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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 sea floor (Maiti et al., 2010). The seasons strongly shape the OM fluxes to the sea floor in the Arctic marine ecosystems. Phytoplankton and ice algae are two principal sources of primary production (PP) in the Arctic Ocean with ice algae being the first food source available after polar night (Søreide et al., 2006, 2008; Leu et al., 2010). Although phytoplankton is quantitatively dominant, ice algal blooms tend to occur earlier in the seasonally ice-covered Arctic seas and may contribute up to 50–60% of total PP (Gosselin et al., 1997; McMinn et al., 2010; Fernandez-Mendez et al., 2015; Van Leeuwe et al., 2018). During the spring, PP is typically greater than zooplankton consumption and thus highest vertical carbon fluxes are recorded (Andreassen and Wassmann, 1998; Tamelander et al., 2006). Later in the season, the zooplankton grazing reduces the OM flux but also adds to it by producing fecal pellets, which helps phytoplankton sink rapidly to the sea bottom (Olli et al., 2002). In fjords and on the shelf, benthic communities can also be fueled by terrestrial OM carried by rivers and/or glaciers, mainly during summer (Bourgeois et al., 2016). Benthic organisms act as temporal couplers in the seasonal systems, since they can consume variable carbon sources over the different seasons (McMeans et al., 2015), therefore benthic communities reflect rather long term (months to years) water column production, while the benthic activities reflect short term (days to weeks) environmental conditions (Morata and Renaud, 2008).

Bioturbation occurs when an organism moves through the sediment, constructs and maintains burrows, and ingests and defecates. This process results in mixing of particles and solutes within the substratum (Kristensen et al., 2012), and alters sediment structure (e.g., grain size distribution; Montserrat et al., 2009), and production, mineralization and redistribution of OM (Kure and Forbes, 1997). Life habit, motility, and manner of feeding of infaunal species induce either random particle movement over a short distance (biodiffusion (Db) hereafter) (Gérino et al., 2007; Meysman et al., 2003) or biologically induced discontinuous particle transfer between the sediment surface and deeper sediment layers, for example via burrowing or feeding behavior (non-local transport (r) hereafter) (Boudreau, 1986; Meysman et al., 2003; Duport et al., 2007; Gogina et al., 2017). According to the mode of particle mixing, benthic organisms can be classified into five functional groups of sediment reworking which may include biodiffusion and/or non-local transport: biodiffusors, gallery-diffusors, upward- and downward-conveyors, and regenerators (François et al., 1997). The presence and intensity of these bioturbation modes are therefore mediated by fauna characteristics like biomass, density, burrowing depth or feeding behavior (François et al., 1999; Gérino et al., 1998; Sandnes et al., 2000; Gilbert et al., 2007; Michaud et al., 2005, 2006; Duport et al., 2007; Aschenbroich et al., 2017). In turn, species composition, nature and intensity of their effects on sediment mixing depends on temperature (Ouelette et al., 2004; Duport et al., 2007; Maire et al., 2007), food inputs (Nogaro et al., 2008) and sediment characteristics (Needham et al., 2011). Changes in species composition and activities, and therefore in bioturbation mode and/or intensity, are expected to influence biochemical processes near the sediment-water interface, including carbon cycling. Bioturbation rate can therefore be influenced by seasonal changes in PP in the above water column and deposited OM in the seafloor (food bank; Morata et al., 2015).

Only a few studies of bioturbation exist in the Arctic Ocean. Teal et al. (2008) created the database with global bioturbation intensity coefficient (Db) and layer depth (L), where they showed that the Arctic, Central Pacific and most tropical regions are missing bioturbation data. In polar regions, it has been shown that sediment mixing rates were higher through biological transports in the shallow sediments directly impacted by the OM input along the marginal ice covered area of the Barents Sea (Maiti et al., 2010) and in the Svalbard fjords (Konovalov et al., 2010). On the contrary, the deep sediments of the Arctic Ocean were marked by lower sediment mixing rates in relation to a lower benthic biomass correlated with lower OM inputs (Clough et al., 1997). Soltwedel et al. (2019), however, did not confirm a higher bioturbation activity in the high productive Marginal Ice Zone (MIZ) in Fram Strait compared to the less productive ice zone. Seasonal aspects of bioturbation in the Arctic were preliminarily studied by Morata et al. (2015), whose experiments showed that the bioturbation activity was positively correlated with fresh food input during the polar night. McClintic et al. (2008) found no seasonal variation in bioturbation intensity during June and October in West Antarctic continental shelf which suggests that deposit feeders are able to access food particles accumulated during high PP periods. Still, our knowledge on benthic communities responsible for bioturbation processes and their relation to OM inputs in the Arctic Ocean and adjacent shelves remains limited, particularly during the spring bloom.

The main aim of this study was to understand the impacts of differences in environmental conditions on benthic communities and their bioturbation function during the spring to summer transition. We focused on the Svalbard area where fjords, shelf and deep Nansen Basin differ considerably in terms of physical forcing affecting the quality and quantity of the OM inputs to the seafloor. Sediment reworking rates were quantified in relation to taxonomic and functional composition of the benthic macrofaunal communities, and in relation to the environmental variables. This work is the first study on bioturbation processes conducted in the Arctic Ocean during spring to summer transition time over a large depth gradient. It will contribute to our understanding of response of macrofauna and their activity to the quality and quantity of OM in the Arctic seabed.

2. Material and methods

2.1. Study area

Sampling was conducted in the Svalbard Archipelago, the Barents Sea and deep Nansen Basin north of Svalbard (Fig. 1, Table 1). This area is highly influenced by cold Arctic Water coming from the north and warm Atlantic Waters coming from the south, and the relative influence of those two water masses varies largely in the study area.

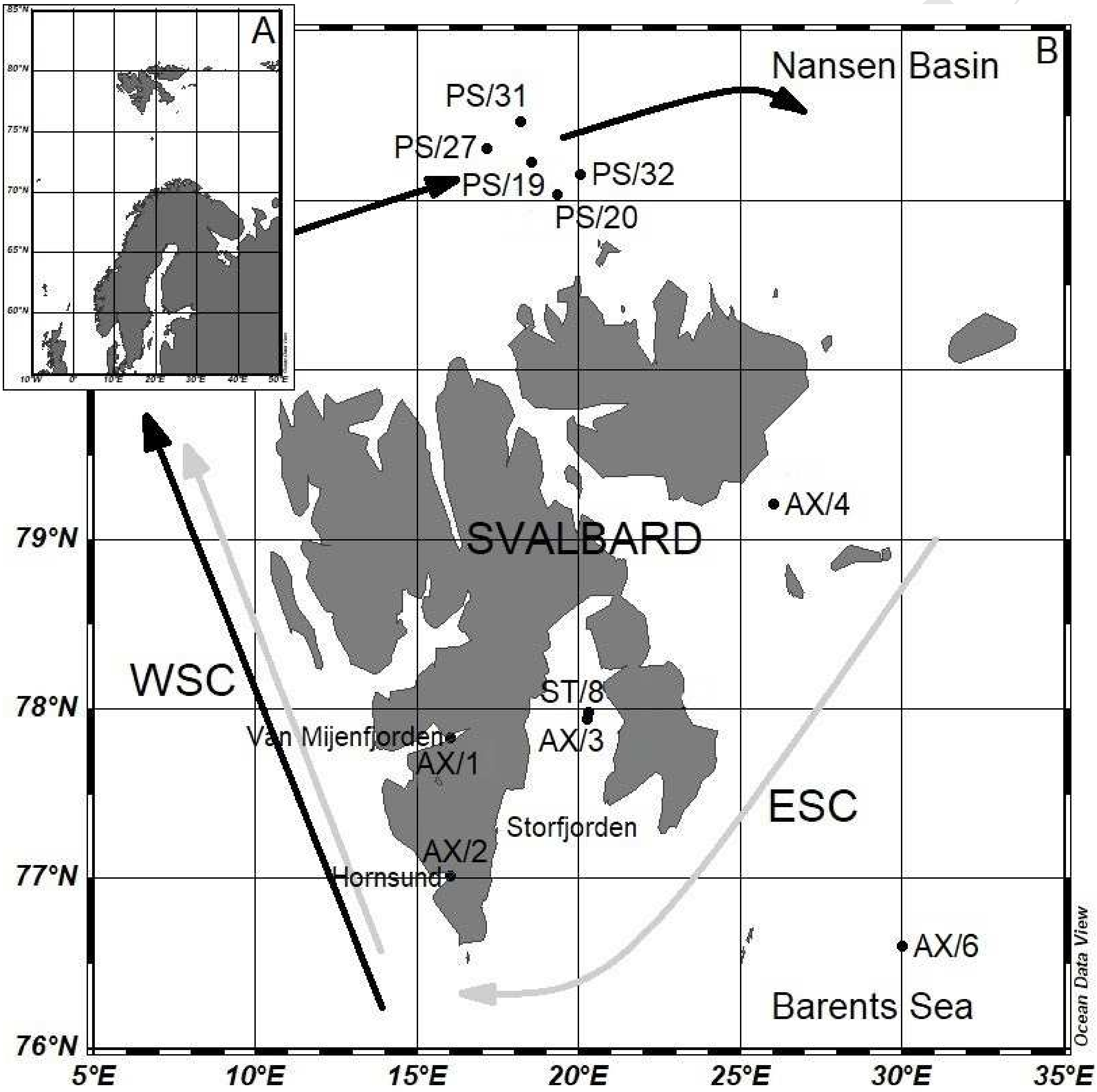

Fig. 1. Geographical location of the study region (A) and (B) sampling locations during two cruises (AX – ARCEx, PS – TRANSSIZ) with two major currents surrounding Svalbard:

