.05$;

565   significant differences (post hoc test) between group A:D and C:D) (Fig. 6A). Non-local

566   transport rates ranged from 0.21 y^{-1} ± 0.20 SE (station AX/2) to 0.60 y^{-1} ± 0.23 SE (station

567   AX/1) in group A. In group B non-local transport rates was 2.12 y^{-1} ± 1 SE (station AX/3). In

568   group C non-local transport rates ranged from 0.75 y^{-1} ± 0.25 SE (station PS/32) to 2.08 y^{-1} ±

569   0.58 SE (station AX/6). In group D non-local transport rates ranged from 0.28 y^{-1} ± 0.04 SE

570   (station PS/31) to 0.68 y^{-1} ± 0.31 SE (station PS/19). There were significant differences in

571   non-local transport (Kruskal-Wallis test; $p<0.05$; significant differences (post hoc test)

572   between group A:C and C:D) (Fig. 6B). Biodiffusive transport values were significantly

573   related with depth, Sed C_{org} and BW C/N ratio Spearman correlation: -0.6, 0.6 and 0.6, p<0.05

574   respectively). Non-local transport values were significantly related to benthic taxa richness,

575   biomass, mud and Sed N_{tot} (Spearman correlation: 0.5, 0.5, 0.5 and 0.5 p<0.05 respectively)

576   (Table 8).

577

578   Fig. 6. Mean bioturbation coefficients: Db - biodiffusion (cm^{-2} y^{-1}) (A) and r – non-local (y^{-1})

579   (B); ± SE, n=no of cores (Table 1) at stations sampled in Van Mijenfjorden, Hornsund (group

580   A); Storfjorden (group B); Barents Sea shelf (group C); northern Barents Sea and Nansen

581   Basin (group D). Station ST/8 marked with * was sampled in summer season. Kruskal –

582   Wallis results for differences between sampling sites are given; significant test results are

583   marked with ** (p<0.05).

584   Table 8. Spearman's rank correlation analyses among biological and physical parameters. Significant values are marked in bold (p<0.05).

	No of taxa	Density	Biomass	Non-local (r)	Biodiffusion (Db)	Depth	Salinity	Temperature	Gravel	Sand	Mud	BW C_{org}	BW N_{tot}	BW $\delta^{13}C$	BW $\delta^{15}N$	BW C/N	Sed C_{org}	Sed N_{tot}	Sed $\delta^{13}C$	Sed $\delta^{15}N$	Sed C/N	SOM	Chl a	Chl a/Phaeo
No of taxa	-	**0.9**	**0.5**	**0.5**	0.0	-0.1	0.2	0.1	0.0	-0.1	**0.3**	-0.1	0.0	-0.1	-0.2	0.0	-0.2	**0.3**	**0.5**	-0.1	**-0.6**	0.1	**0.6**	0.2
Density	**0.9**	-	**0.5**	**0.4**	-0.1	-0.2	-0.1	0.0	0.0	-0.1	0.2	-0.1	0.1	-0.1	-0.2	-0.1	-0.2	0.1	0.3	-0.1	**-0.3**	0.1	**0.5**	**0.3**
Biomass	**0.5**	**0.5**	-	**0.5**	**0.4**	**-0.5**	-0.2	**-0.3**	-0.3	**-0.4**	**0.6**	**0.3**	0.0	0.2	**0.4**	**0.4**	**0.4**	**0.6**	0.2	-0.1	-0.1	**0.3**	**0.4**	0.3
Non-local (r)	**0.5**	**0.4**	**0.5**	-	0.3	-0.2	0.1	0.0	-0.1	**-0.4**	**0.5**	0.2	0.1	0.1	0.2	0.2	0.2	**0.5**	**0.4**	-0.1	**-0.3**	0.3	**0.4**	0.1
Biodiffusion (Db)	0.0	-0.1	**0.4**	0.3	-	**-0.6**	**-0.4**	**-0.3**	**-0.3**	0.0	0.2	0.2	-0.2	0.0	**0.5**	**0.6**	**0.6**	**0.4**	-0.2	0.2	**0.4**	**0.3**	0.0	0.0

585

586   *3.4. Storfjorden – seasonal changes*

587

588   Bottom water salinity was similar in spring and summer in Storfjorden, respectively

589   34.5 and 34.1. Bottom water temperature in spring season was -0.8 °C and increased to 4.5 °C

590   (Table 1). Benthic density decreased from 3625.3 ind./m^2 ± 83.9 SE in spring (AX/3) to

591   1812.7 ind./m^2 ± 229.7 SE in summer (ST/8). Biomass was similar in both seasons (172.3

