Clim. Past Discuss., 11, 3665–3698, 2015 www.clim-past-discuss.net/11/3665/2015/ doi:10.5194/cpd-11-3665-2015 © Author(s) 2015. CC Attribution 3.0 License.



This discussion paper is/has been under review for the journal Climate of the Past (CP). Please refer to the corresponding final paper in CP if available.

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

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Received: 30 May 2015 - Accepted: 15 July 2015 - Published: 13 August 2015

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Published by Copernicus Publications on behalf of the European Geosciences Union.



#### Abstract

This paper presents the reconstruction of climate-driven environmental changes of the last millennium from Hornsund Fjord (Svalbard) based on sedimentological and micropalaeontological records. Our palaeo-investigation was supported by the analysis of foraminiferal ancient DNA (aDNA), focusing on non-fossilised monothalamous species.

- The main climatic fluctuations over the last millennium were the Medieval Warm Period (MWP, 1000–1600 AD), the Little Ice Age (LIA, 1600–1900 AD), and the Modern Warming (MW, 1900 AD–present). Our study indicated that environmental conditions in Hornsund during the MWP and the early LIA (before ~ 1800 AD) were relatively
- stable, resulting from the distant position of glaciers. The beginning of the LIA (~ 1600 AD) was poorly evidenced by the micropalaeontological record, but well marked in the aDNA data, by an increased proportion of monothalamous foraminifera, especially *Bathysiphon* sp. The early LIA (~ 1600–~ 1800 AD) was marked by the increase in abundance of sequences of *Hippocrepinella hirudinea* and *Cedhagenia saltatus*. In the
- late LIA (after ~ 1800 AD), conditions in the fjord became glacier-proximal, characterised by increased meltwater outflows, high sedimentation and a high calving rate. This coincided with an increase in the percentages of sequences of *Micrometula* sp. and *Vellaria pellucidus*. During the MW, major glaciers fronts retreated rapidly to the inner bays, limiting the iceberg discharge to the fjord centre and causing the shift in the
   foraminiferal community reflected in both fossil and aDNA records.

Palaeoceanographic changes in the Hornsund Fjord over the last millennium were driven mainly by the inflow of shelf-originated water masses and glaciers' activity. However, the environmental changes were poorly evidenced in the micropalaeontological record, but well documented in our aDNA data. We considerably increased the number

<sup>25</sup> of potential proxy species by including monothalamous foraminifera in the palaeoecological studies.



#### 1 Introduction

The general outline of climate development over the last millennium is the Medieval Warm Period (MWP), followed by cooling during the Little Ice Age (LIA) and warming in the 20th and 21st centuries (Modern Warming; MW). In the European Arctic, the temperature increase during the the Modern Warming and MW correlated with the

strong influence of the Atlantic Water inflow and associated heat transport (Wanamaker et al., 2012). In contrary, the weakening of the Atlantic Meridional Overturning Circulation (AMOC) and lower heat transport to the Arctic might be responsible for the LIA cooling (Lund et al., 2006). Changes in the Arctic Ocean heat budget were associated with significant changes in the cryosphere, especially the gradual decreases in glacier mass balance and the extent of the sea-ice cover in the last century (e.g., D'Andrea et al., 2012; Jernas et al., 2013).

However, to fully understand the consequences of climate changes in the Arctic, it is necessary to study the long-term high-resolution record of environmental changes

reflecting influences of both marine and terrestrial components. Fjord records provide a large body of information from these two systems; however, the major effort in studying the Holocene history of Svalbard was mainly focused on the shelf area (e.g., Hald et al., 2007; Rasmussen et al., 2012; Łącka et al., 2015). There were only a few high resolution studies of the sedimentary record of Svalbard fjords from the last millennium
 (e.g., Majewski and Zajączkowski, 2007; Majewski et al., 2009).

The environmental changes during the last millennium observed in the Svalbard shelf were correlated with the interplay of Atlantic and Arctic water masses (Kubischta et al., 2011; Jernas et al., 2013). Hornsund Fjord is strongly influenced by tidewater glaciers and thus the sedimentary record in this fjord might indicate that enhanced melt-water

delivery increased the sediment accumulation and restricted the sea productivity during the periods of glaciers advance or retreat. Therefore, it is crucial to create a network of proxies carrying different but complementary information to provide a complete model of past environmental changes in the Arctic fjords.



Foraminifera are widely used as proxies of past and present environmental changes in all types of marine environments. However, palaeoceanographic reconstructions are focused on the multi-chambered hard-shelled taxa, ignoring soft-walled, monothalamous species, which often dominate the foraminifera assemblages in deep sea and high latitude regions (Gooday, 2002). Monothalamous foraminifera, with organic or predom-

- inantly organic test walls, are traditionally defined as "allogromiids" (Gooday, 2002). However, morphological and molecular evidence indicate that "allogromiids" do not refer to a coherent taxonomic group, but they are scattered between several monothalamous clades (Pawlowski et al., 2002; Lejzerowicz et al., 2013a). The group includes
- organic-walled ("naked") and agglutinated forms of various shapes (Cedhagen et al., 2002). Monothalamous foraminifera with a test build of agglutinated particles are referred to as "saccamminids" or "psammosphaerids." The term "allogromiid" is sometimes applied to monothalamous taxa, irrespective of the wall type. Therefore, literature reports might include "saccamminids" and "psammosphaerids" in the "allogromiids"
   group (Gooday, 2002).