WSC - West Spitsbergen Current, warm Atlantic waters (black) and the ESC – East Spitsbergen Current, cold Arctic waters (gray) (after Svendsen et al., 2002).

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

Van Mijenfjorden and Hornsund are located on the west coast of Spitsbergen, Svalbard. Van Mijenfjorden is a small fjord, nearly closed by an island at its mouth. It is separated into two basins: the outer (115 m depth) and inner (74 m depth), and by 45 m deep sill that restricts exchange of water between the fjord and the coastal waters (Skarđhamar and Svendsen, 2010). Hornsund is a large open glacial fjord with eight major tidal glaciers located in the central and inner parts and large terrestrial inflow (Błaszczyk et al., 2013; Drewnik et al., 2016). The average depth is 90 m with a maximum of 260 m (Kędra et al., 2013). Strong gradients in sedimentation, PP and benthic fauna occur along the increasing distance to the glaciers (Włodarska-Kowalczuk et al., 2013). These high latitude fjords are productive systems, where PP starts in early spring and continue to late autumn (Fetzer et al., 2002). The annual PP reaches up to 216 g C m^{-2} y^{-1} in Hornsund (Smoła et al., 2017). The Barents Sea is a shelf sea with water depths ranging from 35 m in the Svalbard Bank to up to 400 m or more in deep depressions and proximal canyon boundaries (Cochrane et al., 2012). The southern part of the Barents Sea is relatively warm and ice free while its northern parts are seasonally ice covered, with maximum ice coverage from March to April and minimum ice coverage generally occurring in September (Vinje, 2009; Ozhigin et al., 2011; Jørgensen et al., 2015). It is one of the most productive areas in the Arctic Ocean with average PP about 100 g C m^{-2} y^{-1} and maximum PP reaching over 300 g C m^{-2} y^{-1} on shallow banks (Sakshaug, 2004). Storfjorden is located east of Spitsbergen and has a maximum depth of 190 m (Skogseth et al., 2005). A polynya appears regularly in Storfjorden. It is a very productive area of the Barents Sea, and its productivity is correlated with the duration of the seasonal sea cover (Winkelmann and Knies, 2005). In Storfjorden the production of marine organic carbon may exceed 300 mg C cm^{-2} kyr^{-1}, while the production of total organic carbon (TOC) may exceed 500 mg C cm^{-2} kyr^{-1} (Pathirana et al., 2013; Rasmussen and Thomsen, 2014). Nansen Basin, with a maximum depth of 4000 m, is part of the Eurasian basin of the Arctic Ocean. In general, annual gross PP is within the range of 5–30 g C m^{-2} (Codispoti et al., 2013).

2.2. Sampling

Benthic sampling was conducted during spring cruises of R/V Polarstern PS92 – TRANSSIZ in May and June 2015, and R/V Helmer Hanssen – ARCEx in May 2016 (Table 1). Samples were collected at 10 stations located along the depth gradient, from Svalbard fjord (depth: 59 – 121 m), through the Barents shelf and slope (from 170 to 842 m) to the deep Nansen Basin (max. depth: 1656 m) (Fig. 1). Almost all stations north of Svalbard (P32, PS/19, PS/27 and PS/31) were sea ice covered during sampling, except PS/20 station. One station in Storfjorden (AX/3) was revisited in July 2016 during the cruise of R/V L'Atalante – STeP 2016 (ST/8).

At each station the bottom water temperature and salinity were determined by the shipboard Conductivity Temperature Density (CTD) rosette. Bottom-water samples were collected using Niskin bottles attached to a CTD and were filtered on pre-combusted Whatman GF/F glass microfiber filters in triplicate and frozen at -20 °C for later analyses of bottom water organic carbon (BW C_{org}), total nitrogen (BW N_{tot}), δ^{13}C (BW δ^{13}C), δ^{15}N (BW δ^{15}N), and C/N ratio (BW C/N).

Sediment samples were collected with a box corer of 0.25 m^2 sampling area. The overlying water from box corer was gently removed from sediment surface and push-cores samples (12 cm Ø and 20 cm deep, 113.0940 cm^2 surface layer) were collected. The top 2 cm sediment of the core was sampled for biogeochemical variables (grain size, chlorophyll *a* (Chl *a*) and phaeopigments (Phaeo), organic matter (SOM), organic carbon (Sed C_{org}) and total nitrogen (Sed N_{tot})). Samples were frozen in -20 °C and transported to the laboratory for analysis.

Additional sediment cores were taken from the box corer for bioturbation experiments following procedures described by Morata et al. (2015). Sediment cores (3 to 5 per station, Table 1) were kept in dark cold room on board (i.e., temperature at 2 °C, the average between -0.8°C and 4.5°C being the range of temperatures observed in the bottom waters, Table 1).

Fluorescent luminophores (5 g; 90–120 μm diameter) were homogeneously added to the overlying water and gradually spread on the sediment surface of each core without disturbing the resident infauna. Cores were then filled with bottom water and aerated by bubbling to keep the overlying water saturated with oxygen. Overlying water was renewed every four days. Sediment cores were incubated in those conditions for 10 days which is the minimum time to enable the characterization of the different transport modes. Incubation time that exceeds 15 days increases the probability of complete homogenization of the sedimentary column, and may thus prevent the differentiation of transport modes (François et al., 1997). This choice of 10 days for duration of experiment was a compromise between the response that we were expecting from the benthic communities and the available time on board to process the experiments.

After this time of incubation in stable conditions the surface water was carefully removed and cores were sliced horizontally in 0.5 cm layers from 0 to 2 cm depth, and in 1 cm layers between 2 and 10 cm depth. In total, 12 samples were taken, and each sediment layer was homogenized. A subsample of each sediment layer was directly frozen (-20 °C) and used for bioturbation analyses. The remaining sediment of each core samples were sieved onboard through 0.5 mm sieve for benthic community structure analysis, and fixed with 10 % buffered formaldehyde.

2.3. Biogeochemical environmental analyses

Sediments for grain size analysis were freeze-dried at -70 °C, homogenized and dry sieved into coarse-grained fractions (>0.250 mm) and fine-grained (<0.250 mm). For the fine fraction, analyses were performed using a Malvern Mastersizer 2000 laser particle analyzer and presented as volume percent. Mean grain size parameters were calculated using the geometric method of moments in the program GRADISTAT 8.0 (Blott and Pye, 2001).

Pigment concentrations were analyzed fluorometrically following methods described in Holm-Hansen et al. (1965) to determine Chl *a* and Phaeo concentrations. About 1 g of dried sediment was extracted with 10 ml of 90 % acetone at 4 °C in the dark. After 24 h, sediment was then centrifuged (3000 rpm for 2 min), and analysed using a Turner Designs AU-10 fluorometer before and after acidification with 100 µl 0.3 M HCl.

For sediment and bottom water biogeochemical parameters analyses, sediments and filters were dried, homogenized and weighed into silver capsules. For sediment and bottom water $\delta^{13}C$ and $\delta^{15}N$, C_{org} and N_{tot} analyses, samples were acidified with 2 M HCl to remove inorganic carbon and dried at 60 °C for 24 h. The analyses were performed on an Elemental Analyzer Flash EA 1112 Series combined with an Isotopic Ratio Mass Spectrometer IRMS Delta V Advantage (Thermo Electron Corp., Germany). SOM content was measured as loss on ignition at 450°C for 4 h (Zaborska et al., 2006). Sed C_{org} content was measured following the method of Kennedy et al. (2005). About 10 mg of dried sediment was acidified with 50 µl of 1 N HCl three times. Analyses were run on a Thermo Quest Flash EA 1112 CHN analyzer.

