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Multiproxy evidence of the Neoglacial expansion of Atlantic Water to eastern Svalbard: Does ancient environmental DNA complement sedimentary and microfossil records?

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Abstract. The main goal of this study was to reconstruct the paleoceanographic development of Storfjorden during the Neoglacial (~ 4 cal ka BP). A multiproxy approach was applied to provide evidence for interactions between the inflow of Atlantic Water (AW) and sea-ice coverage, which are the major drivers of environmental changes in Storfjorden. The sedimentary and microfossil records indicate that a major reorganization of oceanographic conditions in Storfjorden occurred at ~ 2.7 cal ka BP. A general cooling and the less pronounced presence of AW in Storfjorden during the early phase of the Neoglacial are prerequisite conditions for the formation of an extensive sea-ice cover. The period after ~ 2.7 cal ka BP was characterized by alternating short-term cooling and warming intervals. Warming was associated with pulsed inflows of AW and sea-ice melting that stimulated phytoplankton blooms and organic matter supply to the bottom. The cold phases were characterized by heavy and densely packed sea ice resulting in a decrease in productivity. The ancient environmental DNA (aDNA) records of foraminifera and diatoms reveal the timing of the major pulses of AW (~2.3 and ~1.7 cal ka BP) and the variation in sea-ice cover. The AW inflow was marked by an increase in the percentage of DNA sequences of monothalamous foraminifera associated with the presence of fresh phytodetritus, while cold and less productive intervals were marked by an increased proportion of monothalamous taxa known only from environmental sequencing. The diatom aDNA record indicates that primary production was continuous during the Neoglacial regardless of sea-ice conditions. However,

the colder periods were characterized by the presence of diatom taxa associated with sea ice, whereas the present-day diatom assemblage is dominated by open-water taxa.

1. Introduction

The flow of Atlantic Water (AW) is one of the major heat contributors to the Arctic Ocean (Polyakov et al., 2017). Recent oceanographic data indicate warming due to an increase in AW in the Arctic Ocean (Rudels et al., 2015, Polyakov et al., 2017). AW has been present along the western margin of Svalbard during at least the last 12,000 years (e.g., Werner et al., 2011; Rasmussen et al., 2014). One of the major intrusions of AW occurred during the early Holocene (10.8 – 6.8 cal ka BP). A distinct cooling and freshening of the bottom water masses occurred during the mid-late Holocene (6.8–1 cal ka BP) and was accompanied by glacier readvances in Svalbard leading to present-day conditions (Ślubowska-Woldengen et al., 2007; Telesiński et al., 2018). The paleoceanographic conditions in the Svalbard margins correlate closely to the sea surface temperature (SST) variations in the Nordic Seas and confirm that the Svalbard area is highly sensitive to fluctuations in the inflow of AW (Ślubowska-Woldengen et al., 2007). Conversely, until the 1990s eastern Svalbard was recognized as an area exclusively influenced by the East Spitsbergen Current (ESC), which carries cold and less saline Arctic Water (ArW) from the Barents Sea (e.g., Quadfasel et al., 1988; Piechura et al., 1996). Recent studies have revealed that the oceanography of the area is much more complicated (e.g. Skogseth et al., 2007; Geyer et al., 2010). Oceanographic data obtained from conductivity–temperature sensors attached to *Delphinapterus leucas* show a substantial contribution of AW to Storfjorden (east Spitsbergen; Lydersen et al., 2002). Recently, a suggestion by Hansen et al. (2011) that AW was present in Storfjorden during the early Holocene warming (11 – 6.8 cal ka BP) was confirmed by Łącka et al. (2015). However, the limited amount of data available for eastern Svalbard often makes paleoceanographic reconstructions of the area speculative.

The latter part of the Holocene, the so-called Neoglacial cooling (~ 4 cal ka BP), in the European Arctic is correlated with a decline in the summer insolation at northern latitudes (Berger, 1978) and a decline in summer SST (Andersen et al., 2004; Risebrobakken et al., 2010; Rasmussen et al., 2014). The cooling of the surface waters and the limited AW inflow to the Nordic Seas led to the formation of an extended sea-ice cover (Müller et al., 2012). In addition, the southwestern and eastern shelf of Spitsbergen experienced a strengthening of the East Spitsbergen Current leading to an intensification of ArW inflow and the formation of an extensive sea-ice cover (Sarnthein et al., 2003). Therefore, the Neoglacial has usually considered a constantly cold period, with a culmination of cooling during the Little Ice Age. However, the records from Storfjorden and the Barents Sea suggest that the Neoglacial was a period of variable oceanographic conditions with strong temperature and salinity gradients (Calvo et al., 2002; Martrat et al., 2003; Sarnthein et al., 2003; Łącka et al., 2015). There is also evidence of episodic intensifications of the warm AW inflow to western Svalbard at that time (e.g. Risebrobakken et al. 2010; Rasmussen et al., 2012).

According to Nilsen et al. (2008), the critical parameter controlling the fjord–shelf exchange is the density difference between the fjord water masses and the AW. The local winter ice production and formation of brine-enriched waters determines the density of local water masses, which is a key factor that enables AW to penetrate into fjords during the spring and summer. Moreover, the production of brine-enriched waters and associated deep-water overflow is a key contributor to large-scale ocean circulation (Killworth, 1983). In this respect, Storfjorden is especially important because it is one of the few areas where brine-enriched waters have been frequently observed (Haarpainter et al., 2001). In the last decades, reduced brine formation occurred during periods with the most intensive AW advection to Storfjorden and reduced sea-ice formation in the Barents Sea, while intense brine formation was re-established during periods of recurrent cooling (Årthun et al., 2011).

