

1 **Palaeoceanographic changes in Hornsund Fjord (Spitsbergen, Svalbard) over the last**
2 **millennium: new insights from ancient DNA.**

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1 **Abstract**

2 This paper presents a reconstruction of climate-driven environmental changes over the
3 last millennium in Hornsund Fjord (Svalbard), based on sedimentological and
4 micropalaeontological records. Our palaeo-investigation was supported by an analysis of
5 foraminiferal ancient DNA (aDNA), focusing on the non-fossilized monothalamous species.
6 The main climatic fluctuations during the last millennium were the Medieval Warm Period
7 (MWP, 1000 AD – 1600 AD), the Little Ice Age (LIA, 1600 AD – 1900 AD) and the Modern
8 Warming (MW, 1900 AD – present). Our study indicates that the environmental conditions in
9 Hornsund during the MWP and the early LIA (before ~ 1800 AD) were relatively stable. The
10 beginning of the LIA (~ 1600 AD) was poorly evidenced by the micropalaeontological record
11 but was well marked in the aDNA data by an increased proportion of monothalamous
12 foraminifera, especially *Bathysiphon* sp. The early LIA (~ 1600 AD – ~ 1800 AD) was
13 marked by an increase in the abundance of sequences of *Hippocrepinella hirudinea* and
14 *Cedhagenia saltatus*. In the late LIA (after ~ 1800 AD), the conditions in the fjord became
15 glacier-proximal and were characterized by increased meltwater outflows, high sedimentation
16 and a high calving rate. This coincided with an increase in the percentages of sequences of
17 *Micrometula* sp. and *Vellaria pellucidus*. During the MW, the major glacier fronts retreated
18 rapidly to the inner bays, which limited the iceberg discharge to the fjord's centre and caused
19 a shift in the foraminiferal community that was reflected in both the fossil and aDNA records.

20 The palaeoceanographic changes in the Hornsund fjord over the last millennium were
21 driven mainly by the inflow of shelf-originated water masses and glacial activity. However,
22 the environmental changes were poorly evidenced in the micropalaeontological record, but
23 they were well documented in our aDNA data. We considerably increased the number of
24 potential proxy species by including monothalamous foraminifera in the palaeoecological
25 studies.

1 **1 Introduction**

2 The general outline of climate development over the last millennium is the Medieval
3 Warm Period (MWP), followed by cooling during the Little Ice Age (LIA) and warming in
4 the 20th and 21st centuries (Modern Warming; MW). In the European Arctic, the temperature
5 increase during the MWP and MW was correlated with the strong influence of the Atlantic
6 Water inflow and associated heat transport (Wanamaker et al., 2012). In contrast, the
7 weakening of the Atlantic Meridional Overturning Circulation (AMOC) and the lower heat
8 transport to the Arctic might have been responsible for the LIA cooling (Lund et al., 2006).
9 Changes in the Arctic Ocean heat budget were associated with significant changes in the
10 cryosphere, especially the gradual decreases in glacier mass balance and the extent of the sea-
11 ice cover in the last century (e.g., D'Andrea et al., 2012; Jernas et al., 2013).

12 Fjords are a unique form of coastline that are under the influence of the glaciated land
13 and the ocean. Hence, fjord systems are sensitive indicators of climate change phenomena.
14 However, the greatest effort in studying the Holocene history of Svalbard has mainly focused
15 on the shelf area (e.g., Hald et al., 2007; Rasmussen et al., 2012; Łacka et al., 2015). There
16 have been only a few high-resolution studies of the sedimentary record of the Svalbard fjords
17 from the last millennium (e.g., Majewski and Zajączkowski, 2007; Majewski et al., 2009).

18 The environmental changes during the last millennium observed in the Svalbard shelf
19 were correlated with the interplay of Atlantic and Arctic water masses (Kubischta et al., 2011;
20 Jernas et al., 2013). The Hornsund fjord is strongly influenced by tidewater glaciers, and thus
21 the sedimentary record in this fjord might indicate that enhanced melt-water delivery
22 increased the sediment accumulation and restricted the sea productivity during the periods of
23 glacial retreat. To accurately study climate-driven environmental variability in the past, it is
24 crucial to create a network of proxies that carry different but complementary information.

1 Foraminifera are widely used as proxies of past and present environmental changes in
2 all types of marine environments. However, palaeoceanographic reconstructions have focused
3 on multi-chambered hard-shelled taxa and have ignored soft-walled, monothalamous species,
4 which often dominate foraminifera assemblages in high latitude regions (Gooday, 2002).
5 Monothalamous foraminifera with organic or predominantly organic test walls are
6 traditionally defined as allogromiids (Gooday, 2002). However, morphological and molecular
7 evidence indicate that ‘allogromiids’ does not refer to a coherent taxonomic group but rather a
8 group what is scattered between several monothalamous clades (Pawlowski et al., 2002;
9 Lejzerowicz et al., 2013a). The group includes organic-walled (‘naked’) and agglutinated
10 forms of various shapes (Cedhagen et al., 2002). Monothalamous foraminifera with a test
11 build of agglutinated particles are referred to as ‘saccamminids’ or ‘psammosphaerids.’ The
12 term ‘allogromiid’ is sometimes applied to monothalamous taxa, irrespective of wall type.
13 Therefore, literature reports might include saccamminids and psammosphaerids in the
14 allogromiids group (Gooday, 2002).

15 Previous studies have shown that it is possible to consider monothalamous and
16 polythalamous foraminifera (Lejzerowicz et al., 2013b) and other groups of non-fossilized
17 eukaryotes (e.g., Coolen et al., 2013, 2006; Boere et al., 2011) in palaeoecological surveys
18 using an ancient environmental DNA (aDNA) approach. To include monothalamids in
19 palaeoecological studies of Arctic foraminifera, we analysed the ancient foraminiferal DNA
20 record from the last millennium from Hornsund (Pawłowska et al., 2014). The richness of the
21 foraminiferal communities revealed by the molecular analysis was much higher than that in
22 the fossil record, mainly due to the detection of a high number of monothalamous species that
23 were not preserved during the fossilization process and small-size species that are not retained
24 on micropalaeontological sieves.

1 The aim of this study was to reconstruct the climate-driven environmental changes
2 over the last millennium in Hornsund, with decadal to multi-decadal resolution. The
3 promising results of our previous study (Pawłowska et al., 2014) encouraged us to use our
4 aDNA data to supplement the palaeoclimatic record based on traditional proxies. We
5 evaluated the potential use of monothalamous foraminifera as palaeoceanographic proxies,
6 showing that they might provide valuable environmental information that is complementary to
7 the data obtained with traditional microfossil proxies.

8

9 **2 Study area**

10 Hornsund is the southernmost fjord of Spitsbergen. It is connected to the open sea by a
11 wide no-sill outlet. The fjord's coastline encompasses several glacier - proximal basins that
12 are separated by sills. In its central part, the water depth exceeds 200 m and varies from 55 m
13 to 180 m in the glacier - proximal basins (Fig. 1).

14 The hydrology of the fjord is under the influence of two main exogenous water
15 masses: the Atlantic Water (AW) and the Arctic Water (ArW). The AW is warm and saline,
16 and its temperature and salinity are usually defined as $\geq 3^{\circ}\text{C}$ and ≥ 34.9 , respectively. The
17 ArW is colder and fresher, and its salinity varies along the Spitsbergen shelf due to the
18 freshwater outflows from fjords (Cottier et al., 2005). The AW and ArW mix over the
19 continental shelf to form the Shelf Transformed Water (STW), which has a temperature and
20 salinity of 1°C and 34.7, respectively. The STW mainly occupies the outer and central parts of
21 the fjord. The Local Water (LW) is formed directly in the fjord by convectational mixing during
22 cooling in the fall and winter or the interaction between the warmer fjord water and glacier
23 fronts (Svendsen et al., 2002).

24 Seventy percent of the Hornsund catchment area is covered by glaciers (Hagen et al.,
25 1993). The melting of the eight major tidewater glaciers results in an important sediment

1 delivery to the fjord. The modern sediment accumulation rate varies from 0.5 to 0.7 cm yr⁻¹ in
2 the central and inner parts, respectively (Szczuciński et al., 2006).