2.4. Benthic community analysis

In the laboratory, macrofaunal organisms were picked from sediments under a binocular microscope and identified to the lowest possible taxonomic level. Each taxon was counted, weighed (g wet weight) and transferred to 70 % ethanol. Mobility and feeding (WoRMS Editorial Board, 2019), and burrowing behavior (for references see Table 4) were attributed to each taxon. Benthic fauna was classified into five bioturbation functional groups based on the type of the sediment mixing: biodiffusors, gallery-diffusors, upward- or downward-conveyors, and regenerators. Biodiffusors move particles in a random manner in short distances (Gérino, 1992). Gallery-diffusors transport material from the surface sediment layer to deeper by constructing tubes or tunnels system (François et al., 2002). Upward-conveyors transport material from depth to the sediment surface and downward-conveyors transport sediment non-locally to deeper layers (Fisher et al., 1980; Knaust and Bromley, 2012). Regenerators create a biodiffusion-like process, with large amounts of sediment transported out of the reworked zone with a strong input to the overlying water column, as well as passive downward transport of surface sediment to the bottom of the burrow after burrow abandonment (Gardner et al., 1987; Knaust and Bromley, 2012). Organism density and biomass were evaluated per taxon, trophic and bioturbation functional group, and in total for each sediment core, and subsequently converted per 1 m^{-2} (area) in order to provide relevant surface values. The biomass to density (B/D) ratio was calculated per core as a proxy of the mean organism size.

2.5. Bioturbation analyses

After the sediment cores were sliced, part of the sediment from each sediment layer was freeze-dried at -70 °C, and homogenized with a mortar and pestle. Three replicates of 0.2 g sediment from each layer were taken and placed on a black box (9.5 cm x 7 cm) under a constant UV light source (350 ± 370 nm, Tube UV BLB G5T5 6 W). Images were taken with a digital camera (Nikon digital captor 2.342.016 pixels) with 28 µm per pixel resolution from a constant 12 cm from the sediment sample to assure identical acquisition conditions for all images (aperture time 1 s; diaphragm aperture f/13, ISO 200). Images were saved in red-green-blue (RGB) colour in jpeg format. The images were analysed using an image processing toolbox (@mathworks) in order to differentiate luminophores from the background sediment by using an appropriate set of RGB threshold levels (Michaud, 2006). Finally, the particle size appropriate for each luminophore was selected (6 pixels × 6 pixels for the smallest luminophores), and the pictures were corrected (cleaned) by removing the particle sizes smaller and larger than the actual size of the specific luminophore (90–120 µm). The sum of areas (in pixels) of the remaining objects and the number of objects (i.e., luminophores) were calculated for each picture and averaged between the three pictures from each sediment layer. Finally, with these abundances for all sediment depths for each core, the results were computed as the percentage of detected pixels per depth according to the total number of pixels detected per core thus representing the luminophores distribution over depth for each sediment core.

The reaction diffusion type model used in this paper to describe luminophore redistribution following macrofaunal reworking is based on the general diagenetic equation (Berner,1980):

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

where Q is the quantity of the tracer (e.g., luminophores), t is the time, z is the depth, Db is the apparent biodiffusion coefficient, and r(Q) is the non-continuous displacement of tracer. The term r(Q) is defined as follows:

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

where z_1 and z_2 define the upper and lower limits of the tracer redistribution, x and z are depth variables and r is the biotransport coefficient that is the percentage of tracer that left the $[0; x_1]$ deposit and was redistributed in the $[z_1; z_2]$ layer. The redistribution of tracer between z_1 and z_2 and the disappearance of tracer from the 0-z_1 layer are, respectively, described by Eqs. (2a) and (2b). Eq. (2c) indicates that no tracer movement occurs below z_2.

This displacement term was originally exemplified in a model describing gallery-diffusion of macrofaunal reworking (François et al., 2002). This biological reworking process describes the diffusive-like mixing of particles in the region of intense burrowing activity and the rapid transport of organic and inorganic material from the upper sediment layers to the lower regions of reworking (i.e. ‘biotransport’ or “non-local transport”).

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

$$Q\,(z,0) = \begin{cases} Q_0 \; if \; z \in [x_1; x_2[\\ 0 \; else \end{cases} \tag{3}$$

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

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

The application of this bioturbation model to tracer redistributions, initially started by François et al. (1997, 2001) and later revised by Duport al., (2007), allowed the quantification of two particle mixing coefficients: an apparent biodiffusion coefficient Db and a biotransport coefficient r. The biodiffusion coefficient Db takes into account the diffusion-like transport due to the activity of the organisms. We assume that the actual concentration dependent diffusion of tracers is negligible. The biotransport coefficient (r) represents a non-local mixing pattern associated with a biologically induced transfer of particles from one place to another in a discontinuous pattern (i.e. a non-continuous transport; Boudreau, 1986; Meysman et al., 2003). Estimates of the parameters Db and r were finally obtained by minimizing a weighted sum of squared differences between observed and calculated tracer concentrations (François et al., 1999, 2002). For each core, many adjustments between the observed and modelled profiles are necessary in order to find the minimum weighted sum of squared differences.

This model was used with MatLab (@mathworks), thus it gives qualitative data (i.e., kind of sediment mixing) and quantitative data (intensity of the sediment mixing) on the sediment mixing function for the entire benthic community at the sediment-water interface.

2.6. Statistical analysis

Bray-Curtis similarity matrix, based on square-root transformed data was used for the multivariate analysis of the macrobenthic community. Principal coordinate analysis (PCO) was conducted to explore multivariate variability among different sampling stations based on the (B/D) ratio community composition data matrix. Pearson rank correlation (>0.5) vectors of species B/D with axes were overlaid on the PCO plots to visualize the relationships between ordination axes and the directions and degrees of variability in the biological variables. Differences in species composition in samples among the groups of stations were explored using non-parametric multivariate methods applied to Bray-Curtis dissimilarity matrix calculated from biomass/density ratio (B/D) (one-way PERMANOVA). Whenever the significant effect of factor was detected by the main PERMANOVA test, pair-wise tests for differences between levels of each significant factor was performed. SIMPER procedure (similarity percentage species contribution) was used to discriminate species responsible for the differences between sites. In all models, a forward-selection procedure was used to determine the best combination of predictor variables for explaining the variations in macrofauna assemblages. The selection criteria chosen for the best-fitting relationship were based on R^2 values (Anderson et al. 2008). A distance-based linear model (DistLM) was used to analyse and model the relationships between the macrofaunal community structure and the environmental factors. A distance-based redundancy analysis (dbRDA) was used to visualize the variability along the two axes that best discriminated groups of samples defined by a priori assigned groups. Superimposed vectors corresponded to Pearson's correlations (>0.5) of environmental factors with the dbRDA axes. Calculations of the pseudo-F and p values were based on 999 permutations of the residuals under a reduced model. The significance level for all the statistical tests was $p = 0.05$.

The normality of environmental factors and biological factors (non-local and biodiffusion coefficients, benthic density and biomass) was verified with use of Shapiro-Wilk test ($p<0.05$). Since data did not have a normal distribution, Spearman correlations were calculated to estimate the relationships between faunal community characteristics (Table 8) and environment (Appendix 1). Differences in benthic density, biomass, non-local and biodiffusion coefficient were evaluated with the use of the nonparametric Kruskal-Wallis test, and the Dunn's post-hoc multiple comparison test was applied to identify the differences among stations groups. Station ST/8, sampled in July, was excluded from those analyses due to lack of environmental information and because it was sampled during a different season than the other stations. Additionally, a non-parametric pairwise Mann-Whitney U-test was performed to compare differences between the spring and summer season in Storfjorden (AX/3 vs ST/8). All analyses were performed using the PRIMER package v. 7 Clarke and Gorley, 2006; Anderson et al., 2008) and the Statsoft software STATISTICA v. 9.