The aim of the presented study is to reconstruct the paleoceanographic development of Storfjorden during the Neoglacial with multicentennial resolution. We assumed that the periodic intensification of the AW inflow to the West Spitsbergen shelf during the Neoglacial resulted in the appearance of AW also in eastern Spitsbergen, similar to the early Holocene (e.g., Łącka et al., 2015), affecting the density and extent of sea-ice cover in the area. A multiproxy approach comprising composed of sedimentary, microfossil and molecular records was applied to provide evidence for interactions between the inflow of AW and sea-ice coverage in Storfjorden. The ancient environmental DNA (aDNA) analysis targeted diatoms and nonfossilized monothalamous foraminifera, groups that are hardly preserved in fossil records from the Spitsbergen fjords (Pawłowska et al., 2014, Łącka M., *pers. commun.*) Recent studies have demonstrated that analyses of genetic material obtained directly from environmental samples (so called environmental DNA) are an efficient method for biodiversity surveys across time and space (Thomsen and Willerslev, 2015). Our previous studies of foraminiferal aDNA revealed the extraordinary richness of the foraminiferal community, primarily due to the detection of soft-walled monothalamous taxa (Pawłowska et al., 2014). Furthermore, aDNA has been proven to be an effective tool in paleoceanographic reconstructions (e.g. Boere et al., 2009; Pawłowska et al., 2016). The molecular data correlated well with environmental changes and even revealed small changes that were not clearly indicated by other proxy records (Pawłowska et al., 2016). The combination of aDNA studies with the analysis of microfossils and sedimentary proxies provides a powerful means to reconstruct past environments more comprehensively.

2. Study area

Storfjorden is located in southeastern Svalbard between the islands of Spitsbergen, Edgeøya and Barentsøya. Storfjorden is ~190 m long and its main basin is ~190 m deep. Two narrow and shallow passages Heleysundet and Freemansundet connect northern Storfjorden to the Barents Sea. To the south, a 120-m-deep sill separates the main basin from the Storfjordrenna Trough. Storfjordrenna is 245 m long, with a depth varying from 150 m to 420 m.

The water masses in Storfjorden are composed primarily of exogenous Atlantic and Arctic waters and mixed waters that have formed locally. Warm AW is transported by the West Spitsbergen Current branches off near Storfjordrenna and enters the southern part of the fjord. Arctic water (ArW) from the Arctic Ocean and the Barents Sea enters Storfjorden via two passages to the northeast and continues along the inner shelf of Svalbard as a coastal currents. AW is characterized by temperatures > 3 °C and salinity > 34.95, while the temperature and salinity of ArW are < 0 °C and 34.3-34.8, respectively. The presence of locally formed water masses is a result of the interactions between AW, ArW and melt water. Skogseth et al. (2005) listed six local water masses: melt water (MW), polar front water (PW), East Spitsbergen water (ESW), brine-enriched shelf water (BSW), Storfjorden surface water (SSW), and modified Atlantic water (MAW). BSW is formed due to the release of large amounts of brines during polynya events and the intensive formation of sea ice (Haarpainter et al., 2001; Skogseth et al., 2004, 2005) and is characterized by salinities exceeding 34.8 and temperatures below -1.5 °C (Skogseth et al., 2005).

The sedimentary environment in Storfjorden classified as a low-energy, high-accumulation environment, characteristic of inner fjords. The area is sheltered from along-shelf bottom currents and is affected by high terrigenous inputs; therefore deposition prevails over sediment removal by bottom currents (Winklemann and Knies, 2005). The primary productivity is high and strongly depends on the sea ice formation and the duration of the marginal ice zone (Winkelman and Knies, 2005).

3. Materials and methods

3.1 Sampling

The 55-cm-long sediment core ST_1.5 was taken with a gravity corer in Storfjorden during cruise of the R/V *Oceania* in August 2014. The sampling station was located at 76° 53,181' N and 19° 27,559' E at a depth of 153 m (Fig. 1). The core was stored at 4°C and shipped to the Institute of Oceanology PAS for further analyses.

In the laboratory, the core was extruded and cut into 1-cm slices. During cutting, sterile subsamples for ancient DNA (aDNA) analyses were taken at 5 cm intervals. To avoid extraneous and/or cross-contamination the thin layers of sediment that were in contact with under- or overlying sediments were removed using a sterile spatula. Samples for aDNA analyses were taken every 5 cm and kept frozen in -20°C.

3.2 Sediment dating

The chronology of the sediment layers is based on high-precision accelerator mass spectrometry (AMS) ^{14}C dating performed on five bivalve shells from the sediment layers at 2.5, 5.5, 14.5, 43.5, 52.5 cm. The shells were identified to the highest possible taxonomic level and processed on the 1.5 SDH-Pelletron Model "Compact Carbon AMS" in the Poznań Radiocarbon Laboratory, Poznań, Poland. The dates were converted into calibrated ages using the calibration program CALIB Rev. 6.1.0 Beta (Stuiver and Reimer, 1993) and the Marine13 calibration dataset (Reimer et al., 2013). A difference (ΔR) in the reservoir age correction of 105 ± 24 was applied (Mangerud et al., 2006). The calibrated results are reported in units of thousand calibrated years BP (cal ka BP), see Table 1.

3.3 Sediment grain size

Samples for the grain size analyses were freeze-dried and milled. Measurements were performed using a Mastersizer 2000 particle laser analyzer coupled to a Hydro MU device (Malvern, UK). Samples were treated with ultrasound to avoid aggregation. Raw data were analyzed using GRADISTAT v.8.0 software (Blott and Pye, 2001). The mean 0-63-µm grain size [φ] was calculated via the logarithmic method of moments. The sediment fraction >500 µm was used for an ice rafted debris (IRD) analysis. Grains were counted under a stereomicroscope and the amount of IRD is reported as the number of grains per gram of dry sediment [grains g^{-1}] and flux [grains cm^{-2} y^{-1}].

3.4 Fossil foraminifera

Prior to fossil foraminifera analysis, samples were wet sieved through a mesh with 500-µm and 100-µm openings and dried at 60°C. Samples with large quantities of tests were divided using a microsplitter. At least 300 specimens of benthic foraminifera were isolated from each sample and collected on micropaleontological slides. Benthic foraminifera specimens were counted and identified to the lowest possible taxonomic level. The quantity of foraminifera is presented as the number of individuals per gram of dry sediment [ind. g^{-1}] and flux [ind. cm^{-2} y^{-1}]. Foraminifera species were grouped according to their ecological tolerances. Four groups of indicators were distinguished: AW/frontal zone indicators, ArW indicators, bottom current indicators and glaciomarine species (Majewski et al., 2009). Morphologically similar species *Islandiella norcrossi* and *Islandiella helenae* are reported as *Islandiella* spp.