3 During the last millennium, Hornsund was subjected to major environmental changes,
4 including the MWP, cooling and glacial advances during the LIA, which culminated in the
5 period from 1600 AD to 1900 AD, and warming and massive glacial retreats during the 20th
6 and 21st centuries (MW; Ziaja, 2001; Pälli et al., 2003). These changes were correlated with
7 the variability in the inflow of the cold ArW and warm AW and were recorded in foraminifera
8 assemblages and the stable isotope compositions from foraminiferal tests (Majewski et al.,
9 2009).

10 The previous aDNA-based investigation on the foraminiferal fauna from Hornsund
11 (Pawłowska et al., 2014) focused mainly on the hard-shelled species. The aDNA sequences
12 assigned to testate foraminifera made 142 out of 394 OTUs (Operational Taxonomic Units).
13 The microfossil record comprised 45 species and 57% of them were found also in the
14 molecular data. Foraminifera detected by both approaches included species reported for
15 Hornsund by previous investigations (e.g., Hald & Korsun 1997; Pogodina 2005) e.g.,
16 *Cassidulina* spp, *Cibicides lobatulus*, *Nonionellina labradorica*, *Elphidium excavatum*,
17 *Reophax scorpiurus*, *Reophax* sp., *Spiroplectammina* sp., *Cribrostomoides crassimargo* and
18 *Quinqueloculina* sp. Among these, *Cassidulina* spp, *C. lobatulus* and *E. excavatum* were
19 noted frequently in microfossil and sequence data, making 8.8 %, 3.4 % and 2.5 % of the
20 sequences, respectively. However, there were four species that were also frequent in the fossil
21 record, but were represented by less than 1 % of aDNA sequences (*N. labradorica* and *C.*
22 *crassimargo*) or were not sequenced (*B. frigida* and *I. helenae*). On the other hand, some taxa
23 belonging to genera *Stainforthia*, *Spiroplectammina*, *Reophax* were found rarely in the
24 microfossil assemblage, but were represented by numerous sequences. The discrepancies

1 between the records were explained by biological features of certain foraminiferal species and
2 by the differences in characteristics of these two approaches (i.e., the analytical procedures).

3

4 **3 Material and methods**

5 A 2 m long sediment core HF_2011 was taken with a gravity corer from the R/V
6 Oceania during a cruise in July 2011. The sampling station was located in the central basin of
7 the fjord, in a flat seabed area at a depth of 135 m (76° 57.238'N; 15° 41.782'E; Fig. 1). The
8 core was subsampled onboard for aDNA analyses and frozen at -20°C until further analyses
9 were conducted at the Institute of Oceanology, Polish Academy of Sciences (Sopot, Poland),
10 as described in Pawłowska et al. (2014). After thawing at 4°C, the core was split into two
11 parts longitudinally, and each half was cut into 1 cm slices for micropalaeontological and
12 sedimentological analyses. Carbonate shells were picked for accelerator mass spectrometry
13 (AMS) ¹⁴C dating.

14

15 **3.1 Grain-size and stable isotope analyses**

16 The grain size analysis of the sediment slices was conducted using a Mastersizer 2000
17 laser analyser coupled with a HydroMU device (Malvern Instruments, Malvern, UK) and
18 supported by the wet sieving of fractions larger than 250 µm. The granulometric data were
19 analysed with the use of the GRADISTAT 8.0 software program (Blott and Pye, 2001). Dried
20 and weighted sediment fractions > 250 and 500 µm were used for IRD analyses, and at least
21 500 mineral grains from each fraction were counted under a stereomicroscope. The IRD was
22 expressed as the number of grains per gram of sediment (grain g⁻¹) and number of grains per
23 square centimetre per year (grain cm⁻² y⁻¹).

24 Stable isotope analyses were performed on foraminiferal tests selected from 54
25 sediment layers. From each layer, 10 to 12 well-preserved specimens of *Cibicidoides*

1 *lobatulus* were selected. The measurements were performed on a Finnigan-MAT 253 mass
2 spectrometer coupled to a Kiel IV carbonate preparation device (Thermo Fischer Scientific,
3 University of Florida). The resulting values were compared to isotopic standard NBS-19 and
4 expressed in standard δ notation relative to Vienna Pee Dee Belemnite (VPDB).

5

6 **3.2 Foraminiferal counts and molecular analysis**

7 Prior to the analysis of the fossil foraminiferal assemblages, 74 selected sediment
8 samples were dried, weighed and wet-washed through sieves with 500 and 100 μm openings.
9 Each sample was divided using a dry microsplitter, and at least 300 specimens from each
10 sample were counted. The foraminiferal counts were reported as percentages of the total
11 assemblage and as the number of individuals per square centimetre per year. The fossil
12 foraminifera assemblage was analysed with an orthogonally rotated (varimax) Q-mode
13 Principal Component (PC) analysis, using commercially distributed software (SYSTAT 11).
14 Taxa with abundances $> 2\%$ of the total assemblage in at least one sample were analysed.
15 Each PC was defined by the dominant (and eventually accessory) species. The PCs were
16 referred to foraminiferal assemblages (FA) named after the dominant species. The PC scores
17 showed the contribution of the selected species to each PC. PC loadings higher than 0.4 were
18 regarded as statistically significant (Malmgren and Haq, 1982).

19 The analysis of molecular data from 12 selected layers was described in detail in
20 Pawłowska et al. (2014). Briefly, the total DNA of each of the 12 sediment samples was
21 extracted with a PowerSoil DNA kit (MoBio). A 3' SSU rDNA fragment including the
22 foraminifera-specific 37f hypervariable region (Pawłowski and Lecroq, 2010) was PCR
23 amplified from environmental DNA. The SSU rDNA sequences were then obtained either
24 based on cloning and Sanger sequencing or after library-preparation and Illumina high-
25 throughput sequencing.

1 For the cloning-based Sanger sequencing, the environmental DNA was PCR amplified
2 with s14F3 forward primer combined with s17, s15.2 or s15ROTEX as reversed primers. The
3 sizes of the resulting fragments were of ca. 400 bp for s14F3/s17 and ca. 200 bp for both the
4 s14F3/s15.2 and s14F3/s15ROTEX amplifications. Nested PCR was performed for samples
5 with s14F3/s17 with the use of a s14F1/s17 primer combination. Positive and controlled PCR
6 products of expected sizes were cloned and Sanger sequenced as in Pawlowski et al. (2011).
7 The resulting raw sequences were manually corrected and edited using Codon Code Aligner
8 and Seaview 4.0 (Gouy et al. 2010).

9 For high-throughput sequencing (HTS), s14F0 and s15 primers tagged with unique
10 sequences of 5 nucleotides were used. The size of the obtained fragment was ca. 100 bp. The
11 amplicons were quantified and pooled in equimolar quantities. A library preparation was
12 performed using a TruSeq library-preparation kit (Illumina) and was loaded onto a HiSeq
13 instrument for a paired-end HTS run of 2*100 cycles at Fasteris SA (Plan-les-Ouates,
14 Switzerland). The processing of the HTS sequence data, including quality filtering, sample
15 demultiplexing, strict dereplication into unique sequences and operational taxonomic units
16 (OTUs) selection was realized according to Lejzerowicz et al. (2013a), except that unique
17 sequences that were composed of up to 10 reads in a sample were removed. The results were
18 presented as OTUs-to-samples tables and transformed in terms of the number of OTUs and
19 the relative abundance (%) of sequences.

20 **4 Sediment dating**

21 The age of the studied core was estimated based on high precision AMS ¹⁴C dating
22 performed on bivalves shells, as presented in Pawłowska et al. (2014). Eleven shells identified
23 to the highest possible taxonomic level were selected and processed on a 1.5 SDH-Pelletron
24 Model 'Compact Carbon AMS' (Poznań Radiocarbon Laboratory, Poland). The dates were
25 converted into calibrated ages using the CALIB Rev. 7.0.2 Beta calibration program (Stuiver

1 and Reimer, 1993) and the Marine13 calibration dataset (Reimer et al., 2013). The difference
2 ΔR in the reservoir age correction of 105 ± 24 was applied (Mangerud et al., 2006).