3. Results

3.1. Environmental patterns

Bottom water salinity ranged from 34.5 to 35.1 and bottom water temperature ranged from -0.8 °C to 2.5 °C during our sampling. The lowest BW C_{org} concentrations were measured in Erik Eriksen Strait (AX/4; 0.1 ± 0.1 %) and the highest in Storfjorden (AX/3; 0.6 ± 0.0 %). The BW $\delta^{13}C$ values ranged from -27.7‰ on the slope north of Svalbard (PS/32) to -22.2 ‰ in Storfjorden. The lowest BW C/N ratio values were found at the deepest station (PS/31: 6.1 ± 0.0) and the highest values were measured in the southern Barents Sea (AX/6: 10.3 ± 1.2) (Table 2). Sandy and muddy sediments dominated in the study area. The lowest SOM concentrations were measured at station PS/32, on slope (2.6% ± 0.1) and the highest in Storfjorden (AX/3; 6.5% ± 0.3). The most depleted sediment $\delta^{13}C$ values occurred in fjords (AX/1: -24.2‰ and AX/2: -25.4‰) while the most enriched values were found on southern Barents Sea shelf (AX/6: -22.2‰). The lowest Sed C/N ratio values were found in deep basin (PS/27: 7.8 ± 0.4) and the highest value occurred in Van Mijenfjorden (AX/1: 18.7 ± 0.5) (Table 3).

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

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 values (mean ± 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

3.2. Macrobenthic community structure

In total, 186 taxa were identified. The number of taxa per station ranged from 9 (AX/2) to 68 (PS/32) (Table 4). Four burrowing and four sediment-mixing types were recorded. Sub-surface burrowing, Cirratulidae (biodiffusor) and *Lumbrineris* sp. (gallery diffusor) dominated in Svalbard fjords in biomass and density, and in Storfjorden in density. The deep burrowing *Yoldia hyperborea* (conveyor) dominated in biomass at AX/3. Two biodiffusors, the tube building polychaete *Myriochele heeri* and the deep burrowing bivalve *Astarte borealis* dominated in Erik Eriksen station (AX/4) in density and biomass respectively. The tube building *Spiochaetopterus typicus* (conveyor) dominated in terms of density and was second dominant in biomass in the Southern Barents Sea (AX/6). The sea star *Ctenodiscus* sp. dominated in biomass at this station. The tube building polychaete, *Maldane glebifex*, dominated in both density and biomass at the shelf station PS/20. Deep burrowing bivalves (*Yoldiella lenticula*, *Yoldia hyperborea*) dominated in density at PS/32 while the tube building polychaete *Galathowenia oculata* dominated in biomass. Burrow-building taxa were mostly biodiffusors and dominated at all shallow stations. Deep burrowing and tube building taxa were mostly conveyor bioturbators and dominated at deeper stations (Table 4). Fourteen mobility-feeding groups were recorded, and sessile and mobile macrofauna dominated at all stations except from the deepest one (PS/31) where discretely mobile fauna dominated. The lowest number of functional groups was found in Hornsund (AX/2) where 4 groups (sessile surface feeders, discretely subsurface feeders, mobile omnivore and mobile subsurface feeders) occurred. Sessile subsurface feeders dominated at PS/20 (30%) and PS/27 (33%). Sessile surface feeders were predominant in fjords (AX/1: 52% ; AX/2: 80%), Storfjorden (AX/3: 35%), in the southern Barents Sea (AX/6: 45%) and on slope (PS/19: 18%). The share of discretely mobile fauna increased with depth, and discretely mobile surface feeders dominated in the Nansen Basin (PS/31: 44%). The highest number of mobile subsurface feeders was found on the shelf (PS/32: 23%). The number of mobile taxa was similar for all stations. The mobile surface fauna dominated in Erik Eriksen Strait (AX/4: 25%) (Fig. 2).

Table 4. Functional traits, relative density and biomass of the three dominant taxa for each sampling station. Class: P – Polychaeta, B – Bivalvia, An – Anthozoa, As – Asteroidea, O – Ophiuroidea, S – Sipunculidea. Mobility and feeding groups (M/F) are marked by codes: mobility type (D - Discretely mobile, M – Mobile, S – Sessile) and feeding type (car - carnivore, omn - omnivore, sub - subsurface feeder, sur - surface feeder, sus - suspension feeder). Burrowing depth (BT): 1 – surface burrowing, 2 – subsurface burrowing, 3 – deep burrowing. Tubes (T): "+" – I-shaped 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

		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

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

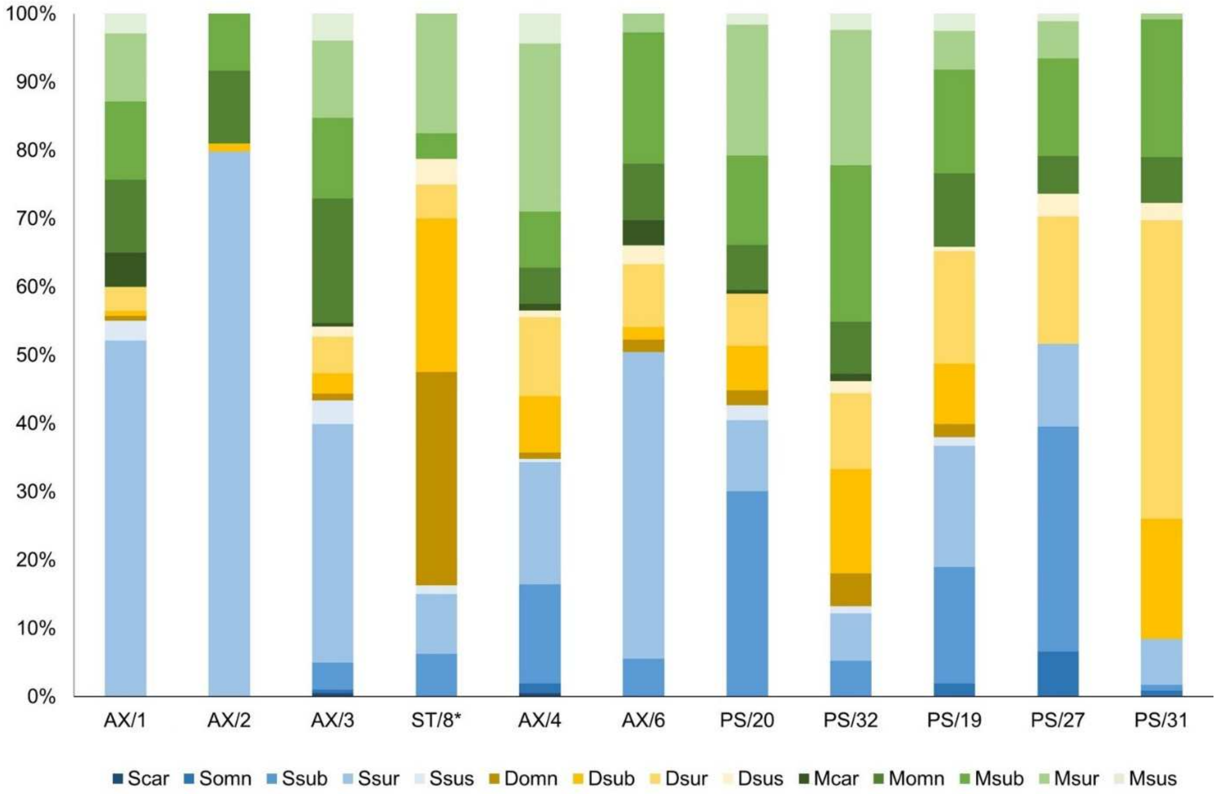

Fig. 2. Percentages of mobility and feeding groups at different sampling stations. Station ST/8 marked with * was sampled in summer season. Functional traits codes: mobility type (D - Discretely mobile (yellow), M – Mobile (green), S – Sessile (blue)) and feeding type (car - carnivore, omn - omnivore,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