3.5 Stable isotopes analysis

Carbon and oxygen stable isotope analyses were performed on *C. lobatulus* tests selected from 27 sediment layers. From 10 to 12 specimens were collected from each sample and subjected to ultrasonic cleaning. The measurements were performed on a Finningan MAT 253 mass spectrometer coupled to a Kiel IV carbonate preparation device at the University of Florida. The resulting values are expressed in standard δ notation relative to Vienna Pee Dee Belemnite (VPDB).

3.6 Ancient DNA analysis

Total DNA was extracted from approximately 10 g sediment using a Power Max Soil DNA extraction kit (MoBio). The foraminiferal SSU rDNA fragment containing the 37f hypervariable region was PCR amplified using primers tagged with unique sequences of five nucleotides appended to their 5' ends (denoted by Xs), namely the foraminifera-specific forward primer s14F1 (5'-XXXXXCGGACACACTGAGGATTGACAG-3') and the reverse primer s15 (5'-XXXXXCCTATCACATAATCATGAAAG-3'). The diatom DNA fragment located in the V4 region was amplified with the forward DIV4for (5'-XXXXXXXXGCGGTAATTCCAGCTCCAATAG-3') and reverse DIV4rev3 (5′-XXXXXXXXCTCTGACAATGGAATACGAATA-3’) primers tagged with a unique combination of eight nucleotides (denoted by Xs) attached at each primer’s 5’-extremity. The amplicons were purified using the High Pure PCR Cleanup Micro Kit (Roche) and quantified using a Qubit 2.0 fluorometer. Samples were pooled in equimolar quantities and the sequence library was prepared using a TruSeq library-preparation kit (Illumina). Samples were then loaded into a MiSeq instrument for a paired-end run of 2*150 cycles (foraminifera) and 2*250 cycles (diatoms). The processing of the HTS sequence data including quality filtering, sample demultiplexing, strict dereplication into unique sequences and operational taxonomic units (OTU) selection was performed according to procedures described by Lejzerowicz et al. (2013) and Pawłowska et al. (2014). The results are presented in OTU-to-sample tables and transformed in terms of the number of sequences, number of OTUs and the percentage (%) of sequences.

4. Results

4.1 Sediment age and type

All dates were in the chronological order and the uppermost layer contained modern, post-bomb carbon indicating a post-1960 age (Table 1). Samples from depths of 2.5 cm and 5.5 cm were not calibrated because they revealed ages that were invalid for the selected calibration curve. The age model was therefore based on the three remaining dates using a linear interpolation. The age of the bottom of the core was estimated to be approximately 9 cal ka BP (Fig. 2). However, the extremely low time resolution between 9 cal ka BP and 4 cal ka BP precluded making any general conclusion about that interval. Therefore, the manuscript focuses only on the last 4 cal ka BP (the Neoglacial).

The sediment accumulation rate (SAR) prior to ~ 2.7 cal ka BP was 0.002 cm y^{-1}. The approximately 10-fold increase in SAR is noted at ~ 2.7 cal ka BP, when it increased to 0.023 cm y^{-1}. During the last 1.5 cal ka BP, SAR decreased to 0.01 cm y^{-1} (Fig. 3). The amount of IRD was the highest prior to ~ 2.7 cal ka BP, reaching up to 83 grains g^{-1}. After 2.7 cal ka BP, the amount of IRD was relatively stable and did not exceed 18 grains g^{-1}. The flux of IRD slightly decreased with time to 0.37 grains g^{-1} cm^{-1}, except for one peak ~ 2.6 cal ka BP, when it reached 0.8 grains g^{-1} cm^{-1} (Fig. 3).

The mean grain size of the 0-63-µm fraction had its highest value (5.8 φ) at ~ 2.7 cal ka BP (Fig. 3) and after 2.4 cal ka BP a slight but continuous reduction in the mean 0-63-µm grain size was noted. The minimum grain size (6.23 φ) was recorded at the top of the core.

4.2 Stable isotopes

The $\delta^{18}O$ values were relatively stable prior to ~ 2.7 cal ka BP, varying slightly between 3.55‰ and 3.69‰ vs. VPDB. Between ~ 2.7 and 1.5 cal ka BP, $\delta^{18}O$ showed the strongest variation, with values ranging from 3.28‰ to 3.77‰ vs. VPDB. After ~ 1.5 cal ka BP, $\delta^{18}O$ became slightly lighter and varied between 3.43‰ and 3.64‰ vs. VPDB except for one peak noted in the uppermost layer of the core, where $\delta^{18}O$ reached 3.87‰ vs. VPDB (Fig. 3). $\delta^{13}C$ values varied throughout the core with slightly lighter values, ranging from 0.92‰ to 1.12‰ vs. VPDB prior to ~ 2.7 cal ka BP. $\delta^{13}C$ values reaching up to 1.46‰ vs. VPDB were noted between ~ 2.7 and ~ 1.5 cal ka BP and gradually decreased from ~ 1.5 cal ka BP to the present, reaching 0.81‰ vs. VPDB at the top of the core (Fig. 3).

4.3 Fossil foraminifera

A total of 8647 fossil foraminifera specimens belonging to 47 species were identified (Supplementary Fig. 1). The foraminiferal assemblages were dominated by calcareous taxa which account for 62–98% of the foraminifera specimens except in the uppermost layer of the core, where the percentage of calcareous foraminifera decreased to 44% (Fig. 3). There were few peaks of agglutinated foraminifera noted at 2.0 cal ka BP, 1.8 cal ka BP and on the sediment surface, where the percentages reached 37%, 37% and 66%, respectively (Fig. 3). The number of foraminiferal individuals varied from 156 to 2610 ind. g^{-1} and the lowest abundances were observed prior to ~ 2.7 cal ka BP (Fig. 3). A short-term decrease in the foraminiferal abundance was observed between 2.1 and 1.9 ka BP, with values reaching as low as 304 ind. g^{-1}. The abundance maxima were noted at 2.3, 1.5, and 0.6 ka BP, with values reaching 2524 ind. g^{-1}, 2584 ind. g^{-1}, and 2610 ind. g^{-1}, respectively. The foraminiferal flux was low and relatively stable throughout the core with values that did not exceed 1 ind cm^{-2} y^{-1}, except for two peaks at 2.3 and 1.5 ka BP, when the flux reached 2.2 ind cm^{-2} y^{-1} (Fig. 3).