Previous studies showed that it was possible to consider monothalamous and polythalamous foraminifera (Lejzerowicz et al., 2013b), as well as other groups of nonfossilised Eukaryotes (e.g., Coolen et al., 2013, 2006; Boere et al., 2011), in palaeoecological surveys using ancient DNA (aDNA) metagenetics. To include monothala-

- <sup>20</sup> mids into palaeoecological studies of the Arctic foraminifera we analysed the ancient foraminiferal DNA record from the last millennium from Hornsund (Pawłowska et al., 2014). The study showed that aDNA record contained almost all of the species reported for Hornsund from previous micropalaeontological investigations (e.g., Hald and Korsun, 1997; Pogodina, 2005). However, the richness of the foraminiferal communi-
- ties revealed by molecular analysis was much higher than in the fossil record because the aDNA data provided a much broader view of benthic foraminifera communities in particular, as they include monothalamous species that were not preserved during the fossilisation process.



The aim of this study was to reconstruct the climate-driven environmental changes over the last millennium in Hornsund, with decadal to multi-decadal resolution. The promising results of our previous study (Pawłowska et al., 2014) encouraged us to use our aDNA data to supplement the palaeoclimatic record based on traditional proxies. We evaluated the potential use of monothalamous foraminifera as palaeoceanographic

proxies, showing that they might provide valuable environmental information, complementary to the data obtained with traditional microfossil proxies.

#### 2 Study area

Hornsund is the southernmost fjord of Spitsbergen. It is connected to the open sea by a wide unlimited outlet, which facilitates its penetration by oceanic waters. The fjords' coastline is variable, encompassing several glacier-proximal basins, separated by sills. In its central part, the water depth exceeds 200 m and varies from 55 to 180 m in the glacier-proximal basins (Fig. 1).

The hydrology of the fjord is under the influence of two main exogenous water <sup>15</sup> masses: the Atlantic Water (AW) and the Arctic Water (ArW). AW is warm and saline, <sup>15</sup> its temperature and salinity are usually defined as ≥ 3 °C and ≥ 34.9, respectively. ArW <sup>16</sup> is colder and fresher, and its salinity varies along the Spitsbergen shelf due to the freshwater outflows from fjords (Cottier et al., 2005). AW and ArW mix over the continental shelf to form the Shelf Transformed Water (STW), with a temperature and salinity of 1 °C and 04.7, mean atticute. CTW

<sup>20</sup> 1 °C and 34.7, respectively. STW mainly occupies the outer and central part of the fjord. Local Water (LW) is formed directly in the fjord by convectional mixing during fall and winter cooling or the interaction between warmer fjord water and glacier fronts (Svendsen et al., 2002).

Seventy percent of the Hornsund catchment area is covered by glaciers (Hagen et al., 1993). The melting of the eight major tidewater glaciers results in an important sediment delivery to the fjord. The modern sediment accumulation rate varies from 0.5 to 0.7 cm yr<sup>-1</sup> in the central and inner parts, respectively (Szczuciński et al., 2006).



During the last millennium Hornsund was subjected to major climatic changes, including the MWP, cooling and glacier advances during the LIA culminating in the period from 1600 to 1900 AD, and warming and massive glacier retreats during the 20th and 21st centuries (MW; Ziaja, 2001; Pälli et al., 2003). These changes correlated with variability of the inflow of cold ArW and warm AW and were recorded in foraminifera assemblages and the stable isotopes composition of foraminiferal tests (Majewski et al., 2009).

#### 3 Material and methods

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The 2 m long sediment core HF\_2011 was taken with a gravity corer from the R/V
 Oceania during the cruise in July 2011. The sampling station was located in the central part of the fjord (Fig. 1). The core was subsampled on board for aDNA analyses and frozen at -20 °C until further analyses at the Institute of Oceanology Polish Academy of Sciences (Sopot, Poland), as described in Pawłowska et al. (2014). After thawing at 4 °C, the core was split in two parts longitudinally, and each half was cut into 1 cm
 slices for micropalaeontological and sedimentological analyses. Carbonate shells were picked for accelerator mass spectrometry (AMS) <sup>14</sup>C dating.

#### 3.1 Grain-size and stable isotope analyses

The grain size analysis of the sediment slices was conducted using the Mastersizer 2000 laser analyser coupled with a HydroMU device (Malvern Instruments, Malvern, UK), supported by the wet sieving of fractions larger than 250 μm. Granulometric data were analysed with the use of GRADISTAT 8.0 software (Blott and Pye, 2001). Dried and weighted sediment fractions > 250 and 500 μm were used for IRD analyses, and at least 500 mineral grains from each fraction were counted under a stereomicroscope. The IRD flux was expressed as number of grains per square centimetre per year (grain cm<sup>-2</sup> yr<sup>-1</sup>).



Stable isotope analyses were performed on foraminiferal tests selected from 54 sediment layers. From each layer, 10 to 12 well-preserved specimens of *Cibicidoides lobatulus* were selected. The measurements were performed on a Finnigan-MAT 253 mass spectrometer coupled to a Kiel IV carbonate preparation device (Thermo Fischer Scientific, University of Florida). The resulting values were compared to the isotopic standard NBS-19 and expressed in standard  $\delta$  notation relative to VPDB.