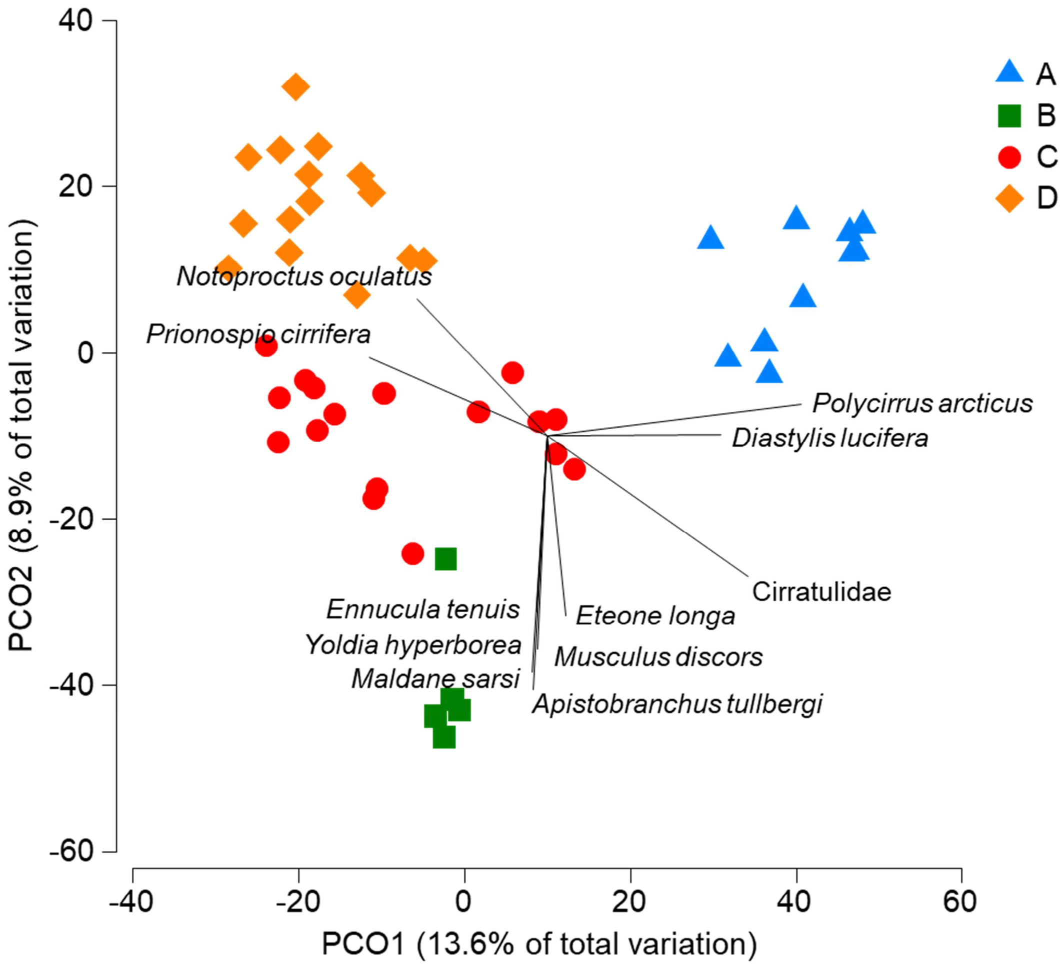

Fig. 3. PCO analysis for macrobenthic communities based on species biomass to density ratio, and the Bray-Curtis similarity among four sampling areas: A (Hornsund, Van Mijenfjorden); B (Storfjorden); C (Barents Sea shelf); D (northern Barents Sea and Nansen Basin). Significantly correlated species with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

Polychaeta dominated at all stations. There were significant differences in density (Kruskal-Wallis test; $p<0.05$; significant differences (post hoc test) between group A:B, A:C and C:D) (Fig. 4A). Benthic density ranged from 1485.5 ind./m^2 ± 168.7 standard error (SE) (station AX/2) to 2475.8 ind./m^2 ± 369.9 SE (station AX/1) in group A. In group B benthic density was 3625.3 ind./m^2 ± 83.9 SE (station AX/3). In group C density ranged from 1927.6 ind./m^2 ± 196.5 SE (station AX/6) to 6388.5 ind./m^2 ± 399.3 SE (station PS/32). In group D density ranged from 1609.3 ind./m^2 ± 295.1 SE (station PS/27) to 2794.1 ind./m^2 ± 404.8 SE (station PS/19). There were significant differences in biomass among areas (Kruskal-Wallis test; $p<0.05$; significant differences (post hoc test) between group A:B, B:D and C:D) (Fig. 4B). Benthic biomass ranged from 2.6 g wet weight/m^2 ± 0.5 SE (station AX/2) to 37 g wet weight/m^2 ± 18.4 SE (station AX/1) in group A. In group B benthic biomass was 172.3 g wet weight/m^2 ± 37.3 SE (station AX/3). In group C biomass ranged from 7.8 g wet weight/m^2 ± 1.1 SE (station PS/32) to 112.9 g wet weight/m^2 ± 61.3 SE (station AX/4). In group D biomass 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 (station PS/27).

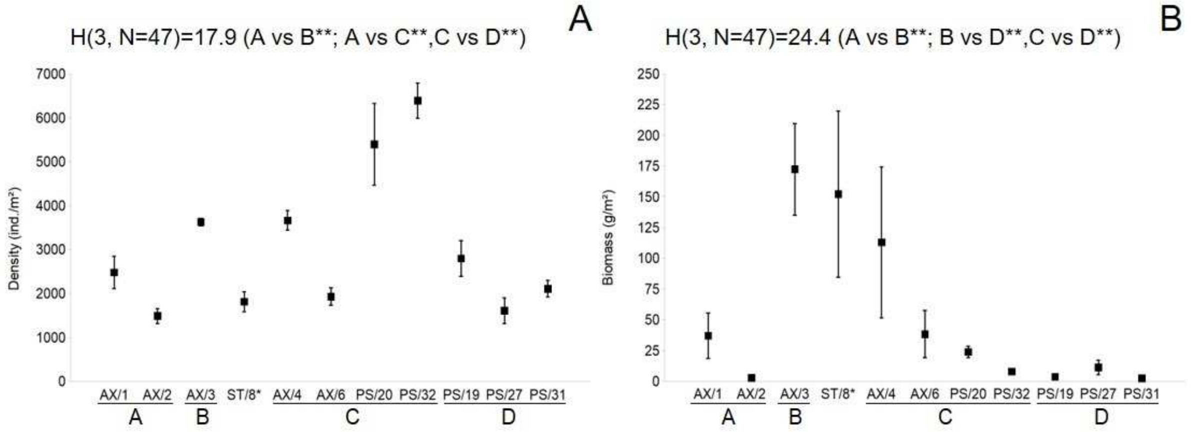

Fig. 4. Mean density (ind./m^{-2}) (A) and biomass (g/m^{-2}) (B); ± SE, n= no of cores (Table 1) at stations sampled in Van Mijenfjorden, Hornsund (group A); Storfjorden (group B); Barents Sea shelf (group C); northern Barents Sea and Nansen Basin (group D). Station ST/8 marked

with * was sampled in summer season. Kruskal – Wallis results for differences between sampling sites are given; significant test results are marked with ** ($p<0.05$).

There were significant differences in the benthic communities structure (biomass/density ratio) among different locations (PERMANOVA test Pseudo-F : 5.07, p=0.001). Significant differences were found for each group (significant pairwise comparisons p=0.001); see Table 5 for details.

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

Benthic taxa that contributed mostly to the groups similarities were: *Polycirrus arcticus* (44.7 %) in fjords (A), *Yoldia hyperborea* (31.7 %) in Storfjorden (B), *Spiochaetopterus typicus* (16.8 %) in the Barents Sea shelf (C) and *Nephasoma diaphanes diaphanes* (16 %) in the northern Barents Sea and Nansen Basin (D) as revealed by SIMPER analysis (Table 6).

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

The results of DistLM analyses showed that salinity explained 10.1% of the variation observed in the macrofauna community while Sed $\delta^{13}C$ (10%) and Sed C/N (9.3%) were next main contributors. Nine variables were included by the DistLM procedure to construct the best fitting model, together explaining 46.8% of total variation. However, one of the variables was not statistically significant (gravel) (Table 7). The most important parameter contributing to the first axis of the dbRDA plot was Sed C/N and explained 17.2% of fitted variation. It also positively correlated with fjords' group (A). The most important parameter contributing to the second axis was sediment Chl *a* and explained 25.7% of fitted flux variation. It was positively correlated with Storfjords group (B) and most stations in group C (shelf) (Fig. 5).