The abundances of certain species followed a general trend with maxima ~ 2.3 cal ka BP and after ~ 1.7 cal ka BP and minima prior to ~ 2.7 cal ka BP and between 2.3 and 1.7 cal ka BP. The most abundant species was *Cassidulina reniforme*, with densities reaching up to 900 ind g^{-1}. The other species that constituted the majority of the foraminiferal assemblage were *Bucella frigida*, *Cibicidoides lobatulus*, *Elphidium excavatum*, *Islandiella* spp, *Melonis barleeanum*, and *Nonionellina labradorica* (Fig. 4).

The foraminiferal assemblage prior to ~ 2.7 cal ka BP was codominated by *Nonionellina labradorica* and *Melonis barleeanum*, which are species that are considered to be indicators of AW inflow and/or frontal zones, and glaciomarine taxa, primarily *Cassidulina reniforme* and *Elphidium excavatum*, which together accounted for up to 60% of the foraminiferal abundance (Fig. 4). After ~ 2.7 cal ka BP, there were AW/frontal zone indicator peaks recorded at 2.4 and 1.8 cal ka BP, where the percentages increased to 33%, 28%, and 42% of the total abundance. The period between ~ 2.4 cal ka BP and ~ 1.8 cal ka BP was characterized by an increase in the percentage of sea-ice indicators (*B. frigida* and *Islandiella* spp), which accounted for up to 25% of the total abundance, and by a short-term peak in the glaciomarine taxa, which accounted for up to 49% of foraminiferal assemblage between 2.5 and 2.1 cal ka BP. A decrease in the relative abundance of glaciomarine species was observed after ~ 0.5 cal ka BP and was followed by an increase in the AW/frontal zone indicators and a single peak in the percentage of bottom current indicators, which reached 19% (Fig. 4).

4.4 Foraminiferal aDNA sequences

A total of 1,499,889 foraminiferal DNA sequences were clustered into 263 OTUs, and 20 remained unassigned. The remaining OTUs were assigned to Globigerinida (5 OTUs), Robertinida (1 OTU), Rotaliida (49 OTUs), Textulariida (18 OTUs), Monothalamea (163 OTUs), and Miliolida (7 OTUs). The majority of sequences belonged to Monothalamea (60%) and Rotaliida (31%) (Supplementary Fig. 2). Herein, we focus on Monothalamea, which is the dominant component of the foraminiferal aDNA record.

The most important components of the monothalamous assemblage were *Micrometula* sp., *Cylindrogullmia* sp., *Hippocrepinella hirudinea*, *Ovammina* sp., *Nemogullmia* sp., *Tinogullmia* sp., *Cedhagenia saltatus*, undetermined allogromiids belonging to clades A and Y (herein called “allogromiids”), and sequences belonging to taxa known exclusively from environmental sequencing (herein called “environmental clades”). The sequences belonging to allogromiids were present throughout the core, accounting for 16–31.7% of all the foraminiferal sequences, except during the intervals prior to ~ 2.4 cal ka BP and ~ 1.7 cal ka BP, when contribution of allogromiid sequences decreased to less than 10% (Fig. 5). The majority of the allogromiids belonged to clade Y, which accounted for up to 100% of the allogromiid sequences, except for the two peaks at 1.6–1.7 cal ka BP and 2.4–2.6 cal ka BP, when the majority of allogromiid sequences belonged to clade A (Fig. 6).

The periods prior to ~ 2.4 cal ka BP and ~ 1.7 cal ka BP were marked by the disappearance of sequences belonging to *C. saltatus*, *Nemogullmia* sp., and the environmental clades, followed by an increase in the percentages of sequences belonging to *Micrometula* sp., *Ovammina* sp., *Tinogullmia* sp., *Shepheardella* sp. and *Cylindrogullmia* sp. (Fig. 5).

4.5 Diatom aDNA sequences

A total of 824,546 diatom DNA sequences were clustered into 177 OTUs. considerable part of the diatom sequences was assigned to only higher taxonomic levels (i.e. Mediophyceae; 34% of diatom sequences) or to raphid pennate forms (13% of diatom sequences; Supplementary Fig. 3). The most abundantly sequenced diatom taxa were *Thalassiosira* spp, *Navicula* sp. and *Chaetoceros* sp. *Navicula* sp. was the most abundant ~3.3 cal ka BP, accounting for up to 25.5% of all diatom sequences. In the following periods, *Navicula* sp. also occurred at ~ 2.6 cal ka BP, ~ 1.7 cal ka BP, ~ 1.3 cal ka BP, and ~ 0.9 cal ka BP, but its abundance did not exceed 5% (Fig. 7). The percentage of sequences of *Chaetoceros* sp. decreased downcore, from 78% at the surface to 3% at ~ 2.2 cal ka BP (Fig. 7). The sequences of *Thalassiosira* spp. were most abundant between ~ 2.6 cal ka BP and ~ 0.9 cal ka BP, accounting for up to 61% of all diatom sequences. The majority of these sequences were assigned to *Thalassiosira* sp., the remaining sequences belonged to *Thalassiosira antarctica* and *Thalassiosira hispida*. Both *Thalassiosira* sp. and *T. antarctica* were detected throughout the core and the percentages of their sequences were the highest prior to ~ 0.9 cal ka BP, reaching up to 50% and 19%, respectively (Fig. 7). Sequences of *T. hispida* were noted only at the sediment core surface, and ~ 2.2 cal ka BP, ~ 1.7 cal ka BP, and ~ 1.6 cal ka BP, accounting for up to 5%, 0.7%, 1.2%, and 0.1% of the diatom sequences (Fig. 7).