#### 3.2 Foraminiferal counts and molecular analysis

Prior to the analysis of fossil foraminiferal assemblages, 74 selected sediment samples were dried, weighed and wet-washed through sieves with 500 and  $100 \,\mu m$  openings.

- Each sample was divided using a dry microsplitter and at least 300 specimens from each sample were counted. The foraminiferal counts were reported as percentages of the total assemblage and as the number of individuals per square centimetre per year. Fossil foraminifera assemblage was analysed with the orthogonally rotated (varimax) Q-mode Principal Component (PC) analysis, using a commercially distributed software
- (SYSTAT 11). Taxa with the abundance > 2 % of the total assemblage in at least one sample were analysed. Each PC was defined by the dominant (and eventually accessory) species. The PCs were referred to foraminiferal assemblages (FA) named after the dominant species.

The analysis of molecular data from 12 selected layers were described in detail in Pawłowska et al. (2014). The molecular data were presented as percentages of sequences.

#### 4 Sediment dating

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The age of the studied core was estimated based on high precision AMS <sup>14</sup>C dating performed on bivalves shells, presented in Pawłowska et al. (2014). Eleven shells identified to the highest possible taxonomic level were selected and processed on the



1.5 SDH-Pelletron Model "Compact Carbon AMS" (Poznań Radiocarbon Laboratory, Poland). The dates were converted into calibrated ages using the calibration program CALIB Rev. 7.0.2 Beta (Stuiver and Reimer, 1993) and the Marine13 calibration dataset (Reimer et al., 2013). The difference  $\Delta R$  in reservoir age correction of  $105 \pm 24$  was applied (Mangerud et al., 2006).

Four out of 11 samples were in chronological order and were used to establish an approximated age model for the sediment core (Fig. 2, Table 1). The age-depth model was made with the use of CLAM-R software (Blaauw, 2010). The age of the oldest layer was estimated to be ~ 965 AD. The sediment accumulation rate (SAR) in the deepest part of the core (i.e., before 1800 AD) ranged from 0.1 to 0.125 cm yr<sup>-1</sup>. At ~ 1800 AD, this rate increased to 1 cm yr<sup>-1</sup>. In the upper layers (after ~ 1890 AD), SAR decreased to 0.3 cm yr<sup>-1</sup>.

#### 5 Foraminifera as environmental indicators

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

- <sup>20</sup> The glaciomarine group comprised *Cassidulina reniforme*, *Elphidium excavatum*, and *Quinqueloculina stalkeri*. The characteristic species of the Atlantic water mass are: *Nonionellina labradorica*, *Bolivina pseudopunctata*, *Buccella frigida*, *Adercotryma glomerata*, *Ammotium cassis* and *Recurvoides turbinatus*. We decided to exclude *Reophax fusiformis* and *Reophax pilulifer* from this group, because there were only
- <sup>25</sup> 2 specimens of *R. fusiformis* in the HF\_2011 core, and *R. pilulifer* was not reported. The Arctic water group was composed of: *Islandiella norcrossi, Elphidium* spp. (excluding *E. excavatum*), *Stainforthia feylingi, Stainforthia loeblichii, Spiroplectammina*



*biformis*, and *Spiroplectammina earlandi*. We decided to add *Islandiella helenae* to this group based on Kelly et al. (1999). The bottom currents indicators group consisted of *Cibicidoides lobatulus* and *Astrononion gallowayi*.

#### 6 Results

#### **5 6.1 Sediment age and characteristics**

Before 1600 AD, the mean grain size fluctuated slightly, except for one peak at ~ 1450 AD, reaching  $5.12\varphi$ . In ~ 1600 AD, the mean grain size increased slightly to  $6.2\varphi$ . After 1800 AD, it varied within a broader range of values and presented three main peaks at 1830, 1850, and 1880 AD. The decrease in the mean grain size was observed from ~ 1940 AD to the end of the 20th century (Fig. 3).

From 1000 to 1800 AD, the IRD flux was relatively stable and did not exceed  $0.5 \,\text{grain}\,\text{cm}^{-2}\,\text{yr}^{-1}$ . After that period the IRD delivery increased considerably, reaching up to 4  $\text{grain}\,\text{cm}^{-2}\,\text{yr}^{-1}$ . From ~ 1900 to ~ 1940 AD IRD flux varied from 0.2 to 1.7  $\text{grain}\,\text{cm}^{-2}\,\text{yr}^{-1}$ . From ~ 1940 AD to the end of the 20th century, the IRD delivery continuously decreased (Fig. 3).

#### 6.2 Stable isotopes

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From 1000 to 1600 AD, the  $\delta^{18}$ O showed relatively stable values varying slightly from 2.63‰ vs. VPDB to 2.88‰ vs. VPDB. After 1600 AD, it fluctuated distinctly from 2.23 to 3.50‰ vs. VPDB. The heavier  $\delta^{18}$ O was observed before 1600 AD and in the 20th century. The period from 1600 to 1900 AD was characterised by lighter  $\delta^{18}$ O, with the main peaks at ~ 1600, ~ 1830 and ~ 1860 AD. The measured values of  $\delta^{13}$ C varied from 0.54‰ vs. VPDB to 1.59‰ vs. VPDB and fluctuated along the core. The most important fluctuations occurred between 1550 and 1900 AD, with  $\delta^{13}$ C values ranging from 0.54 to 1.48‰ vs. VPDB (Fig. 3).