3 Four of the eleven samples were used to establish an approximate age model for the
4 sediment core. The upper-most sample contained post-bomb carbon, which indicates a post-
5 1960 age. Samples located in the middle part of the core revealed ages that were not in
6 chronological order. All the samples (shells) revealing age reversals were excluded from the
7 age model as they were likely redeposited (Table 1). Samples out of chronological order
8 occurred at the depths of ~ 15 -55 cm and ~ 80 -115 cm, and, therefore, it is likely that these
9 sediment intervals represent major redeposition events. The age-depth model was made with
10 the use of the CLAM-R software program (Blaauw, 2010; Fig. 2). The age of the oldest layer
11 was estimated to be ~ 965 AD. The sediment accumulation rate (SAR) in the deepest part of
12 the core (i.e., before 1800 AD; up to 120 cm) ranged from 0.1 to 0.125 cm yr⁻¹. At ~ 1800
13 AD (120 cm), the SAR increased to 1 cm yr⁻¹. In the upper layers (after ~ 1850 AD; 70 cm),
14 the SAR decreased to 0.3 cm yr⁻¹.

15

16 **5 Foraminifera as environmental indicators**

17 Due to the differences in the ecological tolerances of particular species, foraminifera
18 are indicators of glaciomarine conditions, Atlantic and Arctic water masses and bottom
19 currents. Herein, we followed the classification that Majewski et al. (2009) established based
20 on ecological and palaeoenvironmental studies from Greenland, Svalbard, Novaya Zemlya
21 and the Kara Sea region (see Majewski et al., 2009 and references therein).

22 The glaciomarine group comprised *Cassidulina reniforme*, *Elphidium excavatum* and
23 *Quinqueloculina stalkerii*. The characteristic species of the Atlantic water mass are
24 *Nonionellina labradorica*, *Bolivina pseudopunctata*, *Buccella frigida*, *Adercotryma*
25 *glomerata*, *Ammotium cassis* and *Recurvoides turbinatus*. We decided to exclude *Reophax*

1 *fusiformis* and *Reophax pilulifer* from this group because there were only 2 specimens of *R.*
2 *fusiformis* in the HF_2011 core, and *R. pilulifer* was not reported. The Arctic water group was
3 composed of *Islandiella norcrossi*, *Elphidium spp* (excluding *E.excavatum*), *Stainforthia*
4 *feylingi*, *Stainforthia loeblichii*, *Spiroplectammina biformis* and *Spiroplectammina earlandi*.
5 We decided to add *Islandiella helenae* to this group based on Kelly et al. (1999). The bottom
6 current indicator group consisted of *Cibicoides lobatulus* and *Astrononion gallowayi*.

7

8 **6 Results**

9

10 **6.1 Sediment age and characteristics**

11 The sediment was composed mainly of glaciomarine mud, with low sand content.
12 Before 1600 AD (145 cm), the mean grain size fluctuated slightly, except for one peak at ~
13 1450 AD (160 cm), which reached 4.5 ϕ . In ~ 1600 AD, the mean grain size increased
14 slightly to 6.2 ϕ . After 1800 AD (122 cm), it varied within a broader range of values and
15 presented three slight peaks between 1800 and 1850 AD (120 cm, 100 cm and 70 cm). A
16 decrease in the mean grain size was observed from the mid to the end of the 20th century (25-0
17 cm; Fig. 3).

18 From 1000 AD to 1800 AD (200-122 cm), the IRD flux was relatively stable and did
19 not exceed 2 grains $\text{cm}^{-2} \text{yr}^{-1}$. After that period, the IRD delivery increased considerably,
20 reaching up to 28 grains $\text{cm}^{-2} \text{yr}^{-1}$. From ~ 1900 to the end of the 20th century, the IRD flux
21 varied from 0.24 to 10 grains $\text{cm}^{-2} \text{yr}^{-1}$ (Fig. 3). There were three distinctive periods when
22 the amount of IRD in the sediment considerably increased (Fig. 3): 1) at the transition from
23 the MWP to the LIA (160-130 cm; up to 30 grains g^{-1}), 2) in the late LIA (115-80 cm; up to
24 24 grains g^{-1}) and 3) in the early 20th century (60-20 cm; up to 24 grains g^{-1}).

25 **6.2 Stable isotopes**

1 From 1000 to 1600 AD (200-145 cm), $\delta^{18}\text{O}$ showed relatively stable values varying
2 slightly from 2.63 ‰ vs. VPDB to 3.32 ‰ vs. VPDB. After 1600 AD, it fluctuated distinctly
3 from 2.23 to 3.50 ‰ vs. VPDB. Larger $\delta^{18}\text{O}$ values were observed before 1600 AD and in
4 the 20th century. The period from 1600 to 1900 AD (145-60 cm) was characterized by a
5 smaller $\delta^{18}\text{O}$, with significant peaks at the beginning of the LIA (~ 1600 AD; 145 cm) and
6 during the late LIA (05 cm and 90 cm). The measured values of $\delta^{13}\text{C}$ varied from 0.54 ‰ vs.
7 VPDB to 1.59 ‰ vs. VPDB and fluctuated along the core. The most important fluctuations
8 occurred between ~ 1600 and 1900 AD (145-60 cm), with $\delta^{13}\text{C}$ values ranging from 0.54 to
9 1.48 ‰ vs. VPDB (Fig. 3).

10

11 **6.3 Foraminiferal abundance and taxonomic composition revealed by the fossil record**

12 The foraminiferal flux varied from 1 to 86 ind cm⁻² yr⁻¹. The most noticeable shift
13 occurred at ~ 1800 AD (120 cm), when it increased from 2.8 to 81 ind cm⁻² yr⁻¹ (Fig. 3). The
14 number of foraminifera per gram of sediment varied from 86 to 3838 ind g⁻¹. The highest
15 values were observed before ~ 1850 AD (70 cm). After 1850 AD, the number of foraminifera
16 declined and did not exceed 1742 ind g⁻¹ (Fig. 3).

17 A total of 28,771 individuals were assigned to 72 species and 38 genera. Most of the
18 species belonged to Rotaliida (34), Textulariida (12) and Lagenida (12). The other species
19 were identified as Miliolida (10), Lituolida (2) and Globigerinida (Table S1 in the
20 Supplement). The most abundant species were *Elphidium excavatum*, *Cassidulina reniforme*,
21 *Cibicides lobatulus* and *Nonionellina labradorica* (Fig. 4). The fossil assemblage was
22 strongly dominated by *E. excavatum* and *C. reniforme*, which together comprised up to 82 %
23 of the total abundance. The abundance of *C. lobatulus* and *N. labradorica* varied slightly
24 along the core, and no evident faunal changes were observed. The highest percentages of *N.*
25 *labradorica* were noted after ~ 1800 AD and at the beginning of the 20th century (110 cm, 50

1 cm and 25 cm), when its relative abundance reached up to 25 %. The highest percentages of
2 *C. lobatulus* were noted before 1600 AD (145 cm), and a notable decrease in that species
3 occurred in the latter part of the 20th century (25-0 cm). The percentage of agglutinated taxa
4 did not exceed 25 % and reached its highest values between 1600 and 1800 AD (145-120 cm)
5 and after ~ 1930 AD (25 cm; Fig. 4).

6 The proposed 4-factor PC explained 98.5 % of the total variability of the tested
7 dataset. The most important PC analysis assemblages were (1) the *E. excavatum* FA, which
8 explained 40.8 % of the total foraminiferal variance, (2) the *C. reniforme* FA, with *E.*
9 *excavatum* as an accessory species, which explained 34.8 % of the variance, (3) the *N.*
10 *labradorica* FA, with *C. lobatulus* as an accessory species, which explained 20.1 % of the
11 variance, and (4) the *C. lobatulus* FA, which explained 2.8 % of the total variance (Table 2).
12 The HF_2011 core was dominated by the *E. excavatum* FA and the *C. reniforme* FA
13 throughout. The *E. excavatum* FA showed the highest factor loadings during the LIA (i.e.,
14 between 1600 and 1900 AD). In the uppermost part of the core, the *E. excavatum* factor
15 loadings decreased, and the role of the *C. reniforme* FA increased. The *N. labradorica* FA
16 was significant during the MWP and the early LIA (before ~ 1800 AD) and was not
17 significant during the late LIA (after ~ 1850 AD). The *N. labradorica* factor loadings started
18 to increase at the beginning of the 20th century. The *C. lobatulus* FA was significant only in
19 two layers dated to the MWP (Fig. 5).