6. Discussion

The ST_1.5 age model is based on the linear interpolation between the three dates, so the age control of the core should be treated with caution, however the timing of the major environmental shifts was well supported by the variation in ST_1.5 grainsize, the abundance of fossil foraminifera and isotope composition of foraminiferal tests and molecular records of diatoms and non-fossilized foraminifera. Moreover, the good correlation with other records from the region (e.g., Sarnthein et al., 2003, Rasmussen and Thomsen, 2014) supports the ST_1.5 age model. The multiproxy record from Storfjorden revealed several intervals of pronounced environmental changes. The major environmental shifts occurred at ~ 2.7, 2.3 and 1.7 cal ka BP, what correlated well with the temperature minimum (2.7 cal ka BP) and maxima (2.3 and 1.7 cal ka BP) recorded in the GISP2 core (Cuffey and Clow, 1997; Alley, 2000) and 23258 core (Sarnthein et al., 2003).

The most pronounced environmental change during the Neoglacial was recorded in Storfjorden ~ 2.7 cal ka BP. During the period prior to ~ 2.7 cal ka BP, the ST_1.5 sedimentary record displayed elevated and variable IRD delivery and coarsening of the 0-63-

µm fraction (Fig. 3). These results are in agreement with the record from Storfjordrenna (Łącka et al., 2015), where peaks in IRD were noted during the Neoglacial and were attributed to increased iceberg rafting due to fluctuations in the glacial fronts (e.g. Forwick et al., 2010). In addition, the relatively high mean grain size of the 0-63-µm fraction (Fig. 3) might have resulted from more vigorous bottom currents and the removal of fine-grained sediment. According to Andruleit et al. (1996) a sudden increase in the hydrodynamic energy occurred during the late Holocene (~ 2.6 cal ka BP) at the SW Spitsbergen shelf. There are multiple explanations for such an intensification of bottom currents activity, including postglacial reorganization of the oceanographic conditions and a southward shift of the Polar Front, relative isostatic lowering of the sea level, or outflows of dense BSW (Andruleit et al., 1996). In Storfjorden, the intensification of bottom currents is most likely related to the presence of coastal polynyas and BSW production (Haarpainter et al., 2001). The most intensive brine production occurred in Storfjorden during the cold climatic intervals and was associated with the presence of extensive sea-ice cover (Rasmussen and Thomsen, 2015).

The ST_1.5 foraminiferal record supports the presence of a sea-ice cover in Storfjorden during the first phase of the Neoglacial (prior to ~ 2.7 cal ka BP). The ST_1.5 foraminiferal assemblage was codominated by glacier-proximal fauna (primarily *C. reniforme*) and indicators of frontal zones (primarily *M. barleeanum*; Fig. 4). The presence of *C. reniforme* and *M. barleeanus* is linked to cooled and salty AW (e.g., Hald and Steinsund, 1996; Jernas et al., 2013). Moreover, these species are also associated with the presence of phytodetritus, which may be related to the high productivity observed in frontal zones and/or near the sea-ice edge (Jennings et al., 2004). Knies et al. (2017) suggested a variable sea-ice cover extent and a fluctuating sea-ice margin in Storfjorden prior to ~ 2.8 cal ka BP. The record of diatom aDNA supports the latter assumption because the dominant components of the diatom assemblages were *Navicula* sp. and *Thalassiosira* spp (Fig. 7), which are genera found within or under sea-ice (Cremer, 1999; Ikävalko, 2004). The presence of these diatom taxa may suggest that primary production at that time was primarily associated with the winter–spring formation of the sea-ice cover.

The typical response of a foraminiferal community to high trophic resources is an increase in diversity and standing stock (Wollenburg and Kuhnt, 2000). However, according to our data, the foraminiferal community showed no clear signs of increased productivity, as the abundance and flux of foraminifera were low prior to ~ 2.7 cal ka BP (Fig. 3). Similarly, Rasmussen and Thomsen (2015) noted a decrease in concentration of benthic foraminifera in Storfjorden at that time, which was attributed to the more extensive seasonal sea-ice cover.

The lack of a growth response in the benthic foraminifera communities to an increased food supply was also observed in the costal polynyas off Greenland (Ahrens et al., 1997). Conversely, Smith et al. (2010) attributed higher abundances of planktonic and benthic foraminifera in the Weddell Sea coastal polynya to organic matter deposition in the seasonally open-marine environment. The periodic melting and freezing of Storfjorden polynya may enhance the primary productivity; however, at the same time production of dense brines may limit the growth and reproduction of foraminifera. This latter assumption needs to be confirmed by further studies.

The environmental conditions in central Storfjorden changed noticeably ~ 2.7 cal ka BP. The increase in SAR was followed by a gradual decrease in the 0-63-µm fraction and a decrease in the IRD delivery after ~ 2.7 cal ka BP (Fig. 3). According to Knies et al. (2017), the distinct surface water cooling during the Neoglacial provides a prerequisite for the presence of more extensive sea-ice cover; therefore inner Storfjorden was covered by densely packed sea ice between ~ 2.8 and 0.5 cal ka BP with low entrainment of terrestrial sediment and diminished surface water productivity. Rasmussen and Thomsen (2015) suggested glacial advance, followed by intensive ice rafting and meltwater delivery at that time. Therefore, the decreasing IRD in the ST_1.5 core may result from the presence of a sea-ice cover that reduced iceberg rafting while the majority of coarse grained material settled in the proximity of the glacial fronts. Similar conclusions have been stated by Forwick and Vorren (2009) and Forwick et al. (2010), who assumed that the enhanced formation of sea ice along the West Spitsbergen coast trapped icebergs inside the Isfjorden system. Furthermore, glaciers supply the fjord with large amounts of turbid meltwater, leading to the intensive settling of sediment and an increase in sediment accumulation (Fig. 3). The accumulation of fine sediment may also be enhanced by the slowdown of the bottom currents, indicated by the decrease in the 0-63-µm fraction after ~ 2.7 cal ka BP (Fig. 3).