592   g/m^2 ± 37.3 SE (spring, AX/3) and 152.1 g/m^2 ± 67.5 SE (summer, ST/8). Non-local transport

593   rates were similar in spring and summer (2.12 ± 1 and 2.09 ± 0.72 y^{-1} respectively) but

594   biodiffusion rates increased in summer (0.06 ± 0.04 in spring and 0.90 ± 0.90 cm^2 y^{-1} in

595   summer). Significant differences were found for the number of taxa and macrofauna density

596   between spring and summer seasons (Mann-Whitney U-test; Z= 2.3; p<0.05 and Z=2.4;

597   p<0.05, respectively).

598

599   **4. Discussion**

600

601   This is the first complex report on bioturbation activities in spring to summer

602   transition time conducted over the large area from Svalbard fjords and Barents Sea to deep

603   basin north off Svalbard. In our study, benthic community variables differentiated four

604   groups of stations, and this separation was to some extent echoed by the environmental

605   factors. The benthic community properties further affected the measured benthic activities i.e.

606   bioturbation rates.

607

608   4.1. *Benthic community characteristics across the sampled area*

609

36

610   The structure and composition of the benthic communities seemed to be grouped in

611 four groups of stations, however, the primary variables of the benthic community structure

612 (e.g., density, biomass) were highly variable within each station. One of the reasons could be

613 the high variability among replicates that covered only small area of sampled sediment.

614 Benthic species richness of the region was not well represented in the cores taken for the

615 experiments at each station due to their small sampling unit (~113 cm²). This may have

616 implications for the results generalization to the sampled areas due to high variability of

617 benthic density, biomass and consequently on the effects of these on the measured

618 bioturbation coefficients. However, we assume that we collected the most abundant taxa,

619 which would likely have the dominant role in mediating bioturbation effect. We have sampled

620 and identified the benthic organisms in each sediment core where the bioturbation

621 experiments were processed meaning that we know the organisms responsible of the

622 measured bioturbation activities.

623   The variability of the quality and quantity of sedimentary OM within each station

624 impacted benthic community structure. For instance, the lowest quality of SOM (C/N~18)

625 was found in sandy sediments of Van Mijenfjorden and Hornsund fjords, highlighting

626 dominance of refractory organic material within the group A. This probably explains the

627 lowest benthic densities and biomass at these stations. This can be the result of geographical

628 locations (e.g., water circulation restrictions) and glacial activity in Hornsund, related high

629 sedimentation rates and high terrestrial OM inputs disturbing benthic fauna (Drewnik et al.,

630 2016; Włodarska-Kowalczuk and Pearson, 2004). These two stations' communities were

631 mainly shaped by presence of polychaete *Polycirrus arcticus* and cumacean *Diastylis lucifera*,

632 and opportunistic cirratulids were among dominants.

633   A high, but variable, B/D ratio was found in Storfjorden (group B), which is the site of

634 a recurring polynya and has some of the highest productivity in the Barents Sea. The low

37

635   temperature, presence of a sea ice-edge bloom, very fine grained sediments (muds) indicating

636   low hydrodynamism, and high C_{org} and Chl a contents in sediments and in bottom waters

637   promote diverse and high biomass benthic communities with larger individuals burrowing and

638   feeding deeper (Winkelmann and Knies, 2005). High Chl a/Phaeo ratio and large quantities of

639   Chl a within sediments show also a more frequent input of fresh OM because of the presence

640   of the polynya (Haarpaintner et al., 2001; Vinje, 2001; Winkelman and Knies, 2005). This

641   community was also diverse, with high dominance of polychaetes (cirratulids, carnivore

642   *Lumbrineris* sp, and subsurface tube-building conveyor *Maldane sarsi*) and bivalves like

643   *Yoldia hyperborea* and *Nuculana radiata*. PCO indicated that samples collected in Storfjorden

644   were correlated with presence of bivalve *Ennucula tenuis* and polychaete *Apistobanchus*

645   *tulbergi*.