20

21 **6.4 Foraminifera in the ancient DNA record**

22 The results of the aDNA analysis are described in detail in Pawłowska et al. (2014).
23 Herein, we summarize the results, focusing on monothalamous foraminifera.

24 We used Sanger and high-throughput sequencing (HTS) to obtain 717 and 8,700,815
25 sequences, respectively. A total of 394 operational taxonomic units (OTUs) were obtained

1 from the sequence clustering. The majority of the OTUs were assigned to Monothalamea (96
2 OTUs) and Rotaliida (93 OTUs). The remaining OTUs were assigned to Textulariida (33
3 OTUs), Miliolida (10 OTUs), Globothalamea (10 OTUs), Robertinida (1 OTU) and
4 Globigerinida (5 OTUs); 146 OTUs remained unassigned (Table S2). Although the sequences
5 of the species that dominated the fossil record were present in most of the samples, their
6 abundances did not reflect the abundances in the fossil specimens (see Pawłowska et al.,
7 2014).

8 The 96 OTUs assigned to monothalamids comprised 39.4 % of the sequences. The
9 percentage of monothalamous sequences varied along the core from 3.5 % to 65 %. (Fig. 5)
10 There were 7 OTUs constituting more than 3 % of all the sequences in at least one sample.
11 They were referred to *Bathysiphon* sp. (clade BM), *Micrometula* sp. (clade BM, 2 OTUs),
12 *Toxisarcon* sp. (clade C) and monothalamous foraminifera of undetermined phylogenetic
13 origin (3 OTUs; Table S2).

14 Monothalamid sequences were assigned to 14 clades, including 10 that were
15 represented by more than 5 % of the monothalamid sequences in at least one sample. The
16 assemblage of monothalamous foraminifera was strongly dominated by clade BM (genera
17 *Micrometula* and *Bathysiphon*), which together comprised up to 90 % of the sequences of
18 monothalamids (Fig. 5). *Bathysiphon* sp. was the most abundantly sequenced in the samples
19 spanning the MWP and the early LIA, whereas sequences of *Micrometula* sp. dominated in
20 the samples spanning the 20th century. The monothalamous assemblage during the MWP was
21 dominated by *Toxisarcon* sp. and environmental monothalamous sequences belonging to
22 clade V. The early LIA (1600 – 1800 AD; 150-125 cm) was marked by an increased
23 proportion of sequences of *Hipocrepinella hirudinea* (clade D) and *Cedhagenia saltatus*
24 (clade O). The monothalamous assemblage during the beginning of the MW (~ 1900 AD; 50
25 cm) was strongly dominated by *Micrometula* sp. (which made up to 75 % of the

1 monothalamous sequences), together with *Vellaria pellucidus*. In the late MW, a high number
2 of monothalamid sequences occurred that belonged to environmental clades or were of
3 undetermined phylogenetic origin (Fig. 6).

4

5 **7 Discussion**

6 Previous studies on the Svalbard Holocene history reported ‘unstable environmental
7 conditions’ during the last thousand years (e.g., Berben et al., 2014; Groot et al., 2014),
8 reflecting the major climatic changes: the MWP (~ 900 – 1500 AD), the LIA (~ 1500 – 1900
9 AD) and the MW (~ 1900 – present) (Oerlemans, 2005). The Svalbard ice core records and
10 sediment records from the shelf adjacent to Hornsund suggested that prolonged cooling
11 started ~ 1600 AD, and the most severe conditions occurred during the 19th century (Isaksson
12 et al., 2003; Majewski et al., 2009). On the contrary, the reconstruction of the Earth’s surface
13 air temperature from Svalbard (Divine et al., 2011) constituted the cooling stage between 800
14 and 1800 AD, with no clear signs of the onset of the LIA. Our foraminiferal and
15 sedimentological records from Hornsund matched the trend described by Divine et al. (2011),
16 as it revealed a sharp change in environmental conditions at ~ 1800 AD.

17

18 **7.1 The Medieval Warm Period and the early Little Ice Age (~ 1000 AD - ~ 1800 AD)**

19 The period from ~ 1000 to ~ 1800 AD was characterized by low and stable fluxes of
20 IRD and foraminifera and slightly heavier $\delta^{18}\text{O}$ (Fig. 3). This might indicate the influence of
21 warmer and more saline waters, probably of Atlantic origin, and low glacial activity (Jernas et
22 al., 2013). The fossil foraminiferal assemblage was fairly stable during the MWP (i.e., before
23 1600 AD) and there was no clear evidence of faunal change. Conversely, the foraminiferal
24 aDNA record featured a high percentage of *Toxisarcon* sp. (Clade C) at ~ 1000 AD (Fig. 5).
25 As reported by Gooday et al. (2005), *Toxisarcon* sp. are commonly found in the Svalbard

1 fjords. In the case of our study, the increase in the *Toxisarcon* sp. percentage coincided with
2 the peak of light $\delta^{18}\text{O}$, followed by lighter $\delta^{13}\text{C}$, which might suggest the presence of a highly
3 productive zone of frontal contact of the AW and ArW water masses. Voltski et al. (2014)
4 noted the presence of diatom frustules in the cytoplasm of *Toxisarcon* sp.. Therefore, we
5 concluded that the occurrence of *Toxisarcon* sp. might be related to the phytoplankton-
6 originated organic matter input.

7 Our data showed a slight peak of lighter $\delta^{18}\text{O}$ at 1600 AD (Fig. 3), which could
8 indicate an increase in melt water delivery to Hornsund, but it was not followed by increases
9 in sediment accumulation and IRD flux. Therefore, we concluded that lighter $\delta^{18}\text{O}$ at ~ 1600
10 AD showed the increased ArW inflow from the Barents Sea to the Svalbard shelf and
11 Hornsund, which is in agreement with previous $\delta^{18}\text{O}$ and fossil foraminiferal records
12 obtained from the outer fjord (Majewski et al., 2009). This event occurred within a period of
13 significant climate changes connected to the transition from the MWP to the LIA. The
14 Humlum et al. (2005) investigation of the frozen *in situ* vegetation below Longyearbyen
15 glacier (central Spitsbergen) indicated the advance of that glacier during the last ~1100 years.
16 Based on the terrestrial record from Hornsund, the WMP was interrupted 600 years ago by an
17 advance of glaciers (Marks and Pękala, 1986; Linder et al., 1990) that lasted until the
18 beginning of the 20th century.

19 The most pronounced changes that occurred at ~ 1600 AD in the HF_2011 fossil
20 assemblage were slight peaks in the abundances of *N. labradorica*, *I. norcrossi* and *I. helena*.
21 Moreover, an increase in the percentage of agglutinated taxa was noted between 1600 AD and
22 1800 AD (Fig. 4). *Nonionellina labradorica* is an AW indicator usually found in relatively
23 warm and saline waters (Lloyd, 2006; Majewski et al., 2009). However, the abundances of
24 these three species seemed to be controlled more by the food supply than by water
25 temperatures (Hald and Korsun, 1997; Lloyd, 2006; Ivanova, 2008). The presence of

1 *Islandiella* spp might indicate a highly productive environment related to the Polar Front
2 (Steinsund, 1994). This supports the evidence of the inflow of the colder and less saline ArW
3 at ~ 1600 AD, which changed the water mass balance and productivity in the fjord.