Both heavy ice cover and meltwater delivery may limit light penetration in the water and therefore suppress primary production and organic matter export to the bottom. However, the foraminiferal fauna in central Storfjorden revealed more than a 10-fold increase in flux and abundance followed by short-term fluctuations after ~ 2.7 cal ka BP (Fig. 3); this may suggest favorable conditions for foraminiferal growth. Paleoceanographic records from the Nordic Seas suggest that the Neoglacial was not a constantly cold period. For example, the western Spitsbergen continental margin experienced periods of a rapidly advancing and retreating sea-ice margin, caused by a temporarily strengthened AW inflow and/or changes in the atmospheric circulation patterns (Müller et al., 2012). Sarnthein et al. (2003) reported two intervals of remarkably warmer sea surface on the western continental margin of the Barents Sea at ~ 2.2 and ~ 1.7 cal ka BP, which was attributed to short-term pulses of warm AW advection. The ST_1.5 micropaleontological and molecular records are in agreement with the findings of Sarnthein et al. (2003). The inflows of AW ~ 2.3 cal ka BP and 1.7 cal ka BP were marked by peaks in the total foraminiferal abundance in general (Fig. 3) and peaks in the percentage of AW foraminiferal indicators, in particular (Fig. 4), followed by the occurrence of sequences of *T. hispida* (Fig. 7), a diatom species characteristic of subpolar and temperate regions (Katsuki et al., 2009).

Knies et al. (2017) have suggested that the pulses of advected AW did not influence the persistent sea-ice cover in Storfjorden between ~ 2.8 and 0.5 cal ka BP. However, the ST_1.5 foraminiferal record indicates that central Storfjorden was not constantly covered by sea ice at that time. A more reasonable scenario is surface water cooling and periodic melting and freezing of the sea surface and consequent production of brines, which launched convective water mixing and nutrient resupply to the surface, thereby stimulating primary production (Łącka et al., *in prep.*). The presence of diatom aDNA sequences throughout the Neoglacial (Fig. 7) may suggest continuous primary production. It is likely that pulses of AW inflow at 2.3 cal ka BP and 1.7 cal ka BP induced melting of the ice cover, leading to the formation of ice-free areas and highly productive ice marginal zones. This conjecture may be supported by peaks in the light δ^{18}O in benthic foraminiferal tests, the maxima of the foraminiferal flux (Fig. 3) and peaks in the abundance of species associated with highly productive environments such as *M. barleeanum* and *N. labradorica* (Fig. 4). Similarly, the foraminiferal flux and abundance were elevated and slightly variable after ~ 1.7 cal ka BP. The foraminiferal assemblage was codominated by AW/frontal zone indicators and glaciomarine species (Fig. 4) at that time, which may suggest rather ameliorated environmental conditions. In contrast, the interval between 2.3 and 1.7 cal ka BP featured slightly heavier δ^{13}C and δ^{18}O followed by a decrease in the foraminiferal flux and abundance (Fig. 3). The foraminiferal assemblage at this time was dominated by glaciomarine and sea-ice taxa (Fig. 4), which indicate more severe environmental conditions with extensive ice cover and suppressed productivity. The sea-ice formation led to a more intensive release of brines and consequently, stronger bottom current activity reflected in a slight increase in the percentage of *C. lobatulus*, which is considered to be a bottom current indicator (Fig. 4).

The above-described environmental changes were also reflected in the aDNA record of monothalamous foraminifera. During the time intervals of 2.2–1.9 cal ka BP and 1.3–0.4 cal ka BP, monothalamous foraminifera was dominated by allogromiids belonging to clade Y, *Nemogullmia* sp., *C. saltatus* and monothalamids belonging to so called "environmental clades" (Fig. 5). Allogromiids are not coherent taxonomic group but are scattered between several monothalamous clades (Gooday 2002; Pawlowski et al., 2002). Considerable part of the allogromiid sequences in the ST_1.5 core belong to clade Y (Fig. 6), which is primarily composed of taxa known only from environmental sequencing. Sequences belonging to clade Y have previously been noted in modern sediments in the Spitsbergen fjords (Pawłowska et al., *in prep.*). Moreover, clade Y has been abundantly sequenced in the coastal areas off Scotland, characterized by high levels of environmental disturbances (Pawlowski et al., 2014a); this might suggest its high tolerance to environmental stress. In addition, so called "environmental clades" comprised of monothalamous taxa known exclusively from environmental sequencing (Lecroq et al., 2011) and may belong to novel, undescribed foraminiferal lineages (Pawlowski et al., 2014b). *C. saltatus* was recently found by Gooday et al. (2011) in the Black Sea and until recently, little has been known about its environmental tolerances; however, its occurrence in areas with high levels of pollution suggests that it is an opportunistic species with a high tolerance to environmental disturbances. Specimens of *Nemogullmia* were also found in the Spitsbergen fjords (Gooday et al., 2005; Majewski et al., 2005); however, data on its abundance and distribution may be incomplete due to the degradation of its fragile, organic-walled tests. The abovementioned taxa nearly disappeared during episodes of enhanced AW inflow ~ 2.4 cal ka BP and ~ 1.7 cal ka BP, and the monothalamous assemblage was dominated at that time by *Micrometula* sp., *Ovammina* sp., *Shepheardella* sp., *Tinogullmia* sp., *Cylindrogullmia* sp., and allogromiids belonging to clade A (Fig. 5; Fig. 6). All these taxa have recently been observed in the fjords of Svalbard (e.g. Gooday et al., 2005; Majewski et al., 2005; Sabbattini et al., 2007; Pawłowska et al., 2014). *Cylindrogullmia* sp. commonly been found in the inner parts of the fjords (Gooday et al., 2005). Hughes and Gooday (2004) suggest that *Cylindrogullmia* sp. is an infaunal species that normally resides in deeper sediment layers of sediment. *Micrometula* sp. was among the abundantly found organic-walled allogromiids in glacier-proximal sites off Novaya Zemlya (Korsun & Hald, 1998; Korsun et al., 2005) and Svalbard (Korsun & Hald, 2000; Gooday et al., 2005; Pawłowska et al., 2014). Moreover, *Cylindrogullmia* and *Micrometula* are dependent on the presence of fresh phytodetritus (Alve, 2010). *Ovammina* sp. feeds on diatoms and other forms of microalgae (Goldstein & Alve, 2011). Similarly, the presence of *Tinogullmia* is largely controlled by the presence of organic material on the seafloor. High concentrations of *Tinogullmia* have been found in coastal (Cornelius & Gooday, 2004) and deep-sea regions (Gooday, 1993) within phytodetrital aggregates.