# 6.3 Foraminiferal abundance and taxonomic composition revealed by the fossil record

The foraminiferal flux varied from 1 to 86 ind cm<sup>-2</sup> yr<sup>-1</sup>. The most noticeable shift occurred at ~ 1800 AD, when it increased from 2.8 to 81 ind cm<sup>-2</sup> yr<sup>-1</sup>. (Fig. 3). The number of foraminifera per gram of sediment varied from 86 to 3838 ind g<sup>-1</sup>. The highest values were observed before ~ 1850 AD. After 1850 AD number of foraminifera declined and did not exceed 1742 ind g<sup>-1</sup> (Fig. 3).

A total of 28 771 individuals were assigned to 72 species and 38 genera. Most of the species belonged to Rotaliida (34), Textulariida (12) and Lagenida (12). The other species were identified as Miliolida (10), Lituolida (2) and Globigerinida (Table S1 in the Supplement). The most abundant species were *Elphidium excavatum*, *Cassidulina reniforme*, *Cibicidoides lobatulus*, and *Nonionellina labradorica* (Fig. 4). The fossil assemblage was strongly dominated by *E. excavatum* and *C. reniforme*, which together made up to 82% of the total abundance. The abundance of *C. lobatulus* and *N. labradorica* varied slightly along the core, and no evident faunal changes were observed. The main peaks of *N. labradorica* occurred at ~ 1850, ~ 1910 and ~ 1940 AD, when its relative abundance reached up to 25%. The highest percentage of *C. lobatu-*

*lus* was noted at ~ 1840 AD (25%), and its notable decrease occurred after 1940. The percentage of agglutinated taxa did not exceed 25% and reached its highest values
 1940 AD between 1600 and 1800 AD, and after 1940 AD (Fig. 4).

The proposed 4-factor PC explained 98.5% of the total variability of the tested dataset. The most important PC analysis assemblages were: (1) *E. excavatum* FA, which explained 40.8% of the total foraminiferal variance, (2) *C. reniforme* FA, with *E. excavatum* as accessory species, which explained 34.8% of the variance, (3) *N. labradorica* FA, with *C. lobatulus* as accessory species, which explained 20.1% of the variance and (4) *C. lobatulus* EA accessory species, which explained 2.8% of the total

the variance, and (4) *C. lobatulus* FA assemblage, which explained 2.8% of the total variance (Table 2). The HF\_2011 core was dominated by *E. excavatum* FA and *C. reniforme* FA throughout. The E. excavatum FA showed the highest factor loadings during

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the LIA (i.e. between 1600 and 1900 AD). In the uppermost part of the core (after  $\sim$  1930 AD) the *E. excavatum* factor loadings decreased and the role of *C. reniforme* FA increased. The *N. labradorica* FA was significant during the MWP and the early LIA (before  $\sim$  1800 AD) and was not significant during the late LIA (after  $\sim$  1850 AD). The

 N. labradorica factor loadings started to increase at the beginning of the 20th century. The *C. lobatulus* FA was significant only in two layers dated to the MWP (Fig. 5).

#### 6.4 Foraminifera in the ancient DNA record

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

We used Sanger and high-throughput sequencing (HTS) to obtain 717 and 8700 815 sequences, respectively. A total of 394 operational taxonomic units (OTUs) were obtained from sequence clustering. The majority of OTUs were assigned to Monothalamea (96 OTUs) and Rotaliida (93 OTUs). The remaining OTUs were assigned to Textulariida (33 OTUs), Miliolida (10 OTUs), Robertinida (1 OTU) and Globigerinida
 (5 OTUs); 146 OTUs remained unassigned (Table S2). Although the sequences of the species that dominated in the fossil record were present in most of the samples, their shundhana did not reflect the shundhana in the fossil record were present in the fossil record set of the samples.

abundance did not reflect the abundance in the fossil specimens (see Pawłowska et al., 2014).

The 96 OTUs assigned to monothalamids made up 39.4% of all the sequences.

- The percentage of monothalamous sequences varied along the core from 3.5 to 65 %. (Fig. 6) There were 7 OTUs constituting more than 3 % of all the sequences in at least one sample. They were referred to *Bathysiphon* sp. (clade BM), *Micrometula* sp. (clade BM, 2 OTUs), *Toxisarcon* sp. (clade C) and monothalamous foraminifera of undetermined phylogenetic origin (3 OTUs; Table S2). Eleven OTUs corresponded to the se-
- quences of species collected in Svalbard: Bathysiphon argenteus, Micrometula sp., Cylindrogullmia alba, Toxisarcon sp., Gloiogullmia sp., Ovammina sp., Psammophaga crystallifera, Crithionina granum, Nemogullmia longevariabilis, Globipelorhiza sp. and an undescribed "mudball" specimen.