4 The foraminiferal flux before ~ 1800 AD was low (Fig. 3) and could be explained by
5 the presence of species with low fossilization potential, e.g., agglutinated taxa (Wollenburg
6 and Kuhnt, 2000). The percentage of agglutinated taxa was relatively low during the MWP
7 and increased significantly after 1600 AD (Fig. 4), which likely reflected the inflow of the
8 ArW and relatively low glacial activity (Hunt and Corliss, 1993; Hald and Korsun, 1997). Our
9 aDNA data suggests that the abundance of agglutinated foraminifera was higher than that
10 shown by the fossil record. Three agglutinated taxa were detected in both the fossil and aDNA
11 record: *C. crassimargo*, *Reophax* spp and *Spiroplectamina* spp (Tables S1 and S2).
12 However, only *C. crassimargo* was detected by both approaches in the corresponding layers.
13 *Reophax* spp and *Spiroplectamina* spp sequences were recorded in all the examined
14 samples, but they were relatively rare or absent in the fossil material (Pawłowska et al., 2014),
15 probably due to the degradation of their tests. Korsun and Hald (2000) regarded *S. biformis*
16 and *S. earlandi* as typical for glaciomarine habitats. They noticed an increase in the
17 abundance of those agglutinated species off glacier. Korsun et al. (2005) and Hald and Korsun
18 (1997) reported *Reophax* spp and *Spiroplectamina* spp in the outer parts of the glacially fed
19 fjords of Svalbard and Novaya Zemlya. Zajączkowski et al. (2010) noted a decrease in the
20 abundance of agglutinated foraminifera in Hornsund with increasing water turbidity. Thus, the
21 presence of those species might indicate a glacier-distant environment.

22 Furthermore, the transition to the LIA between ~ 1600 and ~ 1800 AD was well
23 marked by the increase in the percentage of monothalamous foraminifera aDNA sequences
24 (Fig. 6). Monothalamids are highly adaptable and occur in environments where conditions
25 may be extreme (Gooday, 2002; Sabbattini et al., 2010), which makes them effective

1 colonizers. It is likely that the change in the hydrology and productivity in Hornsund at ~
2 1600 AD might have created a new ecological niche, which was effectively settled by
3 monothalamids. The monothalamous assemblage during the early LIA (from ~ 1600 to ~
4 1800 AD) was dominated by taxa belonging to clade BM, mainly from genus *Bathysiphon*
5 (Fig. 6). Gooday et al. (2005) reported *Bathysiphon* sp. in two glacial influenced fjords, Van
6 Mijenfjorden and Kongsfjorden, at glacier distant sites. Moreover, a sharp peak of heavier
7 $\delta^{13}\text{C}$ was noted in Hornsund at ~ 1600 AD, which might suggest the short-term suppression of
8 primary productivity that resulted in the presence of degraded organic matter and
9 phytodetritus that seemed to be favourable for *Bathysiphon* sp. (Alve et al., 2010). The
10 presence of sequences of *Bathysiphon* sp. and agglutinated *Spiroplectammina* spp and
11 *Reophax* spp support our conclusion that at the onset of the LIA (~ 1600 - ~ 1800 AD), the
12 position of the glacier fronts was relatively distant to the fjord centre, which resulted in a low
13 SAR and a low IRD flux, whereas the fjords' water masses were influenced by the ArW.

14 The transition to the LIA (~ 1600 - ~ 1800 AD) was also marked by increased
15 percentages of sequences assigned to the monothalamid clade D (mainly *Hippocrepinella*
16 *hirudinea*) and to clade O (mainly *Cedhagenia saltatus*; Fig. 5). *Cedhagenia saltatus* is a
17 species recently found by Gooday et al. (2011) in the Black Sea. Little is known about the
18 environmental tolerance of *C. saltatus*. However, its presence in the area is strongly impacted
19 by human activity, which suggests that it is an opportunistic species that has a high tolerance
20 to environmental disturbance. *Hippocrepinella hirudinea* was noted in the fjords of Svalbard
21 by Majewski et al. (2005) and Gooday et al. (2005). It appeared in the central and outer parts
22 of the studied fjords, mainly in the shallow water sites. Korsun et al. (2005) noted the
23 presence of the genus *Hippocrepinella* in Novaya Zemlya; however, it may not have referred to
24 *H. hirudinea*. The scarce data on the ecological tolerances of *H. hirudinea* and *C. saltatus*
25 precluded making any general conclusions.

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7.2 The late Little Ice Age (~ 1800 AD - ~ 1900 AD)

The late LIA was characterized by an increased sediment accumulation rate and strongly fluctuating IRD delivery (Fig. 3). These changes were linked to changes in the particulate matter flux, which in subpolar fjords was governed by glacial meltwater discharge (Syvitski, 1989). Substantial amounts of suspended sediment and IRD might be released from glaciers during rapid deglaciation and during glacial surges (Koppes and Hallet, 2002). Moreover, sediment might be stored in the proglacial zones of land-based glaciers, from where could be eroded, particularly under conditions of increased glacial meltwater runoff and increased precipitation (Szczuciński et al., 2009). Next, the sediment could be redeposited from the sublittoral zone by storm waves. During the LIA, glacial extent reached its Holocene maximum (D'Andrea et al., 2012); thus, calving and melt water delivery could have occurred close to the central part of the fjord. Noticeably, the increase in the IRD delivery during the late LIA was not followed by an increase in the mean grain size, as was observed in both the precedent and following periods. It is likely that the amount of fine-grained sediment delivered to the sea bottom significantly exceeded the amount of coarse ice-rafted sediment (i.e., IRD) and, consequently, almost no change in the mean grain size was observed.

Our data showed a 20-fold increase in the foraminiferal flux at ~ 1800 AD (Fig. 3), whereas the species diversity was relatively low due to the dominance of glaciomarine species, especially *E. excavatum* and *C. reniforme* (Figs. 4 and 5). As a consequence of the maximal range of the glaciers, conditions throughout the fjord became more glacier-proximal.

The aDNA revealed the dramatic increase in the percentage of sequences of monothalamous foraminifera at ~ 1900 AD (Fig. 6). Previous studies revealed that the distribution of monothalamids in Svalbard was closely related to the distance from the glacier at the head of the fjord. The study conducted by Majewski et al. (2005) in Kongsfjorden and

1 Isfjorden showed a distinctive faunal gradient along the fjord axes, with three different
2 monothalamous assemblages at subtidal, shallow-water and deep-water sites. Korsun et al.
3 (2005) and Korsun and Hald (1998, 2000) reported that allogromiids constituted up to 99 %
4 of living foraminifera in the stations close to the glacier termini in Novaya Zemlya and
5 Spitsbergen. Sabbattini et al. (2007) attributed the occurrence of monothalamids in the
6 Svalbard region to inputs of fresh water and a high, changeable sedimentation rate. Gooday et
7 al. (2005) noted that the inner parts of Tempelfjorden and Kongsfjorden, fjords headed by
8 tidewater glaciers, were dominated by organic-walled allogromiids and saccamminids. This
9 was reflected in our data as the percentage of allogromiids (mainly *Micrometula* sp.)
10 increased significantly from 40 % at ~ 1850 AD to 80 % at ~ 1900 AD (Fig. 5). Moreover, the
11 late LIA and the early MW were marked by an increase of the percentage of sequences
12 assigned to clade E, mainly *Vellaria pellucidis*. Majewski et al. (2005) noted the presence of
13 *Vellaria* sp. in subtidal and shallow areas of the Spitsbergen fjords. The increase in the
14 percentage of *Micrometula* sp. and *V. pellucidis* in the period of the highest glacial activity
15 suggests that those species were potential indicators of glacier-proximal settings.