In general, monothalamous foraminifera are highly adaptable and resistant to environmental disturbances. However, the taxa that dominated the monothalamous assemblage during warm intervals seem to be responsive to the delivery of organic matter and may flourish during phytoplankton blooms associated with the settling of organic matter (e.g., Alve, 2010; Sabbattini et al., 2012, 2013). The pulses of AW inflow that are associated with sea-ice melting stimulated phytoplankton blooms and organic matter supply to the bottom. The enhanced primary productivity supported the development of an organic matter-dependent monothalamous community. Conversely, the colder phases of the Neoglacial were characterized by heavy and densely packed sea ice resulting in limited productivity (Knies et al., 2017). Therefore, the monothalamous assemblage was less diverse and was dominated by highly opportunistic taxa.

The decrease in the percentage of foraminiferal sea-ice indicators that started after ~ 1.7 cal ka BP suggests a gradually diminishing sea-ice coverage in Storfjorden (Fig. 4), and Modern-like conditions were established in Storfjorden ~ 0.5 cal ka BP, with seasonally variable sea-ice cover resulting in intensified but variable polynyal activity (Rasmussen and Thomsen, 2014; Knies et al., 2017). the IP_{25} records from the western Spitsbergen shelf indicate variable sea-ice conditions during the last 2 ka (Cabedo-Sanz and Belt, 2016). Moreover, the majority of diatom aDNA sequences after ~ 0.5 cal ka BP belonged to *Chaetoceros* sp., a taxa that is observed in surface waters and is almost entirely absent under sea ice (Różańska et al., 2008). Moreover, high abundances of *Chaetoceros* are often associated with highly productive surface waters (Cremer, 1999), which indicate declining sea-ice cover (Cabedo-Sanz and Belt, 2016). However, the aDNA record of the monothalamous foraminifera ~ 0.4 cal ka BP displayed relatively high percentages of taxa that dominated during colder intervals of the Neoglacial (Fig. 5); this may be related to the recovery from the Little Ice Age and consequently, temporarily deteriorated environmental conditions (D'Andrea et al., 2012). However, further studies are required to confirm the latter conclusion.

7. Conclusions

The ST_1.5 multiproxy record revealed that the environmental variability in Storfjorden during the Neoglacial was steered controlled primarily by the interplay between AW and ArW and changes in the sea-ice cover. The molecular record supports and complements sedimentary and microfossil records, which indicate that major changes in the environmental conditions in Storfjorden occurred at ~ 2.7 cal ka BP. The general cooling at the early phase of the Neoglacial initiated conditions for the formation of extensive sea-ice cover. The latter part of the Neoglacial (after ~ 2.7 cal ka BP) was characterized by alternating short-term cooling and warming periods. Warming was associated with pulsed inflows of AW and sea-ice melting stimulating phytoplankton blooms and organic matter supply to the bottom. The cold phases were characterized by heavy and densely packed sea ice resulting in limited productivity.

Moreover, the aDNA diatom record supports the conclusion that primary production took place continuously during the Neoglacial, regardless of the sea-ice conditions. The early phase of the Neoglacial was characterized by the presence of diatom taxa associated with sea ice, whereas the present-day diatom assemblage was dominated by *Chaetoceros* spp, a taxa characteristic of open water.

The aDNA record of monothalamous foraminifera is in agreement with the microfossil record and revealed the timing of the major pulses of AW at 2.3 and 1.7 cal ka BP. The AW inflow was marked by an increase in the percentage of sequences of monothalamous taxa associated with the presence of fresh phytodetritus. The monothalamous assemblage during cold intervals was less diverse and was dominated by monothalamous foraminifera known only from environmental sequencing.

Author contribution

MZ and Jan P designed the study. Joanna P, MŁ and MZ collected the sediment core. MŁ and MK performed the sedimentological and micropaleontological analyses. Joanna P performed the molecular analyses and prepared the manuscript with contributions from all co-authors.

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Figures captions

Figure 1: Study area and the location of the studied core ST_1.5 and the other cores discussed in this paper.

Figure 2: Age–depth model of the studied core.

Figure 3: Sedimentological and micropaleontological data plotted versus age. The sediment accumulation rate (SAR), mean grain size of the 0-63-µm fraction, ice-rafted debris (IRD) flux and number of grains per gram of sediment, oxygen ($\delta^{18}O$) and carbon ($\delta^{13}C$) stable isotopes in foraminiferal tests, the percentage of calcareous foraminifera individuals and the flux and abundance of foraminifera are presented.

Figure 4: The abundance (expressed as the number of individuals per gram of dry sediment) and the percentage of the dominant testate foraminifera.