Table 7. Results of DistLM procedure for fitting environmental variables to the macofauna community data. %Var - percentage of explained variance; %Cum - cumulative percentage explained by the added variable. Significance level $p < 0.05$. 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 $\delta^{13}C$ – bottom water $\delta^{13}C$ BW, BW $\delta^{15}N$ –

bottom water δ^{15}N, BW C/N – bottom water C/N, Sed C_{org} – C_{org} concentration in sediment, 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 – sediment C/N, SOM – sediment organic matter, Chl *a* – sediment Chlorophyll *a* and Chl *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

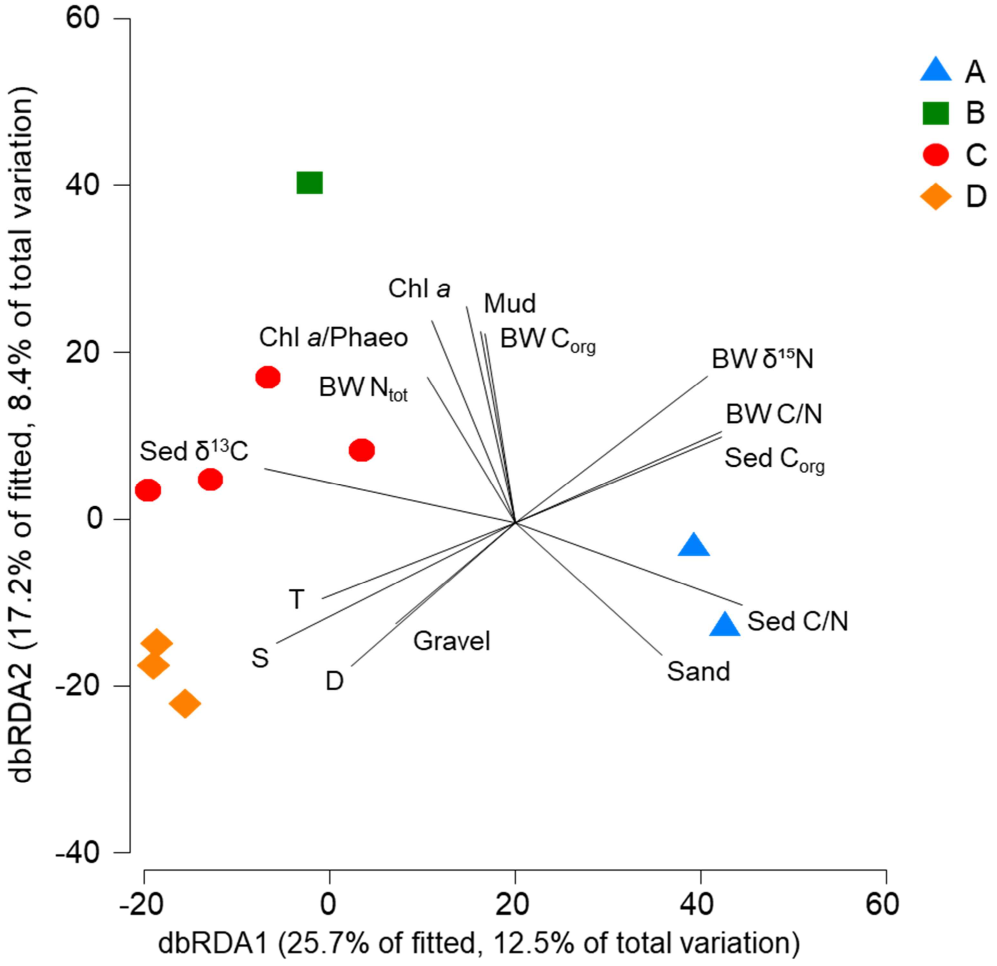

Fig. 5. Distance-based Redundancy Analysis (dbRDA) plot of the DistLM model visualizing the relationships between the environmental parameters and the biomass/density ratio of species between four sampling areas: A (Hornsund, Van Mijenfjorden); B (Storfjorden); C (Barents Sea shelf); D (northern Barents 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

After 10 days, almost all luminophores (~95%) remained on sediment core surface at all sampling stations meaning that about 5% of luminophores were transported into sediments. The fastest decrease was noted at the B group (Storfjorden : AX/3 and ST/8), and at the C group (Southern Barents Sea station (AX/6) ; Nansen Basin < 400 m (PS/20, PS/32)) where ~15 to 25% of surface luminophores were buried. While luminophores were still present all along the sedimentary column in the Storfjorden station, some subsurface peaks of luminophores were clearly measured below 3 cm in the C group. The lowest decrease of the luminophores over depth was noted in the A group (Svalbard Fjords AX1/1, AX/2) and in the D group at deepest station (PS/31) in the Nansen Basin where 92 to 98% of luminophores remained at surface with slight subsurface peaks of tracers (about: only 0.91 %) between 1 to 3 cm deep .

Biodiffusion rates ranged from 0.04 cm^{-2} y^{-1} ± 0.01 standard error (SE) (station AX/2) to 0.07 cm^{-2} y^{-1} ± 0.03 SE (station AX/1) in group A. In group B biodiffusion rates was 0.06 cm^{-2} y^{-1} ± 0.04 SE (station AX/3). In group C biodiffusion ranged from 0 (station PS/32) to 0.76 cm^{-2} y^{-1} ± 0.71 SE (station AX/6). There was no biodiffusive transport in group D. There were significant differences in biodiffusion among areas (Kruskal-Wallis test; $p<0.05$; significant differences (post hoc test) between group A:D and C:D) (Fig. 6A). Non-local transport rates ranged from 0.21 y^{-1} ± 0.20 SE (station AX/2) to 0.60 y^{-1} ± 0.23 SE (station AX/1) in group A. In group B non-local transport rates was 2.12 y^{-1} ± 1 SE (station AX/3). In group C non-local transport rates ranged from 0.75 y^{-1} ± 0.25 SE (station PS/32) to 2.08 y^{-1} ± 0.58 SE (station AX/6). In group D non-local transport rates ranged from 0.28 y^{-1} ± 0.04 SE (station PS/31) to 0.68 y^{-1} ± 0.31 SE (station PS/19). There were significant differences in non-local transport (Kruskal-Wallis test; $p<0.05$; significant differences (post hoc test) between group A:C and C:D) (Fig. 6B). Biodiffusive transport values were significantly related with depth, Sed C_{org} and BW C/N ratio Spearman correlation: -0.6, 0.6 and 0.6, $p<0.05$ respectively). Non-local transport values were significantly related to benthic taxa richness, biomass, mud and Sed N_{tot} (Spearman correlation: 0.5, 0.5, 0.5 and 0.5 $p<0.05$ respectively) (Table 8).

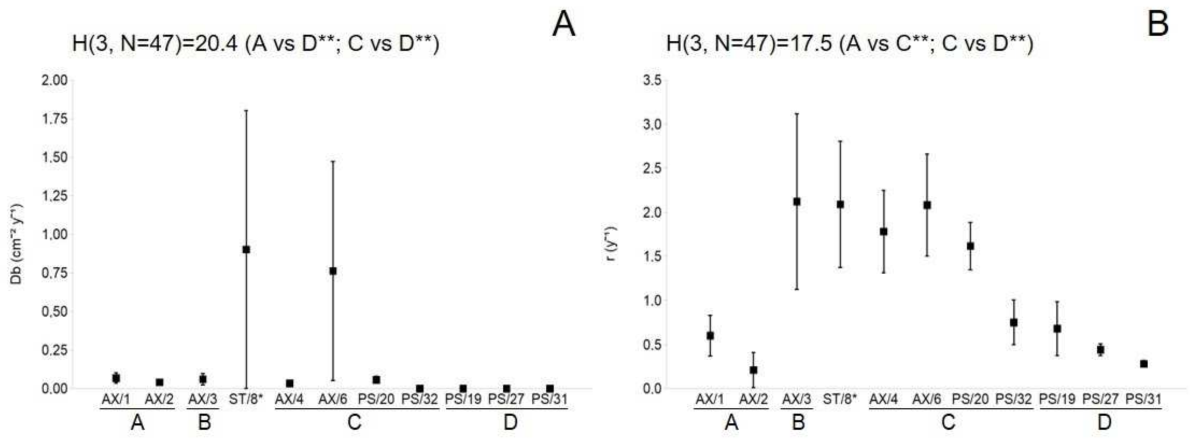

Fig. 6. Mean bioturbation coefficients: Db - biodiffusion (cm^{-2} y^{-1}) (A) and r – non-local (y^{-1}) (B); ± SE, n=no of cores (Table 1) at stations sampled in Van Mijenfjorden, Hornsund (group A); Storfjorden (group B); Barents Sea shelf (group C); northern Barents Sea and Nansen Basin (group D). Station ST/8 marked with * was sampled in summer season. Kruskal – Wallis results for differences between sampling sites are given; significant test results are marked with ** ($p<0.05$).