Monothalamid sequences were assigned to 14 clades, including 10 that were represented by more than 5% of monothalamid sequences in at least one sample. The assemblage of monothalamous for aminifera was strongly dominated by clade BM (genera Micrometula and Bathysiphon), which together made up to 78% of the sequences

- of monothalamids (Fig. 6). Bathysiphon sp. was the most abundantly sequenced in 5 the samples dated before 1840 AD, while sequences of *Micrometula* sp. dominated in the samples spanning the 20th century. The monothalamous assemblage during the MWP was dominated by *Toxisarcon* sp. and environmental monothalamous sequences belonging to clade V. The early LIA (1600–1840 AD) was marked by an increased pro-
- portion of sequences of Hipocrepinella hirudinea (clade D) and Cedhagenia saltatus 10 (clade O). The monothalamous assemblage during the early MW (before 1930 AD) was strongly dominated by Micrometula sp. (which made up to 75% of monothalamous sequences), together with Vellaria pellucidus. After 1930 AD, a high number of monothalamid sequences occurred that belonged to environmental clades or were of 15

undetermined phylogenetic origin (Fig. 6).

#### Discussion 7

Previous studies on the Svalbard Holocene history reported "unstable environmental conditions" during the last thousand years (e.g., Berben et al., 2014; Groot et al., 2014), reflecting the major climatic changes: the Medieval Warm Period (MWP, ~900-1500 AD), the Little Ice Age (LIA,  $\sim$  1500–1900 AD) and the Modern Warming (MW,  $\sim$  1900 20 AD-present) (Oerlemans, 2005). Svalbard ice core records and sediment records from the shelf adjacent to Hornsund suggested that prolonged cooling started  $\sim$  1600 AD, and the most severe conditions occurred during the 19th century (Isaksson et al., 2003; Majewski et al., 2009). On the contrary, the reconstruction of the Earth's surface air temperature from Svalbard (Divine et al., 2011) constituted the cooling stage 25 between 800 and 1800 AD, with no clear signs of the onset of the LIA. Our foraminiferal



and sedimentological records from Hornsund matched the trend described by Divine et al. (2011), as it revealed a sharp change in environmental conditions at  $\sim$  1800 AD.

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

The period from ~ 1000 to ~ 1800 AD was characterized by low and stable fluxes of IRD and foraminifera, and slightly heavier  $\delta^{18}$ O (Fig. 3). This might indicate the influence of warmer and more saline waters, probably of Atlantic origin, and low glacial activity (Jernas et al., 2013). The fossil foraminiferal assemblage was fairly stable during the MWP (i.e., before 1600 AD) with no clear evidence of faunal change. Conversely, the foraminiferal aDNA record featured a high proportion of *Toxisarcon* sp. (Clade C) at ~ 1000 AD (Fig. 6). As reported by Gooday et al. (2005), *Toxisarcon* sp. is commonly found in Svalbard fjords. In case of our study, the increase in the *Toxisarcon* sp. percentage coincided with the peak of light  $\delta^{18}$ O, followed by lighter  $\delta^{13}$ C, which

might suggest the presence of a highly productive zone of frontal contact of AW and ArW water masses. The presence of diatom frustules in the cytoplasm of *Toxisarcon* sp. (Voltski et al., 2014) might suggest that its occurrence was related to the phytoplankton-originated organic matter input.

Our data showed a slight peak of lighter  $\delta^{18}$ O at 1600 AD (Fig. 3), that could indicate an increase of melt water delivery to Hornsund, but it was not followed by the increase of sediment accumulation and IRD flux. Therefore, we concluded that lighter  $\delta^{18}$ O at

- $_{20}$  ~ 1600 AD showed the increased ArW inflow from the Barents Sea to the Svalbard shelf and Hornsund, which is in agreement with previous  $\delta^{18}$ O and fossil foraminiferal records obtained from the outer fjord (Majewski at al., 2009). This event occured within a period of significant climate changes connected to the transition from the MWP to the LIA. The Humlum et al. (2005) investigation of the frozen in situ vegetation below
- Longyearbyen glacier (central Spitsbergen) indicated the advance of this glacier during the last ~ 1100 years. Based on the terrestrial record from Hornsund, the WMP was interrupted 600 years ago by an advance of glaciers (Marks and Pękala, 1986; Linder et al., 1990) that lasted until the beginning of the 20th century.



The most pronounced changes that occurred ~ 1600 AD in the HF\_2011 fossil assemblage were slight peaks in the abundance of *N. labradorica, I. norcrossi* and *I. helenae.* Moreover, the increase in the percentage of agglutinated taxa was noted between 1600 and 1800 AD (Fig. 4). *Nonionellina labradorica* is an AW indicator usually found <sup>5</sup> in relatively warm and saline waters (Lloyd, 2006; Majewski et al., 2009). However, the abundance of these three species seemed to be controlled more by the food supply than by water temperatures (Hald and Korsun, 1997; Lloyd, 2006; Ivanova, 2008). The presence of *Islandiella* spp. might indicate a highly productive environment, related to the Polar Front (Steinsund, 1994). This supported the evidence of the inflow of colder <sup>10</sup> and less saline ArW at ~ 1600 AD, changing the water mass balance and productivity in the fjord.