646   The group C, covering stations sampled over the Barents Sea shelf, was highly

647   variable in terms of community structure and various environmental factors. The southern

648   Barents Sea station (AX/6) was characterized by similar environmental conditions to the

649   Storfjorden resulting in the occurrence of fauna with similar characteristics but with a lower

650   biomass to density ratio. This station was dominated by tube-building conveyor polychaete

651   *Spiochaetopterus typicus* and *Heteromastus* sp. and bivalve *Macoma* sp. It was characterized

652   by high amount of SOM but low Chl a in the sediments, indicating late bloom/post bloom

653   conditions, where most of the fresh OM was already utilized by benthic organisms. Lower

654   Chl a/Phaeo ratio also indicates more degraded OM, possibly a result of intensive pelagic

655   grazing (Morata and Renaud, 2008). This is likely since this station is in the southernmost

656   location, therefore it was under the strong influence of Atlantic waters and was already in the

657   late-phase of the phytoplankton bloom (Krause et al., 2018). The other stations from this

658   group, located in the northern part of Barents Sea e.g. Erik Eriksen Strait, were characterized

659   by high share of sand but relatively fresh and abundant SOM, though low Chl a levels. This is

660 quite similar to stations north of Svalbard (PS/20 and PS/32), although the later was

661 characterized by higher amounts of Chl *a* present in the sediment related to the bloom in

662 progress at the time of sampling (Peeken, 2016). This group was characterized by highly

663 diverse communities (from 36 (AX/6) to 68 (PS/32) number of taxa), however most of them

664 belonged to either biodiffusors or conveyors.

665 The northern Barents Sea and Nansen Basin (group D) were differentiated from the

666 other groups by salinity, temperature, depth and occurrence of gravel. The species shaping

667 communities included polychaetes *Prionospio cirrifera* and *Notoproctus oculatus*. Stations in

668 group D were seasonally ice covered (including during sampling), and deeper than 400 m.

669 They were characterized by low amount of Sed C_{org} but presence of high OM quality in

670 bottom water layer, perhaps indicating recent sedimentation. They were characterized by

671 much lower benthic biomass and higher benthic density which were both decreasing with

672 increasing depth regardless the bloom stage. Decreasing quality and quantity of OM with

673 increasing depth, as it was observed in Nansen Basin, are often reflected in spatial variations

674 in benthic community structure (Carroll et al., 2008) and result in severe energy limitation for

675 deep-seafloor communities, dominated by small sized-individuals in high densities (Gage and

676 Tyler, 1991; Bergmann et al., 2009; Grebmeier et al., 1988; Renaud et al., 2008).

677 Long living Arctic benthic fauna reflects carbon export fluxes to the sea bottom but

678 changes are observed after several years or decades at deep stations (Grebmeier, 2012; Link et

679 al., 2013). Therefore, it is likely that the bloom stage and current OM delivery to the sea floor

680 did not directly influence the benthic community structure which is mainly dependent on the

681 integrated carbon input to the sediments and OM pool available in the sediment. However,

682 fresh OM arriving to the sea floor can trigger fast benthic response in terms of feeding and

683 related movement (Morata et al., 2015; Boetius et al., 2013), thus influence the community

684 functioning.

39

685

4.2. Bioturbation processes (sediment mixing)

687

688   Conducting experiments at the large depth gradient posts a challenge of working in

689 hyperbaric conditions. Although, Glud et al. (1994) showed that in situ measurements of

690 sediment oxygen demand/oxygen penetration depth were uniformly higher than deck

691 incubations, the relative differences among stations did not change with depth. Since other

692 published studies have also not incorporated hyperbaric chambers when estimating sediment

693 oxygen demand (Boetius et al., 2013), metabolism (Linke et al., 1995), and bioturbation

694 (Clough et al., 1997), our results, as the relative rates, remain comparable.

695   Both coefficients of bioturbation (non-local transport (r) and biodiffusion (Db) were

696 quantified in the stations of groups A, B and C where a higher diversity of bioturbation groups

697 was recorded among the dominant taxa (Table 4). Stations of the group D, on the contrary,

698 exhibited lower diversity of functional traits among the dominant taxa with the simultaneous

699 presence of two groups of sediment mixing (conveyors, biodiffusers) but where only non-

700 local transport was observed.

701   Species identity and differences in species characteristics, such as feeding mode and

702 typical burrowing depth, have been previously shown to influence the intensity of

703 bioturbation (Viitasalo-Frösén et al., 2009; Josefson et al., 2012; Näkki et al., 2017) and

704 functional diversity can be considered to have more impacts than taxonomic richness (Harvey

705 et al., 2012; Link et al., 2013). However, interpreting the bioturbation processes and the

706 assignment of the macrofaunal species to the correct functional group can be challenging.