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17 **7.3 The Modern Warming (~ 1900 AD – present)**

18 The sedimentary record of the MW featured a decrease in the SAR and a lower but
19 variable IRD flux (Fig. 3). Peaks in the IRD flux coincided with the increased mean grain size
20 (Fig. 3). This trend was opposite to that of the late LIA, where no clear correlation between
21 the IRD flux and mean grain size was observed. The post-LIA glacial retreat led to an
22 increased distance between the coring station and the main tidewater glacier front. In the
23 Spitsbergen fjords, fine-sized particles from glacial outflows are deposited close to the source
24 (Szczuciński et al., 2009); therefore, the HF_2011 station was impacted mainly by ice-rafted,
25 coarser particles. The IRD flux gradually diminished in the late 20th century, which was

1 probably a result of retreat of the tidewater glaciers' fronts to the inner bays, which limited
2 iceberg drift to the fjord centre. The most noticeable changes in the fossil foraminifera
3 community occurred in the late 20th century, with the gradual increase of *B. frigida* and *I.*
4 *norcrossi* and the decrease of *C. lobatulus* (Fig. 4). *Islandiella norcrossi* and *B. frigida*
5 typically occupied the distal sections of the glacial fjords of Svalbard and Novaya Zemlya
6 (Korsun et al., 2005; Hald and Korsun, 1997; Korsun and Hald, 2000; Pogodina, 2005).
7 Steinsund (1994) linked the presence of *I. norcrossi* and *B. frigida* with high productivity
8 related to a polar front position and seasonal sea-ice cover. Thus, we concluded that since the
9 mid-20th century, Hornsund and the adjacent shelf remained under the influence of the AW,
10 which formed a frontal zone with local waters. This conclusion is supported by the PC
11 analysis, which showed that the significance of the *N. labradorica* FA was increasing during
12 the 20th century (Fig. 5). *Cibicidoides lobatulus* is a relatively shallow-water species and
13 takes advantage of vigorous bottom waters (Hald and Korsun, 1997; Lloyd, 2006); however,
14 it is an epiphytic species that needs a hard substrate to stay attached to the bottom surface.
15 Therefore, the decrease in the percentage of *C. lobatulus* could be connected to a decrease in
16 the near-bottom currents and a low IRD flux and, consequently, an increase in the fine
17 sediment fraction (Fig. 3). The increased abundance of species typical of glacier-distal faunas
18 was followed by a decrease in the abundance of species considered to be bottom current
19 indicators (Fig. 4). These results support our evidence for a rapid glacier retreat, coupled with
20 the decreasing influence of glaciomarine sedimentation and enhanced productivity. It was also
21 reflected in the molecular record, where the number of OTUs and the percentage of
22 monothalamids decreased after ~ 1920 AD, reaching values similar to those during the MWP
23 (Fig. 6). The second half of the 20th century was marked by a significant increase in the
24 unassigned monothalamids sequences belonging to environmental clades. However, without

1 an accurate identification of sequences, it is not possible to make any palaeoecological
2 interpretations.

3 The use of the approach based on aDNA allows the hidden diversity of benthic
4 foraminifera communities to be assessed and, therefore, the information based on traditional
5 palaeoceanographic proxies to be refined. However, current methodological biases associated
6 with the environmental DNA sequencing approach preclude comprehensive analyses of
7 sequence abundance data. The aDNA data should be interpreted carefully as it is not possible
8 to establish the direct relationship between the number of
9 specimens and the number of ribosomal sequences. Some aspects of quantitative DNA
10 analyses were discussed in Weber and Pawlowski (2013). One of the conclusions was that
11 when the species is very abundant, its sequences are also numerous. Therefore, the genuinely
12 dominant species might be associated with high sequence occurrences in the sequencing data.

13

14 **8 Conclusions and Perspectives**

15 The main climatic fluctuations of the last millennium (the MWP, the LIA and the
16 MW) were reflected in the fjord water mass balance and glacial activity. The marine
17 environmental conditions during the MWP and the early LIA were relatively stable, with a
18 low SAR and low IRD flux. The beginning of the LIA (~ 1600 AD) was poorly supported by
19 the fossil record, but it was well evidenced in the aDNA data. It was marked by the increased
20 percentage of sequences of monothalamous foraminifera, mainly *Bathysiphon* sp., which
21 supports our assumption that the terminal positions of the glaciers were relatively distant at
22 the onset of the LIA. The early LIA (~ 1600 – ~ 1800 AD) was also marked by high
23 percentages of *H. hirudinea* and *C. saltatus*. The late LIA (after ~ 1800 AD) was
24 characterized by the increased proximity of tidewater glaciers' fronts, which increased
25 sedimentation from suspension and from the icebergs; thus conditions in the fjord centre

1 became glacier-proximal. The end of the LIA (~ 1900 AD) was marked by increased
2 percentage of *Micrometula* sp. and *V. pellucidus*. Those results revealed their potential as
3 indicators of glacier-proximal environments, which were characterized by melt water
4 outflows, a high sedimentation rate and increased calving. During the MW, the major
5 glaciers' fronts retreated rapidly to the inner bays, limiting the iceberg discharge to the fjord
6 centre and causing the shift in the foraminiferal community reflected in the fossil and aDNA
7 records.

8 The present study was the first attempt to implement an aDNA foraminiferal record for
9 palaeoclimatic reconstruction. The data inferred from the molecular analyses correlated well
10 with environmental changes. The aDNA record even revealed small environmental changes
11 that were not clearly indicated by the fossil record. By including monothalamous foraminifera
12 identified in the aDNA record, we considerably increased the number of potential proxy
13 species. However, to fully benefit from this new source of information, it is essential to
14 improve knowledge of the ecology of monothalamids. The positive results of the present
15 study encourage further applications of ancient foraminiferal DNA sequences to reconstruct
16 past environmental changes in polar regions.

17

18 **Acknowledgements**

19 This study was supported by the Scientific Exchange Programme between Switzerland and
20 the New Member States of the EU (Sciex-NMS) project 10.140 and by the Swiss National
21 Science Foundation grant 31003A_140766. The study was also funded by the Polish Ministry
22 and Higher Education Grants No. 2013/11/B/ST10/00276 and 2014/12/T/ST10/00675. The
23 authors thank the crew of R/V Oceania for their assistance during the fieldwork. Ms.C.
24 Mateusz Ostrowski is thanked for helping with the granulometric analysis.

25

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1 **Table 1.** Raw AMS ^{14}C and calibrated dates used for the age model (after Pawłowska et al.,
 2 2014).

Sediment depth [cm]	Material	Raw AMS ^{14}C	Calibrated years BP $\pm 2\sigma$	Years AD used in age model
8.5	<i>Cilliatocardina cilliatea</i>	105.58 (± 0.35) pMC	-10 - -35	
33.5	Bivalvia nd.	9990 (± 50) BP	10 605-11 040	
48.5	Gastropod nd.	610 (± 30) BP	40-240	
56.5	<i>Nuculana pernula</i>	880 (± 25) BP	315-485	
70.5	<i>Bathyarca glacialis</i>	580 (± 30) BP	1-150	1850
89.5	<i>Macoma calcarea</i>	765 (± 30) BP	230-420	
106.5	<i>Cilliatocardina cilliatea</i>	760 (± 30) BP	230-420	
109.5	<i>Cilliatocardina cilliatea</i>	735 (± 25) BP	180-380	
122.5	Gastropod nd.	615 (± 30) BP	40-250	1800
166.5	<i>Hiatella arctica</i>	1075 (± 30) BP	500-630	1450
173.5	<i>Macoma calcarea</i>	1145 (± 30) BP	540-670	1400

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1 **Table 2.** PC scores and percent of total variance explained by four factor principal component
 2 analysis. The contribution of each analysed species is shown, and species significant for
 3 particular assemblages are marked in bold.