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

3.4. *Storfjorden – seasonal changes*

Bottom water salinity was similar in spring and summer in Storfjorden, respectively 34.5 and 34.1. Bottom water temperature in spring season was -0.8 °C and increased to 4.5 °C (Table 1). Benthic density decreased from 3625.3 ind./m^2 ± 83.9 SE in spring (AX/3) to 1812.7 ind./m^2 ± 229.7 SE in summer (ST/8). Biomass was similar in both seasons (172.3 g/m^2 ± 37.3 SE (spring, AX/3) and 152.1 g/m^2 ± 67.5 SE (summer, ST/8). Non-local transport rates were similar in spring and summer (2.12 ± 1 and 2.09 ± 0.72 y^{-1} respectively) but biodiffusion rates increased in summer (0.06 ± 0.04 in spring and 0.90 ± 0.90 cm^2 y^{-1} in summer). Significant differences were found for the number of taxa and macrofauna density between spring and summer seasons (Mann-Whitney U-test; Z= 2.3; $p<0.05$ and Z=2.4; $p<0.05$, respectively).

4. Discussion

This is the first complex report on bioturbation activities in spring to summer transition time conducted over the large area from Svalbard fjords and Barents Sea to deep basin north off Svalbard. In our study, benthic community variables differentiated four groups of stations, and this separation was to some extent echoed by the environmental factors. The benthic community properties further affected the measured benthic activities i.e. bioturbation rates.

4.1. *Benthic community characteristics across the sampled area*

The structure and composition of the benthic communities seemed to be grouped in four groups of stations, however, the primary variables of the benthic community structure (e.g., density, biomass) were highly variable within each station. One of the reasons could be the high variability among replicates that covered only small area of sampled sediment. Benthic species richness of the region was not well represented in the cores taken for the experiments at each station due to their small sampling unit (~113 cm²). This may have implications for the results generalization to the sampled areas due to high variability of benthic density, biomass and consequently on the effects of these on the measured bioturbation coefficients. However, we assume that we collected the most abundant taxa, which would likely have the dominant role in mediating bioturbation effect. We have sampled and identified the benthic organisms in each sediment core where the bioturbation experiments were processed meaning that we know the organisms responsible of the measured bioturbation activities.

The variability of the quality and quantity of sedimentary OM within each station impacted benthic community structure. For instance, the lowest quality of SOM (C/N~18) was found in sandy sediments of Van Mijenfjorden and Hornsund fjords, highlighting dominance of refractory organic material within the group A. This probably explains the lowest benthic densities and biomass at these stations. This can be the result of geographical locations (e.g., water circulation restrictions) and glacial activity in Hornsund, related high sedimentation rates and high terrestrial OM inputs disturbing benthic fauna (Drewnik et al., 2016; Włodarska-Kowalczuk and Pearson, 2004). These two stations' communities were mainly shaped by presence of polychaete *Polycirrus arcticus* and cumacean *Diastylis lucifera*, and opportunistic cirratulids were among dominants.

A high, but variable, B/D ratio was found in Storfjorden (group B), which is the site of a recurring polynya and has some of the highest productivity in the Barents Sea. The low temperature, presence of a sea ice-edge bloom, very fine grained sediments (muds) indicating low hydrodynamism, and high C_{org} and Chl *a* contents in sediments and in bottom waters promote diverse and high biomass benthic communities with larger individuals burrowing and feeding deeper (Winkelmann and Knies, 2005). High Chl *a*/Phaeo ratio and large quantities of Chl *a* within sediments show also a more frequent input of fresh OM because of the presence of the polynya (Haarpaintner et al., 2001; Vinje, 2001; Winkelman and Knies, 2005). This community was also diverse, with high dominance of polychaetes (cirratulids, carnivore *Lumbrineris* sp, and subsurface tube-building conveyor *Maldane sarsi*) and bivalves like *Yoldia hyperborea* and *Nuculana radiata*. PCO indicated that samples collected in Storfjorden were correlated with presence of bivalve *Ennucula tenuis* and polychaete *Apistobanchus tulbergi.*

The group C, covering stations sampled over the Barents Sea shelf, was highly variable in terms of community structure and various environmental factors. The southern Barents Sea station (AX/6) was characterized by similar environmental conditions to the Storfjorden resulting in the occurrence of fauna with similar characteristics but with a lower biomass to density ratio. This station was dominated by tube-building conveyor polychaete *Spiochaetopterus typicus* and *Heteromastus* sp. and bivalve *Macoma* sp. It was characterized by high amount of SOM but low Chl *a* in the sediments, indicating late bloom/post bloom conditions, where most of the fresh OM was already utilized by benthic organisms. Lower Chl *a*/Phaeo ratio also indicates more degraded OM, possibly a result of intensive pelagic grazing (Morata and Renaud, 2008). This is likely since this station is in the southernmost location, therefore it was under the strong influence of Atlantic waters and was already in the late-phase of the phytoplankton bloom (Krause et al., 2018). The other stations from this group, located in the northern part of Barents Sea e.g. Erik Eriksen Strait, were characterized by high share of sand but relatively fresh and abundant SOM, though low Chl *a* levels. This is quite similar to stations north of Svalbard (PS/20 and PS/32), although the later was characterized by higher amounts of Chl *a* present in the sediment related to the bloom in progress at the time of sampling (Peeken, 2016). This group was characterized by highly diverse communities (from 36 (AX/6) to 68 (PS/32) number of taxa), however most of them belonged to either biodiffusors or conveyors.

The northern Barents Sea and Nansen Basin (group D) were differentiated from the other groups by salinity, temperature, depth and occurrence of gravel. The species shaping communities included polychaetes *Prionospio cirrifera* and *Notoproctus oculatus*. Stations in group D were seasonally ice covered (including during sampling), and deeper than 400 m. They were characterized by low amount of Sed C_{org} but presence of high OM quality in bottom water layer, perhaps indicating recent sedimentation. They were characterized by much lower benthic biomass and higher benthic density which were both decreasing with increasing depth regardless the bloom stage. Decreasing quality and quantity of OM with increasing depth, as it was observed in Nansen Basin, are often reflected in spatial variations in benthic community structure (Carroll et al., 2008) and result in severe energy limitation for deep-seafloor communities, dominated by small sized-individuals in high densities (Gage and Tyler, 1991; Bergmann et al., 2009; Grebmeier et al., 1988; Renaud et al., 2008).

Long living Arctic benthic fauna reflects carbon export fluxes to the sea bottom but changes are observed after several years or decades at deep stations (Grebmeier, 2012; Link et al., 2013). Therefore, it is likely that the bloom stage and current OM delivery to the sea floor did not directly influence the benthic community structure which is mainly dependent on the integrated carbon input to the sediments and OM pool available in the sediment. However, fresh OM arriving to the sea floor can trigger fast benthic response in terms of feeding and related movement (Morata et al., 2015; Boetius et al., 2013), thus influence the community functioning.

4.2. Bioturbation processes (sediment mixing)

Conducting experiments at the large depth gradient posts a challenge of working in hyperbaric conditions. Although, Glud et al. (1994) showed that in situ measurements of sediment oxygen demand/oxygen penetration depth were uniformly higher than deck incubations, the relative differences among stations did not change with depth. Since other published studies have also not incorporated hyperbaric chambers when estimating sediment oxygen demand (Boetius et al., 2013), metabolism (Linke et al., 1995), and bioturbation (Clough et al., 1997), our results, as the relative rates, remain comparable.

Both coefficients of bioturbation (non-local transport (r) and biodiffusion (Db) were quantified in the stations of groups A, B and C where a higher diversity of bioturbation groups was recorded among the dominant taxa (Table 4). Stations of the group D, on the contrary, exhibited lower diversity of functional traits among the dominant taxa with the simultaneous presence of two groups of sediment mixing (conveyors, biodiffusers) but where only non-local transport was observed.

Species identity and differences in species characteristics, such as feeding mode and typical burrowing depth, have been previously shown to influence the intensity of bioturbation (Viitasalo-Frösén et al., 2009; Josefson et al., 2012; Näkki et al., 2017) and functional diversity can be considered to have more impacts than taxonomic richness (Harvey et al., 2012; Link et al., 2013). However, interpreting the bioturbation processes and the assignment of the macrofaunal species to the correct functional group can be challenging. Short-term experimental studies of sediment mixing provide just essential data for only few species and results are hard to compare with longer time-scale processes in natural ecosystems. Also, the same species can have different behavior and belong to another sediment mixing groups across their ranges since species are known to be able to feed in several different ways and change their feeding and mobility to exploit the food resources available (Biles et al., 2002). Change in organism feeding behavior will also mean a change in bioturbation which is reduced as a result of decreasing species diversity and community biomass, as well as diversity of feeding and bioturbation groups (Mazik and Elliott, 2000). In general, in our study, the high number of sub-surface deposit feeders, which feed at depth and transport material to the surface can explain dominance of non-local mixing (Boudreau, 1997; Gérino et al., 1998). Conveyors were actually omnipresent and the intensity of non-local transport was variable between stations, and was increasing with increasing species richness, density and biomass, but also with increasing percentage of mud presence and Chl *a* contents (Table 8). Since non-local transport is non-continuous, it is usually difficult to link it directly to benthic biomass (or biovolume) since some movements of particles do not depend only on animal movements, but also on animal-independent effects (e.g., particles falling down into the burrows, initial burrows construction). In our study, increasing benthic biomass generated by high labile OM inputs, seems to have positive effects on the conveying activities and consequently on the non-local transport rates.