707 Short-term experimental studies of sediment mixing provide just essential data for only few

708 species and results are hard to compare with longer time-scale processes in natural

709 ecosystems. Also, the same species can have different behavior and belong to another

40

710   sediment mixing groups across their ranges since species are known to be able to feed in

711   several different ways and change their feeding and mobility to exploit the food resources

712   available (Biles et al., 2002). Change in organism feeding behavior will also mean a change in

713   bioturbation which is reduced as a result of decreasing species diversity and community

714   biomass, as well as diversity of feeding and bioturbation groups (Mazik and Elliott, 2000). In

715   general, in our study, the high number of sub-surface deposit feeders, which feed at depth and

716   transport material to the surface can explain dominance of non-local mixing (Boudreau, 1997;

717   Gérino et al., 1998). Conveyors were actually omnipresent and the intensity of non-local

718   transport was variable between stations, and was increasing with increasing species richness,

719   density and biomass, but also with increasing percentage of mud presence and Chl *a* contents

720   (Table 8). Since non-local transport is non-continuous, it is usually difficult to link it directly

721   to benthic biomass (or biovolume) since some movements of particles do not depend only on

722   animal movements, but also on animal-independent effects (e.g., particles falling down into

723   the burrows, initial burrows construction). In our study, increasing benthic biomass generated

724   by high labile OM inputs, seems to have positive effects on the conveying activities and

725   consequently on the non-local transport rates.

726   In shallow fjords (Van Mijenfjorden and Hornsund, Group A), the benthic

727   communities were characterized by low bioturbation rates (non-local transport from $0.21 \pm$

728   0.20 to 0.60 ± 0.23 y^{-1} and biodiffusion from 0.04 ± 0.01 to 0.07 ± 0.03 cm^{-2} y^{-1}). This

729   similarity between the AX/1 and AX/2 stations of the group A can be explained by the

730   occurrence of a similar benthic community whose the species have the same functional traits

731   combination (i.e., feeding, mobility, burrowing depth, burrowing mode and sediment mixing

732   mode; Table 4) but present in low density and biomass. Biodiffusors (Cirratulidae; Gérino et

733   al., 1992, 2007), conveyors (*P. arcticus*) and gallery diffusors (*Lumbrineris* sp.; Petch, 1986),

41

734 both present in those fjords, were probably limited by the lack of fresh OM in the sediments at

735 the time of sampling.

736 Storfjorden (AX/3, group B), Erik Eriksen Strait (AX/4) and PS/20 (group C) had

737 similar measured bioturbation rates with high non-local transport and low biodiffusion, and

738 shared a high biomass contribution of bivalves and maldanid polychaetes. Yoldiids and

739 maldanids, burrowing deeper into the sediment, are known to be effective conveyors which

740 can either actively transfer sediment directly into deep layers from the surface, or into surface

741 layers from deeper layers of the sediments (Bender and Davis, 1984; Smith and Schafer,

742 1984), respectively. This can explain high non-local transport in these areas.

743 The southern Barents Sea, AX/6, group C, had higher but strongly spatially variable

744 Db and r by station within the group, with a relatively higher biomass and density of the

745 organisms (*Spiochaetopterus typicus* (conveyor, Smith and Shafer, 1984) dominating in the

746 density and *Astarte* sp. (biodiffusor, Queirós at al., 2013) dominating in the biomass. The

747 reason for that was most likely earlier occurrence of the phytoplankton bloom due to the lack

748 of sea ice, so at the time of the cruise, late spring/post-bloom conditions and abundant OM

749 activated rapidly benthic organisms.

750 All deeper and sea ice covered stations in group D, including sea ice covered PS/32

751 (group C), were dominated by biodiffusors and conveyors (Table 4). Those stations were

752 characterized by significant non-local transport and unmeasurable biodiffusion. This suggests

753 that the sediment transport mode by conveyors dominated in the sampled deeper areas

754 adapted to scarce fresh food availability despite the presence of biodiffusers. This implies a

755 very low activity by biodiffusers undetectable at the time scale of 10 days of experiment, or

756 an interfering of such activities with the conveyors species. Typically for communities living

757 in OM limited environments, these benthic communities were characterized by a low number

758 of species with low biomass. Giving the low bioturbation rates in the deeper stations, we

759 could actually suppose that time incubation with luminophores superior to 10 days could be

760 tested in the future experiments in order to insure a more complete transport of tracers

761 towards deep layers where the benthic community is less active. Since the bioturbation model

762 takes into account in its calculation this time duration, the final bioturbation coefficient is

763 however normalized to this time scale, signifying the similar relative comparison between

764 stations for our experiment remains valid. If we were able to detect measurable biodiffusive

765 coefficient for the deeper stations for a longer time scale, normalized to the same time unit,

766 the biodiffusion would be still low because of weak benthic infauna dynamic in such

767 environments. Our results are, however, similar to the patterns showed by Clough et al.