The foraminiferal flux before  $\sim$  1800 AD was low (Fig. 3) and could be explained by the presence of species with low fossilisation potential, e.g., agglutinated taxa (Wollenburg and Kuhnt, 2000). The percentage of agglutinated tests was relatively low during the MMD and is again and investigation of the test of agglutinated tests was relatively low during

- the MWP and increased significantly after 1600 AD (Fig. 4), which likely reflected the inflow of ArW and relatively low glacial activity (Hunt and Corliss, 1993; Hald and Korsun, 1997). Our aDNA data suggested that the abundance of agglutinated foraminifera was higher than it was as shown by the fossil record. Three agglutinated taxa were detected by both fossil and aDNA record: *C. crassimargo, Reophax* spp, and *Spiro-*
- *plectammina* spp. (Tables S1 and S2). However, only *C. crassimargo* was detected by both approaches in the corresponding layers. *Reophax* spp. and *Spiroplectammina* spp. sequences were recorded in all of the examined samples, but they were relatively rare or absent in fossil material (Pawłowska et al., 2014), probably due to the degradation of their tests. Korsun and Hald (2000) regarded *S. biformis* and *S. earlandi* as
- typical for glaciomarine habitats. They noticed an increase in the abundance of those agglutinated species off glacier. Korsun et al. (2005) and Hald and Korsun (1997) reported *Reophax* spp. and *Spiroplectammina* spp. in the outer parts of glacially fed fjords of Svalbard and Novaya Zemlya. Zajączkowski et al. (2010) noted the decrease



of abundance of agglutinated foraminifera in Hornsund with increasing water turbidity. Thus, the presence of those species might indicate a glacier-distant environment.

Furthermore, the transition to the LIA between  $\sim$  1600 and  $\sim$  1800 AD was well marked by the increase of the percentage of monothalamous foraminifera aDNA se-

- <sup>5</sup> quences (Fig. 5). Monothalamids are highly adaptable and they occur in environments where conditions may be extreme (Gooday et al., 2002; Sabbattini et al., 2010), which makes them effective colonizers. It is likely that the change in hydrology and productivity in Hornsund at ~ 1600 AD might have created a new ecological niche, which was effectively settled by monothalamids. The monothalamous assemblage during the
- <sup>10</sup> early LIA (from ~ 1550 to ~ 1840 AD) was dominated by taxa belonging to clade BM, mainly from genus *Bathysiphon* (Fig. 6). Gooday et al. (2005) reported *Bathysiphon* sp. in two glacial influenced fjords, Van Mijenfjorden and Kongsfjorden, at glacier distant sites. Moreover, a sharp peak of heavier  $\delta^{13}$ C was noted in Hornsund at ~ 1600 AD, which might suggest the short-term suppression of primary productivity resulting in the
- <sup>15</sup> presence of degraded organic matter and phytodetritus that seems to be favourable for *Bathysiphon* sp. (Alve et al., 2010). The presence of sequences of *Bathysiphon* sp. and agglutinated *Spiroplectammina* spp. and *Reophax* spp. supported our conclusion that at the onset of the LIA (~ 1600–~ 1800 AD), the position of glacier fronts was relatively distant to the fjord centre, which resulted in low SAR and low IRD flux, while fjords water masses were influenced by the ArW.

The transition to the LIA (~ 1600–~ 1800 AD) was also marked by increased percentages of sequences assigned to the monothalamid clade D (mainly *Hippocrepinella hirudinea*) and to clade O (mainly *Cedhagenia saltatus*; Fig. 6).*Cedhagenia saltatus* is a species recently found by Gooday et al. (2011) in the Black Sea. Little is known <sup>25</sup> about the environmental tolerance of *C. saltatus*. However, its presence in the area strongly impacted by human activity, suggested that it was an opportunistic species, with a high tolerance to environmental disturbance. *Hipocrepinella hirudinea* was noted in the fjords of Svalbard by Majewski et al. (2005) and Gooday et al. (2005). It appeared



in the central and outer parts of the studied fjords, mainly in the shallow water sites.

Korsun et al. (2005) noted the presence of the genus *Hipocrepinella* in Novaya Zemlya, however; it may not have referred to *H. hirudinea*. The scarce data on *H. hirudinea* and *C. saltatus* ecological tolerance precluded making any general conclusions.

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

- <sup>5</sup> 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 tidewater glaciers during rapid deglaciation, as well as during glacial surges (Koppes and Hallet, 2002). Moreover, sediment might be stored in proglacial
- zone of land-based glaciers, from where could be eroded, particularly under conditions of increased glacial meltwater runoff and increased precipitation (Szczuciński et al., 2009) and next redeposited from the sublittoral zone by storm waves. During the LIA, the glaciers extent reached its Holocene maximum (D'Andrea et al., 2012); thus,
- the calving and melt water delivery could occur close to the central part of the fjord. The HF\_2011 core was located close to the southern shore of Hornsund, therefore we concluded that the observed increase in SAR resulted mainly from the sediment delivery from land.