In shallow fjords (Van Mijenfjorden and Hornsund, Group A), the benthic communities were characterized by low bioturbation rates (non-local transport from 0.21 ± 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 similarity between the AX/1 and AX/2 stations of the group A can be explained by the occurrence of a similar benthic community whose the species have the same functional traits combination (i.e., feeding, mobility, burrowing depth, burrowing mode and sediment mixing mode; Table 4) but present in low density and biomass. Biodiffusors (Cirratulidae; Gérino et al., 1992, 2007), conveyors (*P. arcticus*) and gallery diffusors (*Lumbrineris* sp.; Petch, 1986), both present in those fjords, were probably limited by the lack of fresh OM in the sediments at the time of sampling.

Storfjorden (AX/3, group B), Erik Eriksen Strait (AX/4) and PS/20 (group C) had similar measured bioturbation rates with high non-local transport and low biodiffusion, and shared a high biomass contribution of bivalves and maldanid polychaetes. Yoldiids and maldanids, burrowing deeper into the sediment, are known to be effective conveyors which can either actively transfer sediment directly into deep layers from the surface, or into surface layers from deeper layers of the sediments (Bender and Davis, 1984; Smith and Schafer, 1984), respectively. This can explain high non-local transport in these areas.

The southern Barents Sea, AX/6, group C, had higher but strongly spatially variable Db and r by station within the group, with a relatively higher biomass and density of the organisms (*Spiochaetopterus typicus* (conveyor, Smith and Shafer, 1984) dominating in the density and *Astarte* sp. (biodiffusor, Queirós at al., 2013) dominating in the biomass. The reason for that was most likely earlier occurrence of the phytoplankton bloom due to the lack of sea ice, so at the time of the cruise, late spring/post-bloom conditions and abundant OM activated rapidly benthic organisms.

All deeper and sea ice covered stations in group D, including sea ice covered PS/32 (group C), were dominated by biodiffusors and conveyors (Table 4). Those stations were characterized by significant non-local transport and unmeasurable biodiffusion. This suggests that the sediment transport mode by conveyors dominated in the sampled deeper areas adapted to scarce fresh food availability despite the presence of biodiffusers. This implies a very low activity by biodiffusers undetectable at the time scale of 10 days of experiment, or an interfering of such activities with the conveyors species. Typically for communities living in OM limited environments, these benthic communities were characterized by a low number of species with low biomass. Giving the low bioturbation rates in the deeper stations, we could actually suppose that time incubation with luminophores superior to 10 days could be tested in the future experiments in order to insure a more complete transport of tracers towards deep layers where the benthic community is less active. Since the bioturbation model takes into account in its calculation this time duration, the final bioturbation coefficient is however normalized to this time scale, signifying the similar relative comparison between stations for our experiment remains valid. If we were able to detect measurable biodiffusive coefficient for the deeper stations for a longer time scale, normalized to the same time unit, the biodiffusion would be still low because of weak benthic infauna dynamic in such environments. Our results are, however, similar to the patterns showed by Clough et al. (1997) who noted low biodiffusive transport (0.01 to 0.11 cm^{-2} y^{-1}) by using radioactive tracer for its deep portions in relationships to the lower benthic biomass due to lower fresh OM inputs. They found, however, higher surficial sediment biological mixing rates than the natural sedimentation rates in the Arctic deep sediments, highlighting the importance of quantifying bioturbation in the Arctic Ocean taking into account its spatial variability. Also, Soltwedel et al. (2019), using luminophores for experiments that lasted 2 and 4 years, found low biodiffusion mixing rates at the Long-Term Ecological Research (LTER) observatory HAUSGARTEN in Fram Strait (~ 0.2 cm^{-2} y^{-1}). They concluded that the meiofauna, and to a certain extent megafauna, were the main bioturbators in the deep sea environments. Although, only macrofauna (>500 µm) was identified and was presented as the main responsible of the bioturbation activities in our study, meiofaunal activities may also explain some of the patterns that could not be attributed to the changes in the environment or macrofaunal communities in the deep sea stations. Since the model quantifies bioturbation coefficients of the entire benthic community, it includes here also the meiofauna activities. Meiofauna is actually known as the most abundant infauna (Heip et al., 1985; Vanreusel et al., 2010; Rosli et al., 2016; own data) and as having impact on the bioturbation activities in the first few centimeters of the sediment (Aller and Aller, 1992; Piot el al., 2014; Aschenbroich et al., 2017; Mäkelä et al., 2018). Therefore, we suggest that also the smaller benthic fractions should be identified in future studies on Arctic deep infaunal activity in order to find better infauna variables for explaining the bioturbation measurements.

4.3. Seasonal changes (Storfjorden station)

The highest values of non-local transport were reported for Storfjorden and remained stable during both spring and summer time. The biodiffusion coefficient measured in Storfjorden during summer was about fifteen times higher compared to measurements conducted during spring, probably because of the changes in species and functional groups between the two seasons associated with the more labile OM reaching the seafloor in summer (Chl *a*/Phaeo~52, Table 3). The dominant taxa in density were Cirratullidae (biodiffusor) both during spring and summer (31.2 % and 11 %, respectively) and Lumbrineris sp. (gallery diffusor) (14.1 % and 18.3 %, respectively) while in biomass, Yoldia hyperborea (convoyer) dominated during both seasons (57.4 % and 30.5 %, respectively) (Table 4). Such changes, i.e. replacement of one large specimen by another large specimen of different species, should be rather accounted to spatial variability of benthic communities than due to seasonal change in sampled communities. Also, species such as *Nereis diversicolor* or *M. balthica* are able to change their feeding mode (suspensive-feeder versus deposit feeder) depending on environmental conditions (De Goej and Luttikhuizen, 1998; Christensen et al., 2000). It is also possible that taxa such as Cirratulidae, *Lumbrinereis*, *Yoldia* and *Nuculana* change their feeding mode with increased OM input from the polynya during the summer just after the spring bloom, as was observed in other ecosystems or experiments (e.g., Bender and Davis, 1984 for *Yoldia* spp; Rouse and Pleijel, 2001; Kędra et al., 2012 for Cirratulidae).

Benthic activities are related to the supply of OM to the seabed (Grassle and Grassle, 1994; Levin and Gooday, 2003; Blake et al., 2009) and biodiffusion intensity can be strongly dependent on flux of fresh food from overlying waters (Gérino et al., 1998). In shallow sediments of temperate areas, Duport et al. (2007) found the highest intensity of sediment mixing (non-local and biodiffusion) during summer in the Thau Lagoon. Also Gérino et al. (2007) found more rapid non-local transport in spring than in autumn in the Venice Lagoon. Organic carbon supply generally increases when the PP starts in spring, and peaks with the bloom and afterwards, over the summer. In the polar areas, Morata et al. (2015) found minimum biodiffusive activity during the polar night, and high non-local transport after a pulse of fresh food in experiments conducted in high Arctic fjord in Svalbard. This result suggests that behavior of benthic species change with the OM input. Also, laboratory experiments showed that macrofauna can react quickly to food input by increasing their bioturbation activities (Nogaro et al., 2008). Furthermore, Dauwe et al. (1998) reported maximum sediment mixing with medium food quality in the study comparing macrofaunal benthic activity with contrasting food supply in the North Sea. They also showed that the minimal mixing was observed at the station with high quality OM, and no mixing when low quality OM was present. This can result from combination of physical and biochemical factors influencing bioturbation, or changes in species behavior. The other possible explanation is related to the oxygen conditions in different areas. Both North and Baltic Sea are areas with high PP and eutrophication. Higher amounts of new OM reaching the sea floor often result in low oxygen levels leading to anoxic conditions affecting faunal behavior or even survival (Carstensen et al., 2014). Svalbard fjords and adjacent areas are largely oligo- and meso- trophic, and well oxygenated regardless the time of the year and intensity of the spring bloom deposition. We, thus, expect minimal negative impacts of OM deposition on benthic communities. Our results from this limited seasonal comparison suggest that large inputs of fresh OM to the seabed can trigger bioturbation activities.

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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**	-

- 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.