768 (1997) who noted low biodiffusive transport (0.01 to 0.11 $cm^{-2} y^{-1}$) by using radioactive tracer

769 for its deep portions in relationships to the lower benthic biomass due to lower fresh OM

770 inputs. They found, however, higher surficial sediment biological mixing rates than the

771 natural sedimentation rates in the Arctic deep sediments, highlighting the importance of

772 quantifying bioturbation in the Arctic Ocean taking into account its spatial variability. Also,

773 Soltwedel et al. (2019), using luminophores for experiments that lasted 2 and 4 years, found

774 low biodiffusion mixing rates at the Long-Term Ecological Research (LTER) observatory

775 HAUSGARTEN in Fram Strait (~ 0.2 $cm^{-2} y^{-1}$). They concluded that the meiofauna, and to a

776 certain extent megafauna, were the main bioturbators in the deep sea environments. Although,

777 only macrofauna (>500 µm) was identified and was presented as the main responsible of the

778 bioturbation activities in our study, meiofaunal activities may also explain some of the

779 patterns that could not be attributed to the changes in the environment or macrofaunal

780 communities in the deep sea stations. Since the model quantifies bioturbation coefficients of

781 the entire benthic community, it includes here also the meiofauna activities. Meiofauna is

782 actually known as the most abundant infauna (Heip et al., 1985; Vanreusel et al., 2010; Rosli

783 et al., 2016; own data) and as having impact on the bioturbation activities in the first few

43

784 centimeters of the sediment (Aller and Aller, 1992; Piot el al., 2014; Aschenbroich et al.,

785 2017; Mäkelä et al., 2018). Therefore, we suggest that also the smaller benthic fractions

786 should be identified in future studies on Arctic deep infaunal activity in order to find better

787 infauna variables for explaining the bioturbation measurements.

788

789 *4.3. Seasonal changes (Storfjorden station)*

790

791 The highest values of non-local transport were reported for Storfjorden and remained

792 stable during both spring and summer time. The biodiffusion coefficient measured in

793 Storfjorden during summer was about fifteen times higher compared to measurements

794 conducted during spring, probably because of the changes in species and functional groups

795 between the two seasons associated with the more labile OM reaching the seafloor in summer

796 (Chl a/Phaeo~52, Table 3). The dominant taxa in density were Cirratullidae (biodiffusor)

797 both during spring and summer (31.2 % and 11 %, respectively) and Lumbrineris sp. (gallery

798 diffusor) (14.1 % and 18.3 %, respectively) while in biomass, Yoldia hyperborea (convoyer)

799 dominated during both seasons (57.4 % and 30.5 %, respectively) (Table 4). Such changes,

800 i.e. replacement of one large specimen by another large specimen of different species, should

801 be rather accounted to spatial variability of benthic communities than due to seasonal change

802 in sampled communities. Also, species such as *Nereis diversicolor* or *M. balthica* are able to

803 change their feeding mode (suspensive-feeder versus deposit feeder) depending on

804 environmental conditions (De Goej and Luttikhuizen, 1998; Christensen et al., 2000). It is

805 also possible that taxa such as Cirratulidae, *Lumbrinereis*, *Yoldia* and *Nuculana* change their

806 feeding mode with increased OM input from the polynya during the summer just after the

807 spring bloom, as was observed in other ecosystems or experiments (e.g., Bender and Davis,

808 1984 for *Yoldia* spp; Rouse and Pleijel, 2001; Kędra et al., 2012 for Cirratulidae).

44

809   Benthic activities are related to the supply of OM to the seabed (Grassle and Grassle,

810   1994; Levin and Gooday, 2003; Blake et al., 2009) and biodiffusion intensity can be strongly

811   dependent on flux of fresh food from overlying waters (Gérino et al., 1998). In shallow

812   sediments of temperate areas, Duport et al. (2007) found the highest intensity of sediment

813   mixing (non-local and biodiffusion) during summer in the Thau Lagoon. Also Gérino et al.

814   (2007) found more rapid non-local transport in spring than in autumn in the Venice Lagoon.