	PC 1	PC 2	PC 3	PC 4
Percent of total variance explained	40.8 %	34.8 %	20.1 %	2.8 %
<i>Adercotryma glomerata</i>	-0,1857	-0,13401	-0,75184	-0,06062
<i>Buccella frigida</i>	-0,40847	0,081688	-0,13456	-0,34934
<i>Cassidulina reniforme</i>	-1,44681	2,923605	0,894126	0,480619
<i>Cibicidoides lobatulus</i>	-0,22008	-1,29993	1,821983	2,252356
<i>Cribrostomoides crassimargo</i>	0,13799	0,418817	-0,63454	-1,15662
<i>Elphidium bartletti</i>	-0,06081	-0,41644	-0,64903	0,130446
<i>Elphidium excavatum</i>	3,21345	1,108558	0,281919	0,526077
<i>Islandiella helenae</i>	-0,39509	-0,39785	0,267723	0,366261
<i>Islandiella norcrossi</i>	-0,21596	-0,31512	-0,5112	0,091585
<i>Nonionellina labradorica</i>	0,124046	-0,71182	2,242218	-2,40609
<i>Quinqueloculina stalkerii</i>	-0,23152	-0,30084	-0,57036	0,05742
<i>Recurvoides turbinatus</i>	-0,15527	-0,33373	-0,6666	0,055335
<i>Spiroplectammina biformis</i>	-0,08015	-0,30205	-0,80459	0,020384
<i>Spiroplectammina</i> sp.	-0,07563	-0,32089	-0,78525	-0,00781

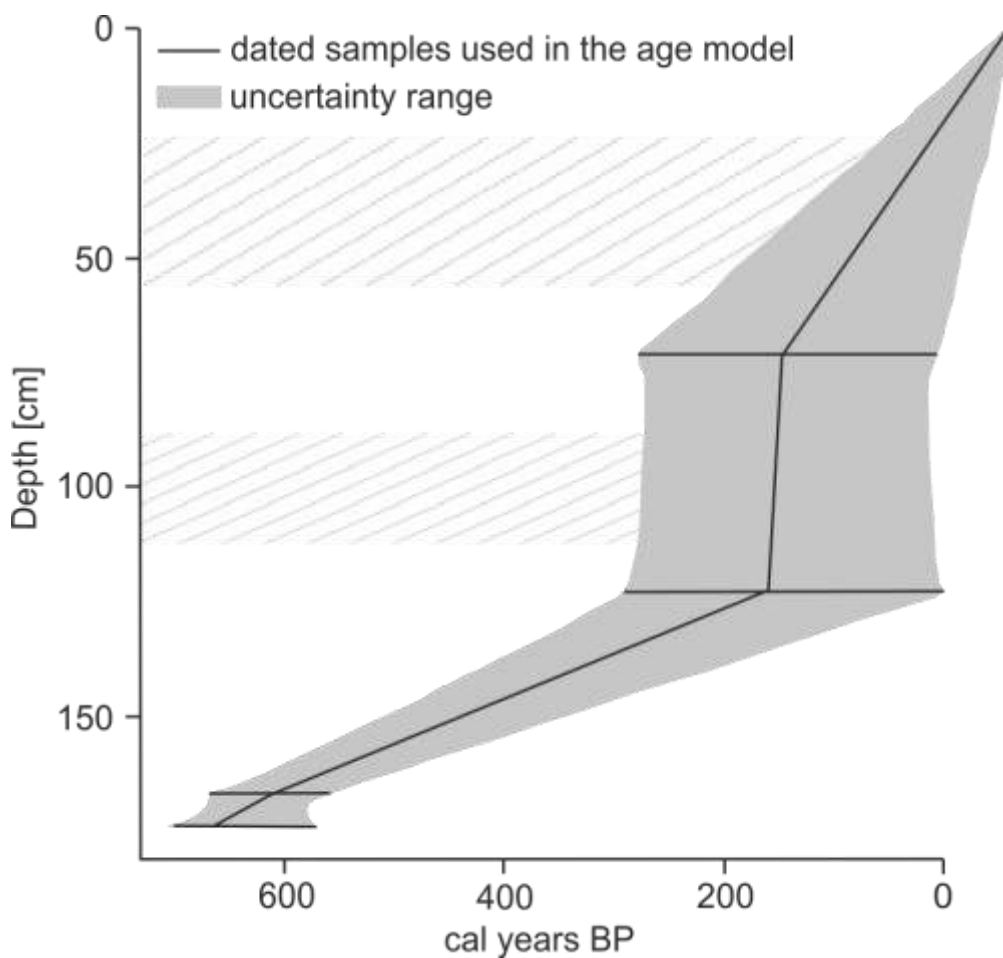
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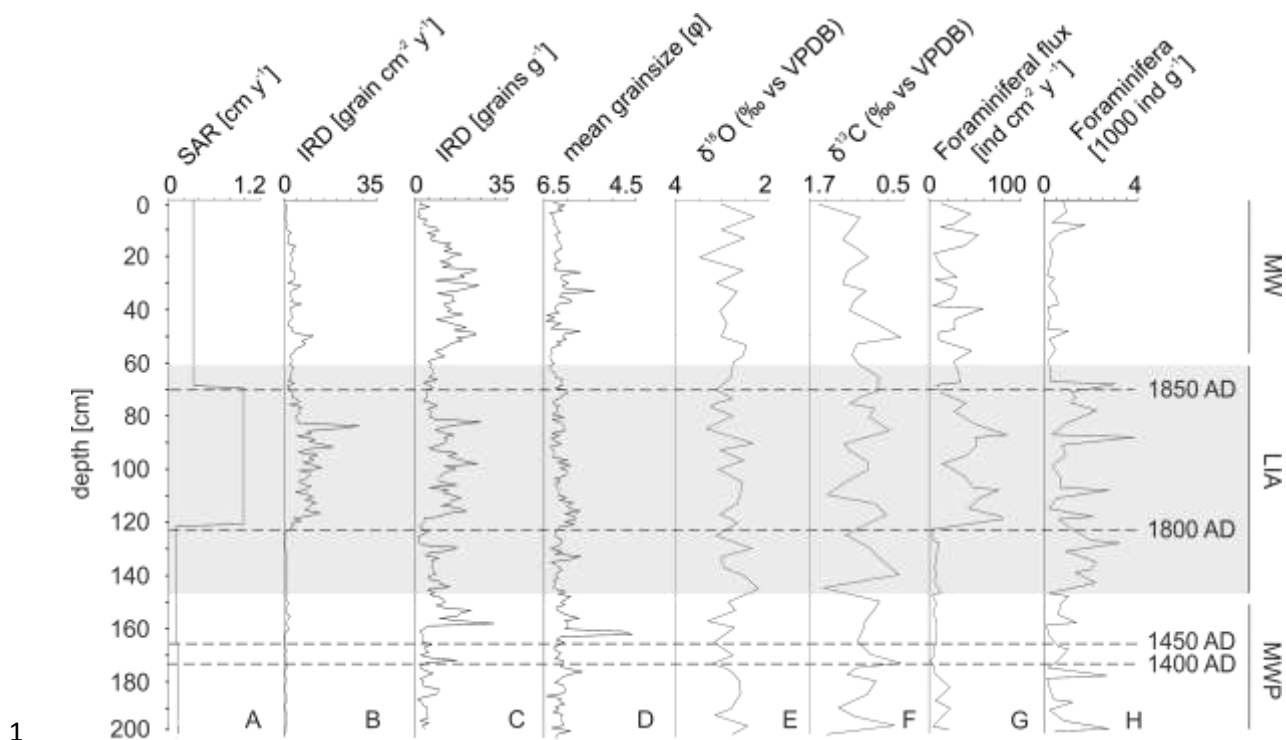
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 2 **Figure 1.** Bathymetric map of Hornsund with sampling station HF 2011. The position of core
 3 HR 3 studied by Majewski et al. (2009) is shown. Glaciers are shown in white. WSC – West
 4 Spitsbergen Current, ESC – East Spitsbergen Current.