Our data showed an 25-fold increase of foraminiferal flux at  $\sim$  1800 AD (Fig. 3), while

- the species diversity was relatively low due to the dominance of glaciomarine species, especially *E. excavatum* and *C. reniforme* (Figs. 4 and 5). Moreover, the *N. labradorica* FA became not significant (Fig. 5). As a consequence of the maximal glaciers range, conditions in the whole fjord became not significant after ~ 1850 AD 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 Isfjorden showed a distinctive faunal gradient along the fjord axes, with three different monothalamous assemblages at subtidal, shallow- and deep-water sites. Korsun et al. (2005) and Korsun and Hald (1998, 2000) reported that allogromiids constituted up to 99% of living foraminifera in the stations close to the glacier ter-

- <sup>5</sup> mini in Novaya Zemlya and Spitsbergen. Sabbattini et al. (2007) attributed the occurrence of monothalamids in the Svalbard region to the inputs of fresh water and a high, changeable sedimentation rate. Gooday et al. (2005) noted that the inner parts of Tempelfjorden and Kongsfjorden, fjords headed by tidewater glaciers, were dominated by organic-walled allogromiids and saccamminids. This was reflected in our data, as the
- proportion of allogromiids (mainly *Micrometula* sp.) increased significantly from 40 % at ~ 1870 AD to 80 % at ~ 1900 AD (Fig. 6). Moreover, the late LIA and the early MW were marked by an increase in the proportion of sequences assigned to clade E, mainly *Vellaria pellucidis*. Majewski et al. (2005) noted the presence of *Vellaria* sp. in subtidal and shallow *Vellaria pellucidus* area of Spitsbergen fjords. The increase in the percentage
- <sup>15</sup> of *Micrometula* sp. and *Vellaria pellucidus* in the period of the highest glacial activity, suggested that those species were potential indicators of glacier-proximal settings.

#### 7.3 The Modern Warming (~ 1900 AD-present)

The sedimentary record of the MW featured decrease in the SAR and lower, yet variable IRD flux (Fig. 3).

- The peaks of IRD flux were noted along with the increased mean grain size (Fig. 3). This trend was opposite to that of the late LIA, where no clear correlation between the IRD flux and mean grain size was observed. The post-LIA glacial retreat led to an increased distance between the coring station and the main tidewater glacier front. In Spitsbergen fjords, fine-sized particles from glacial outflows are deposited close to
- the source (Szczuciński et al., 2006); therefore, the HF\_2011 station was impacted mainly by ice-rafted, coarser particles. The IRD flux gradually diminished from ~ 1940 AD, what probably resulted from a tidewater glaciers' fronts retreat to the inner bays, limiting iceberg drift to the fjord centre.



The most noticeable changes in the fossil foraminifera community during the 20th century occurred after 1940 AD, with the gradual increase of *B. frigida* and *I. norcrossi* and decrease of *C. lobatulus* (Fig. 4). *Islandiella norcrossi* and *B. frigida* typically occupied the distal sections of glacial fjords of Svalbard and Novaya Zemlya (Korsun et al., 2005; Hald and Korsun, 1997; Korsun and Hald, 2000; Pogodina, 2005). Steinsund (1994) linked the presence of *I. norcrossi* and *B. frigida* with high productivity related to a polar front position and seasonal sea-ice cover. Thus, we concluded that since

- 1940 AD, Hornsund and the adjacent shelf remained under Atlantic water influence, forming the frontal zone with local waters. This conclusion was supported by PC anal-
- <sup>10</sup> ysis, where significance of *N. labradorica* FA was increasing during the 20th century (Fig. 5). *Cibicidoides lobatulus* is a relatively shallow-water species, taking advantage of vigorous bottom waters (Hald and Korsun, 1997; Lloyd, 2006); however, it is an epiphytic species, which needs a hard substrate to stay attached to the bottom surface. Therefore, the decrease in the percentage of *C. lobatulus* could be connected to the 15 decrease of near-bottom currents and low IRD flux and, consequently, an increase in
- the fine sediment fraction (Fig. 3).

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The increased abundance of species typical for glacier-distal faunas, followed by a decrease in the abundance of species considered to be bottom current indicators (Fig. 4) supported our evidence of rapid glacier retreat, coupled with the decreasing influence of glaciomarine sedimentation and enhanced productivity. It was reflected in the molecular record, where the number of OTUs and the percentage of monothala-

mids decreased after ~ 1920 AD, reaching the values similar to those during the MWP (Fig. 6). The second half of the 20th century was marked by the significant increase in the unassigned monothalamids sequences belonging to environmental clades. How-

<sup>25</sup> ever, without the accurate identification of sequences, it is not possible to make any palaeoecological interpretations.

The use of aDNA approach gained an access to hidden diversity of benthic foraminifera community and allowed to refine the paleoclimatic reconstruction based on traditional proxies. However, current methodology allowed to perform only qualita-



tive analysis of ancient foraminiferal DNA. The aDNA data should be interpreted carefully, as it is not possible to establish the direct relationship between the number of specimens and the number of ribosomal sequences. In aDNA studies major difficulties arise from DNA degradation and chemical modification. Moreover, the DNA damage and degradation rate is strongly dependent on the physical, chemical and biological properties of the microenvironment (Pederesen et al., 2015). The absolute number of sequences should be interpreted with caution; however, it is possible to identify the

dominant species based on the sequence proportion (Weber and Pawlowski, 2013).