815   Organic carbon supply generally increases when the PP starts in spring, and peaks with the

816   bloom and afterwards, over the summer. In the polar areas, Morata et al. (2015) found

817   minimum biodiffusive activity during the polar night, and high non-local transport after a

818   pulse of fresh food in experiments conducted in high Arctic fjord in Svalbard. This result

819   suggests that behavior of benthic species change with the OM input. Also, laboratory

820   experiments showed that macrofauna can react quickly to food input by increasing their

821   bioturbation activities (Nogaro et al., 2008). Furthermore, Dauwe et al. (1998) reported

822   maximum sediment mixing with medium food quality in the study comparing macrofaunal

823   benthic activity with contrasting food supply in the North Sea. They also showed that the

824   minimal mixing was observed at the station with high quality OM, and no mixing when low

825   quality OM was present. This can result from combination of physical and biochemical

826   factors influencing bioturbation, or changes in species behavior. The other possible

827   explanation is related to the oxygen conditions in different areas. Both North and Baltic Sea

828   are areas with high PP and eutrophication. Higher amounts of new OM reaching the sea floor

829   often result in low oxygen levels leading to anoxic conditions affecting faunal behavior or

830   even survival (Carstensen et al., 2014). Svalbard fjords and adjacent areas are largely oligo-

831   and meso- trophic, and well oxygenated regardless the time of the year and intensity of the

832   spring bloom deposition. We, thus, expect minimal negative impacts of OM deposition on

833 benthic communities. Our results from this limited seasonal comparison suggest that large

834 inputs of fresh OM to the seabed can trigger bioturbation activities.

835

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1292

1293   **Figures and tables:**

1294   List of tables:

1295   Table 1. Main characteristics of the sampling stations.

1296   Table 2. Bottom water (BW) characteristics for each sampling station: C_{org}, N_{tot}, $\delta^{13}C$, $\delta^{15}N$ (in

1297   %) and C/N values (mean ± SD, n=3).

1298   Table 3. Sediment variables for each sampling station: sediment type, C_{org}, N_{tot}, $\delta^{13}C$, $\delta^{15}N$,

1299   OM (in %), C/N, Chl a (µg DW g^{-1}) and Chl a/Phaeo values (mean ± SD, n=no of cores).

1300   Table 4. Functional traits, relative density and biomass of the three dominant taxa for each

1301   sampling station. Class: P – Polychaeta, B – Bivalvia, An – Anthozoa, As – Asteroidea, O –

1302   Ophiuroidea, S – Sipunculidea. Mobility and feeding groups (M/F) are marked by codes:

1303   mobility type (D - Discretely mobile, M – Mobile, S – Sessile) and feeding type (car -

1304   carnivore, omn - omnivore, sub - subsurface feeder, sur - surface feeder, sus - suspension

1305   feeder). Burrowing depth (BT): 1 – surface burrowing, 2 – subsurface burrowing, 3 – deep

1306   burrowing. Tubes (T): "+" – I-shaped tube, "-" – no tube. Sediment mixing types (SMix):

1307   biodiffusor (B), upward conveyor (UC), gallery diffusor (GD), downward conveyor (DC).

1308   Table 5. PERMANOVA results for the multivariate descriptors of benthic communities with

1309   significant pair-wise comparisons results for different groups.

1310   Table 6. SIMPER analysis B/D ratio faunal percentage contribution to the average similarity

1311   for different sampling stations groups. Species that contributed more than 5% are listed.

1312   Table 7. Results of DistLM procedure for fitting environmental variables to the macofauna

1313   community data. %Var - percentage of explained variance; %Cum - cumulative percentage

1314   explained by the added variable. Significance level $p < 0.05$. Environmental factors: D –

1315   depth, S – salinity, T – temperature, types of sediment (mud, sand, gravel), BW C_{org} – bottom

1316   water C_{org}, BW N_{tot} – bottom water N_{tot}, BW $\delta^{13}C$ – bottom water $\delta^{13}C$ BW, BW $\delta^{15}N$ –

1317   bottom water $\delta^{15}N$, BW C/N – bottom water C/N, Sed C_{org} – C_{org} concentration in sediment,

1318   Sed N_{tot} – sediment N_{tot}, Sed $\delta^{13}C$ – sediment $\delta^{13}C$, Sed $\delta^{15}N$ – sediment $\delta^{15}N$, Sed C/N –

1319   sediment C/N, SOM – sediment organic matter, Chl a – sediment Chlorophyll a and Chl

1320 a/Phaeo – sediment Phaeopigments.

1321   Table 8. Spearman's rank correlation analyses among biological and physical parameters.

1322   Significant values are marked in bold ($p < 0.05$).

1323

1324   List of figures:

1325   Fig. 1. Geographical location of the study region (A) and (B) sampling locations during two

1326   cruises (AX – ARCEx, PS – TRANSSIZ) with two major currents surrounding Svalbard:

1327   WSC - West Spitsbergen Current, warm Atlantic waters (black) and the ESC – East

1328   Spitsbergen Current, cold Arctic waters (gray) (after Svendsen et al., 2002).

1329   Fig. 2. Percentages of mobility and feeding groups at different sampling stations. Station ST/8

1330   marked with * was sampled in summer season. Functional traits codes: mobility type (D -

1331   Discretely mobile (yellow), M – Mobile (green), S – Sessile (blue)) and feeding type (car -

carnivore, omn - omnivore, sub - subsurface feeder, sur - surface feeder, sus - suspension feeder).