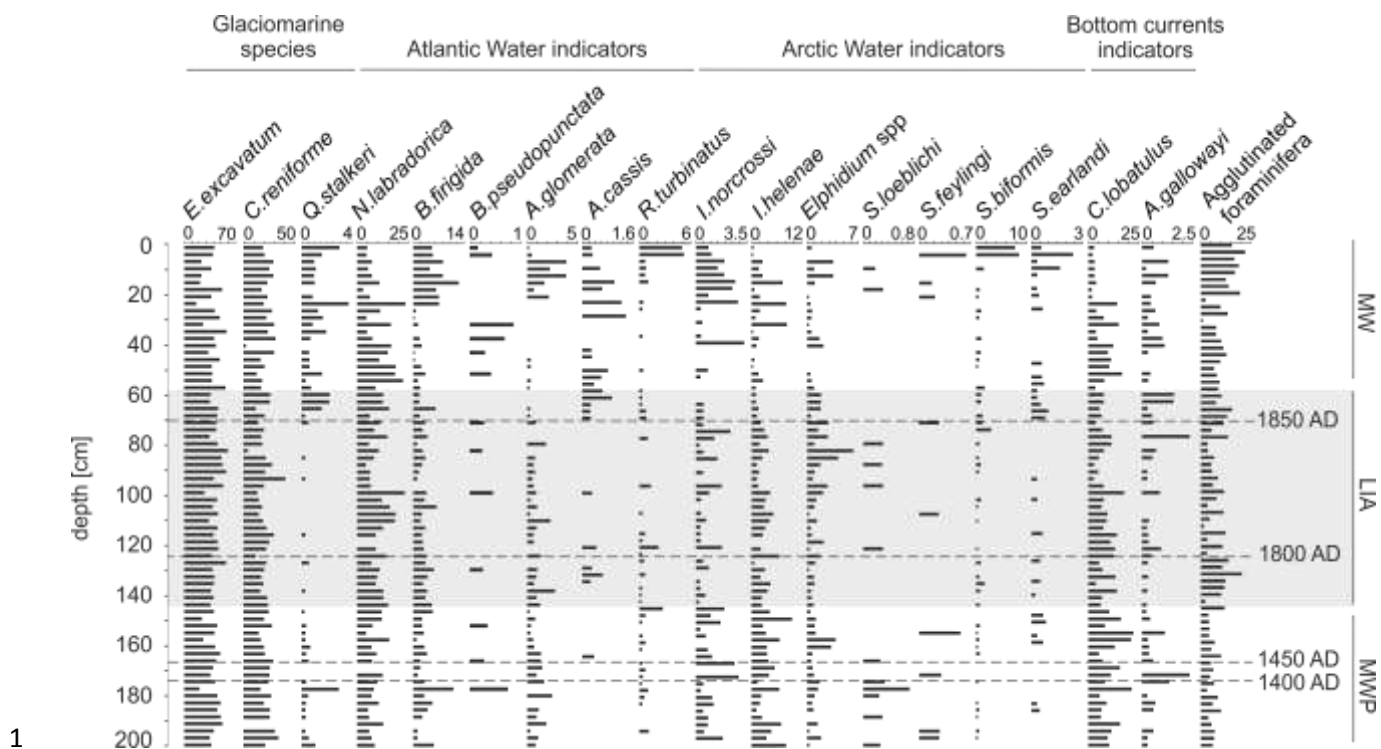


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 2 **Figure 2.** Age model of the studied core. The black line indicates the age-depth model
 3 derived from a linear interpolation. The grey fields show the probability distributions of
 4 calendar dates obtained by the calibration of individual ^{14}C dates used for the age model. The
 5 shaded areas mark sediment intervals which most likely represent major redeposition events
 6 (after Pawłowska et al. 2014, modified).



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2 **Figure 3.** Sediment accumulation rate (A), IRD delivery, expressed as IRD flux (B) and
3 number of IRD grains per gram of sediment (C), mean grainsize (D), stable oxygen (E) and
4 carbon (F) isotopes, flux of total fossil foraminifera (G) and number of foraminifera per gram
5 of sediment (H). MWP: Medieval Warm Period, LIA: Little Ice Age, MW: Modern Warming.
6 The time ranges of the MWP, LIA and MW are presented after Majewski et al. (2009).

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2 **Figure 4.** The abundances of selected foraminifera species expressed as percentages (%) of
3 the total assemblage. The foraminiferal taxa were grouped based on their ecological
4 tolerances (see Sect. 5: Foraminifera as palaeoenvironmental indicators). MWP: Medieval
5 Warm Period, LIA: Little Ice Age, MW: Modern Warming. The time ranges of MWP, LIA
6 and MW are presented after Majewski et al. (2009).

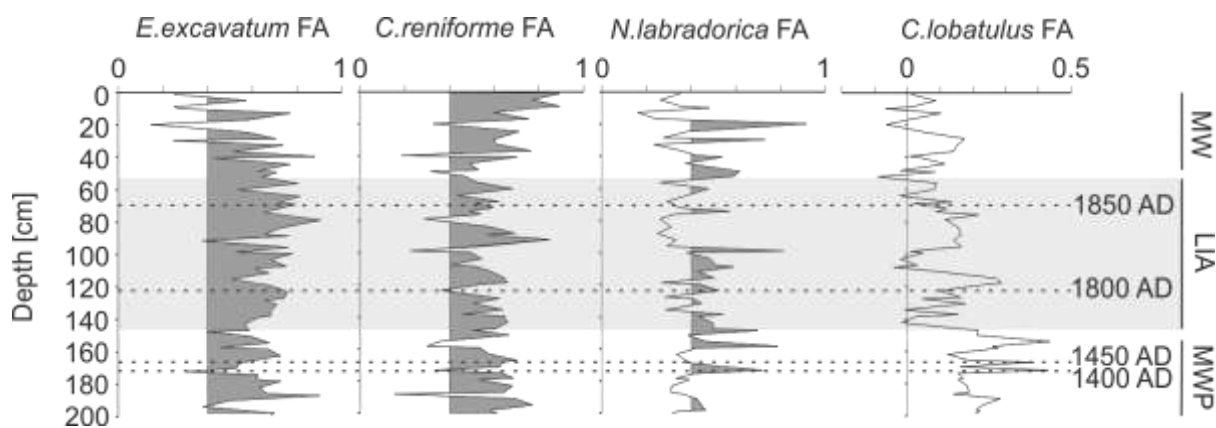
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2 **Figure 5.** PC loading values for four foraminiferal assemblages found in the HF_2011 core.
3 The statistically significant loadings are marked in grey. MWP: Medieval Warm Period, LIA:
4 Little Ice Age, MW: Modern Warming. The time ranges of the MWP, LIA and MW are
5 presented after Majewski et al. (2009).

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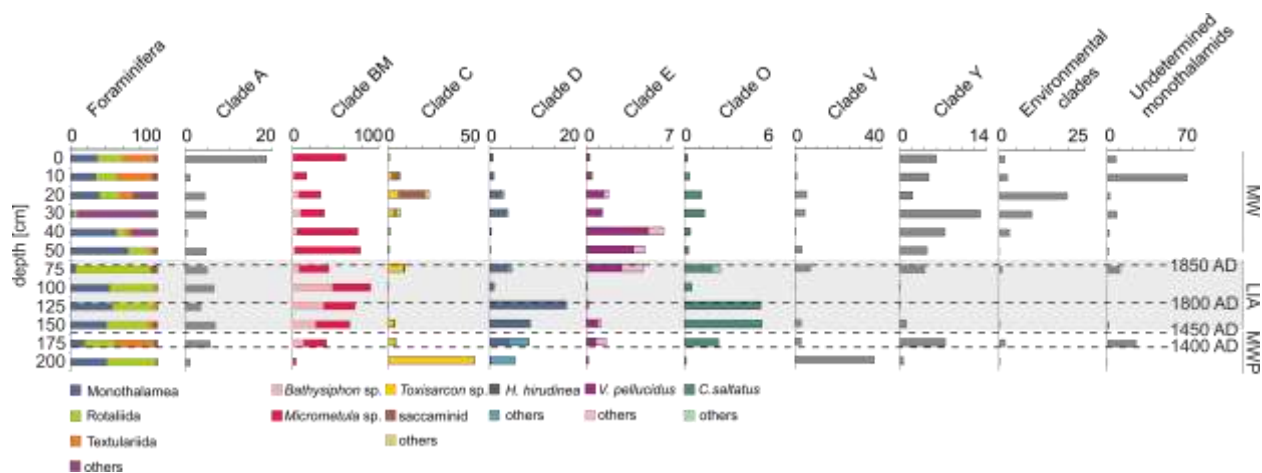
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 2 **Figure 6.** The relative abundance of the monothalamid sequences, expressed as the
 3 percentage of all foraminiferal sequences, and the composition of the monothalamid
 4 assemblage, expressed as percentages of sequences within clades. Clades that constitute more
 5 than 5 % of the monothalamid sequences in at least one sample are presented. ‘Environmental
 6 clades’ relate to foraminifera known only from environmental sequencing.

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9 **Electronic supplementary material**

10 **Table S1.** List of fossil foraminifera species and number of individuals in core HF_2011.

11 **Table S2.** OTU richness and number of foraminiferal sequences in core HF_2011.

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