#### 8 Conclusions and perspectives

- <sup>10</sup> The main climatic fluctuations of the last millennium (the MWP, the LIA and the MW) were reflected in the fjord water mass balance and glaciers' activity. The marine environmental conditions during the MWP and the early LIA were relatively stable, with a low SAR and low IRD flux. The beginning of the LIA (~ 1600 AD) was poorly supported by the fossil record, but it was well evidenced in the aDNA data. It was <sup>15</sup> marked by the increased proportion of sequences of monothalamous foraminifera, mainly *Bathysiphon* sp., supporting our assumption, that the terminal position of the glaciers was relatively distant at the onset of the LIA. The early LIA (~ 1600–~ 1800 AD) was also marked by high percentages of *H. hirudinea* and *C. saltatus*. The late LIA (after ~ 1800 AD) was characterised by the increased proximity of tidewater glaciers'
- fronts, increased sedimentation from suspension and from the icebergs; thus conditions in the fjord centre became glacier-proximal. The end of the LIA (~ 1900 AD) was marked by increased proportions of *Micrometula* sp. and *V. pellucidus*. Those results revealed their potential as indicators of glacier-proximal environments, characterised by melt water outflows, a high sedimentation rate and increased calving. During the
- MW, major glaciers' fronts retreated rapidly to the inner bays, limiting the iceberg discharge to the fjord centre and causing the shift in the foraminiferal community reflected in fossil and aDNA records.



The present study was the first attempt to implement the aDNA for a miniferal record in the palaeoclimatic reconstruction. The data inferred from molecular analyses correlated well with environmental changes. The aDNA record revealed even small environmental changes that were not clearly indicated by the fossil record. By including 5 monothalamous foraminifera identified in the aDNA record, we considerably increased the number of potential proxy species. However, to fully benefit from this new source of information, it is essential to improve the knowledge of monothalamids ecology. The positive results of the present study encourage further applications of ancient foraminiferal DNA sequences to reconstruct past environmental changes in polar regions.

#### The Supplement related to this article is available online at doi:10.5194/cpd-11-3665-2015-supplement.

Acknowledgements. This study was supported by the Scientific Exchange Programme between Switzerland and the New Member States of the EU (Sciex-NMS) project 10.140 and by the Swiss National Science Foundation grant 31003A 140766. The study was funded also by the Polish Ministry and Higher Education Grant No. 2013/11/B/ST10/00276. The crew of R/V Oceania is thanked for help during the fieldwork. The authors thank Witold Szczuciński for help with refining the age model and for valuable discussions.

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 Table 1. Raw AMS <sup>14</sup>C and calibrated dates used for the age model.

Sediment depth[cm]	Material (shells)	Raw AMS <sup>14</sup> C	Calibrated years AD $\pm 2\sigma$	Cal. yr AD used in age model
70.5	Bathyarca glacialis	580 ± 30 BP	1799–1949	1880
122.5	Gastropod nd.	615 ± 30 BP	1703–1910	1820
166.5	Hiatella arctica	1075 ± 30 BP	1318–1447	1400
173.5	Macoma calcarea	1145 ± 30 BP	1281–1414	1320

**Table 2.** PC scores and percent of total variance explained by four factor principal component analysis. The contribution of each analysed species is shown, species significant for particular assemblage 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%
Adercotryma glomerata	-0.1857	-0.13401	-0.75184	-0.06062
Buccella frigida	-0.40847	0.081688	-0.13456	-0.34934
Cassidulina reniforme	-1.44681	2.923605	0.894126	0.480619
Cibicidoides lobatulus	-0.22008	-1.29993	1.821983	2.252356
Cribrostomoides crassimargo	0.13799	0.418817	-0.63454	-1.15662
Elphidium bartletti	-0.06081	-0.41644	-0.64903	0.130446
Elphidium excavatum	3.21345	1.108558	0.281919	0.526077
Islandiella helenae	-0.39509	-0.39785	0.267723	0.366261
Islandiella norcrossi	-0.21596	-0.31512	-0.5112	0.091585
Nonionellina labradorica	0.124046	-0.71182	2.242218	-2.40609
Quinqueloculina stalkeri	-0.23152	-0.30084	-0.57036	0.05742
Recurvoides turbinatus	-0.15527	-0.33373	-0.6666	0.055335
Spiroplectammina biformis	-0.08015	-0.30205	-0.80459	0.020384
Spiroplectammina sp.	-0.07563	-0.32089	-0.78525	-0.00781





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











**Figure 3.** Sediment accumulation rate (a), IRD flux (b), mean grainsize (c), stable oxygen (d) and carbon (e) isotopes, fossil foraminifera flux (f) and number of foraminifera per gram of sediment (g). MWP: Medieval Warm Period, LIA: Little Ice Age, MW: Modern Warming. The time range of MWP, LIA and MW is presented after Majewski et al. (2009).





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



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**Figure 5.** PC loading values for four foraminiferal assemblages found in the HF\_2011 core. Statistically significant loadings were marked grey. MWP: Medieval Warm Period, LIA: Little Ice Age, MW: Modern Warming. The time range of MWP, LIA and MW is presented after Majewski et al. (2009).





**Figure 6.** The relative abundance of monothalamid sequences, expressed as the percentage of all foraminiferal sequences (A) and the composition of the monothalamid assemblage, expressed as percentages of sequences within clades (B–K). Clades that constitute more than 5% of the monothalamid sequences in at least one sample are presented. "Environmental clades" relate to foraminifera known only from environmental sequencing.