Fig. 3. PCO analysis for macrobenthic communities based on species biomass to density ratio, and the Bray-Curtis similarity among four sampling areas: A (Hornsund, Van Mijenfjorden); B (Storfjorden); C (Barents Sea shelf); D (northern Barents Sea and Nansen Basin). Significantly correlated species with the PCO coordinates (r>0. 5) are shown on the plot.

Fig. 4. Mean density (ind./m^{-2}) (A) and biomass (g/m^{-2}) (B); ± SE, n= no of cores (Table 1) at stations sampled in Van Mijenfjorden, Hornsund (group A); Storfjorden (group B); Barents Sea shelf (group C); northern Barents Sea and Nansen Basin (group D). Station ST/8 marked with * was sampled in summer season. Kruskal – Wallis results for differences between sampling sites are given; significant test results are marked with ** (p<0.05).

Fig. 5. Distance-based Redundancy Analysis (dbRDA) plot of the DistLM model visualizing the relationships between the environmental parameters and the biomass/density ratio of species between four sampling areas: A (Hornsund, Van Mijenfjorden); B (Storfjorden); C (Barents Sea shelf); D (northern Barents Sea and Nansen Basin). Environmental variables with Pearson rank correlations with dbRDA axes > 0.5 are shown. Environmental factors: D – depth, S – salinity, T – temperature, types of sediment (mud, sand, gravel), BW C$_{org}$ – bottom water C$_{org}$, BW N$_{tot}$ – bottom water N$_{tot}$, BW δ^{15}N – bottom water δ^{15}N, BW C/N – bottom water C/N, Sed C$_{org}$ – C$_{org}$ concentration in sediment, Sed δ^{13}C – sediment δ^{13}C, Sed C/N – sediment C/N, Chl a – sediment Chlorophyll a and Chl a/Phaeo – sediment Phaeopigments.

Fig. 6. Mean bioturbation coefficients: Db - biodiffusion (cm^{-2} y^{-1}) (A) and r – non-local (y^{-1}) (B); ± SE, n=no of cores (Table 1) at stations sampled in Van Mijenfjorden, Hornsund (group A); Storfjorden (group B); Barents Sea shelf (group C); northern Barents Sea and Nansen Basin (group D). Station ST/8 marked with * was sampled in summer season. Kruskal –

66

1356   Wallis results for differences between sampling sites are given; significant test results are

1357   marked with ** (p<0.05).

1358 Appendix 1. Spearman's rank correlation analyses among physical and biogeochemical variables. Significant values are marked in bold (p<0.05).

	Depth	Salinity	Temperature	Gravel	Sand	Mud	BW C_{org}	BW N_{tot}	BW $\delta^{13}C$	BW $\delta^{15}N$	BW C/N	Sed C_{org}	Sed N_{tot}	Sed $\delta^{13}C$	Sed $\delta^{15}N$	Sed C/N	SOM	Chl a	Chl a/Phaeo
Depth	-	**0.8**	**0.8**	**0.7**	-0.2	-0.0	-0.1	**0.3**	0.1	**-0.5**	**-0.6**	**-0.6**	**-0.3**	**0.4**	-0.2	**-0.5**	**-0.4**	-0.2	**-0.5**
Salinity	**0.8**	-	**0.7**	**0.3**	**-0.4**	**0.4**	0.2	**0.3**	-0.0	-0.3	**-0.3**	-0.2	0.3	**0.8**	-0.1	**-0.5**	0.1	0.2	**-0.3**
Temperature	**0.8**	**0.7**	-	**0.6**	-0.3	-0.0	-0.0	0.1	-0.2	-0.2	**-0.3**	**-0.3**	-0.2	**0.5**	0.0	-0.3	-0.2	-0.1	**-0.5**
Gravel	**0.7**	**0.3**	**0.6**	-	-0.2	-0.0	-0.1	0.2	**0.3**	**-0.5**	**-0.6**	**-0.7**	**-0.5**	-0.0	-0.3	**-0.5**	**-0.7**	**-0.4**	**-0.4**
Sand	-0.2	**-0.4**	-0.3	-0.2	-	**-0.9**	**-0.8**	**-0.7**	**-0.6**	-0.1	0.2	-0.2	**-0.5**	**-0.5**	0.5	0.2	-0.2	**-0.3**	0.0
Mud	-0.0	**0.4**	-0.0	-0.0	**-0.9**	-	**0.7**	**0.6**	**0.6**	0.2	0.0	**0.3**	**0.7**	**0.5**	**-0.4**	**-0.3**	**0.4**	**0.5**	0.1
BW C_{org}	-0.1	0.2	-0.0	-0.1	**-0.8**	**0.7**	-	**0.8**	**0.6**	0.1	-0.2	**0.4**	**0.4**	**0.4**	**-0.7**	0.2	0.3	**0.4**	**0.3**
BW N_{tot}	**0.3**	**0.3**	0.1	0.2	**-0.7**	**0.6**	**0.8**	-	**0.7**	**-0.4**	**-0.7**	-0.1	0.1	**0.4**	**-0.8**	-0.1	0.1	**0.4**	**0.4**
BW $\delta^{13}C$	0.1	-0.0	-0.2	**0.3**	**-0.6**	**0.6**	**0.6**	**0.7**	-	-0.1	**-0.4**	-0.1	0.1	-0.1	**-0.5**	-0.2	-0.1	0.0	0.1
BW $\delta^{15}N$	**-0.5**	-0.3	-0.2	**-0.5**	-0.1	0.2	0.1	**-0.4**	-0.1	-	**0.8**	**0.8**	**0.5**	-0.2	**0.5**	**0.5**	**0.5**	-0.2	**-0.3**
BW C/N	**-0.6**	**-0.3**	**-0.3**	**-0.6**	0.2	0.0	-0.2	**-0.7**	**-0.4**	**0.8**	-	**0.7**	**0.5**	-0.1	**0.6**	**0.3**	**0.4**	-0.0	-0.1
Sed C_{org}	**-0.6**	-0.2	**-0.3**	**-0.7**	-0.2	**0.3**	**0.4**	-0.1	-0.1	**0.8**	**0.7**	-	**0.7**	0.1	**0.3**	**0.6**	**0.8**	0.1	0.0
Sed N_{tot}	**-0.3**	0.3	-0.2	**-0.5**	**-0.5**	**0.7**	**0.4**	0.1	0.1	**0.5**	**0.5**	**0.7**	-	**0.5**	0.2	-0.1	**0.8**	**0.5**	0.0
Sed $\delta^{13}C$	**0.4**	**0.8**	**0.5**	-0.0	**-0.5**	**0.5**	**0.4**	**0.4**	-0.1	-0.2	-0.1	0.1	**0.5**	-	-0.2	**-0.5**	**0.3**	**0.7**	0.1
Sed $\delta^{15}N$	-0.2	-0.1	0.0	-0.3	**0.5**	**-0.4**	**-0.7**	**-0.8**	**-0.5**	**0.5**	**0.6**	**0.3**	0.2	-0.2	-	0.2	**0.3**	**-0.4**	**-0.6**
Sed C/N	**-0.5**	**-0.5**	-0.3	**-0.5**	0.2	**-0.3**	0.2	-0.1	-0.2	**0.5**	**0.3**	**0.6**	-0.1	**-0.5**	0.2	-	**0.3**	**-0.4**	0.0
SOM	**-0.4**	0.1	-0.2	**-0.7**	-0.2	**0.4**	0.3	0.1	-0.1	**0.5**	**0.4**	**0.8**	**0.8**	**0.3**	**0.3**	**0.3**	-	**0.3**	-0.0
Chl a	-0.2	0.2	-0.1	**-0.4**	**-0.3**	**0.5**	**0.4**	**0.4**	0.0	-0.2	-0.0	0.1	**0.5**	**0.7**	**-0.4**	**-0.4**	**0.3**	-	**0.7**
Chl a/Phaeo	**-0.5**	**-0.3**	**-0.5**	**-0.4**	0.0	0.1	**0.3**	**0.4**	0.1	**-0.3**	-0.1	0.0	0.0	0.1	**-0.6**	0.0	-0.0	**0.7**	-

1359

- This is the first complex report on bioturbation in spring to summer transition conducted over a large depth gradient in the Arctic Ocean.

- Benthic community structure and related biodiffusion and non-local transport varied in Svalbard fjords, Barents Sea and Nansen Basin.

- Changes in environmental conditions, and related changes in quality and quantity of available organic matter, had impact on benthic communities and bioturbation.

- Large inputs of fresh OM to the seabed can trigger bioturbation activities.