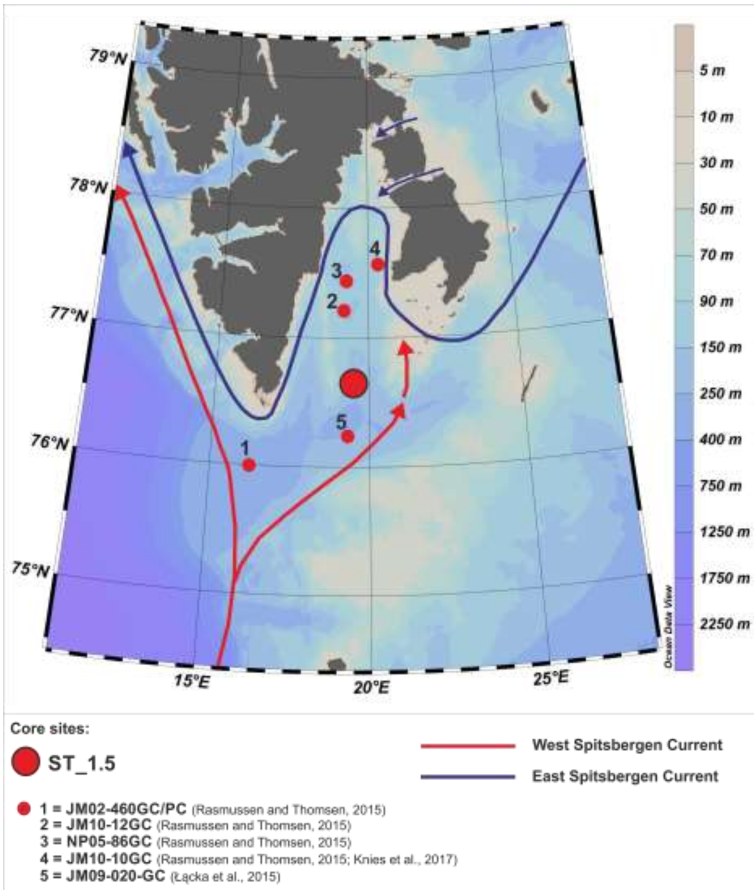
Figure 5: The dominant components of the monothalamous assemblages. The abundance is expressed as the percentage of the monothalamous sequences and the most abundantly sequenced taxa are presented. The trend is indicated with the dashed line.

Figure 6: The percentage share of certain clades in the allogromiid sequences.

Figure 7: The percentage of sequences of dominant diatom taxa vs. time. The trend is indicated with the dashed line.

Tables captions

Table 1: Raw and calibrated AMS^{14}C dates used in the age model.



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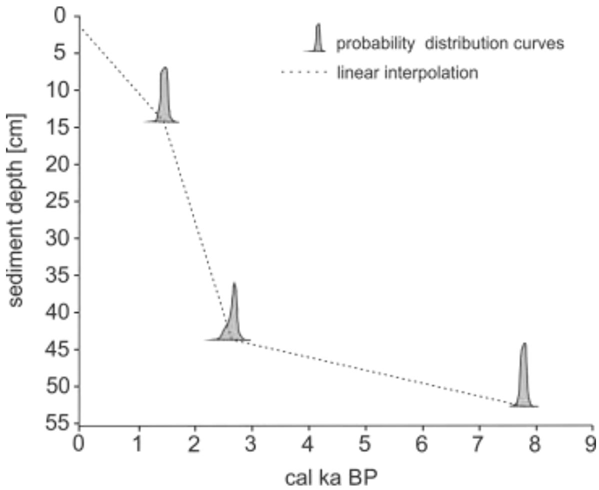

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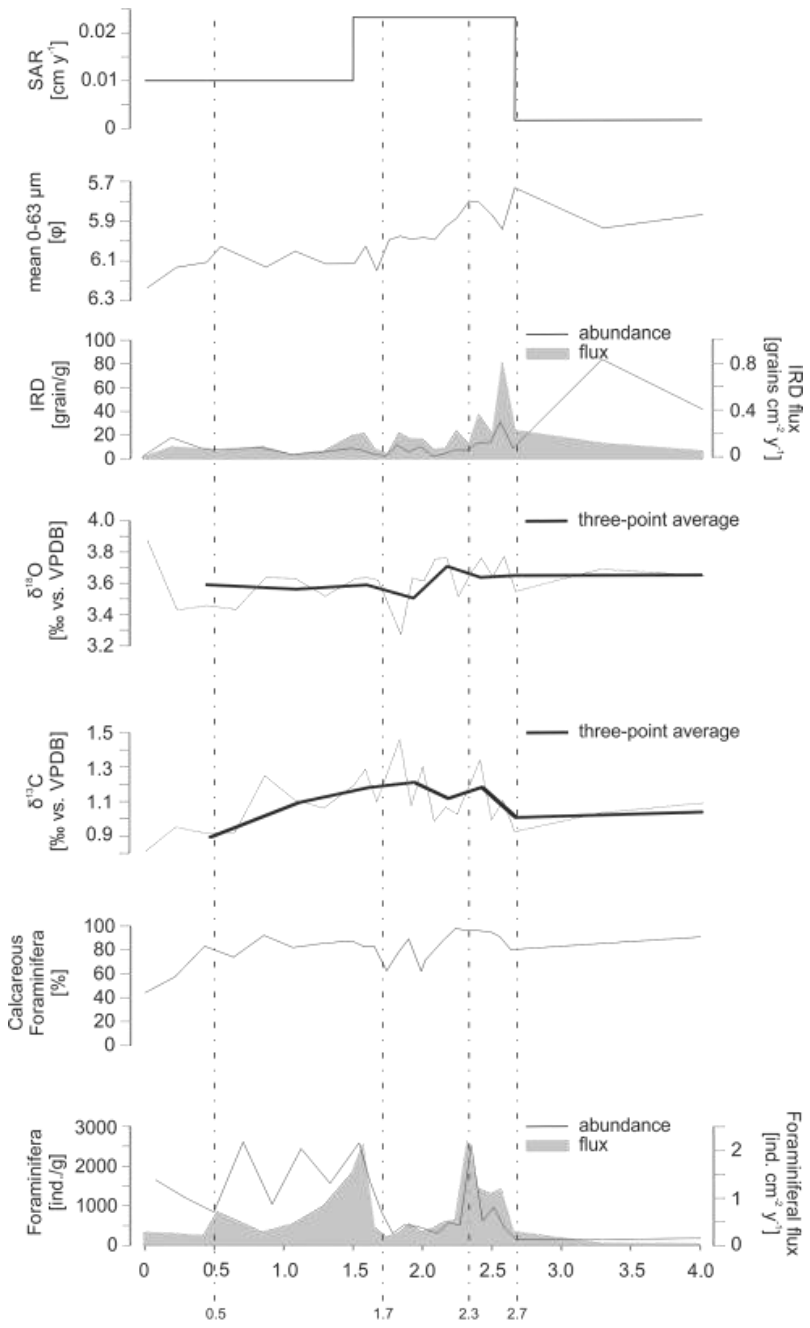

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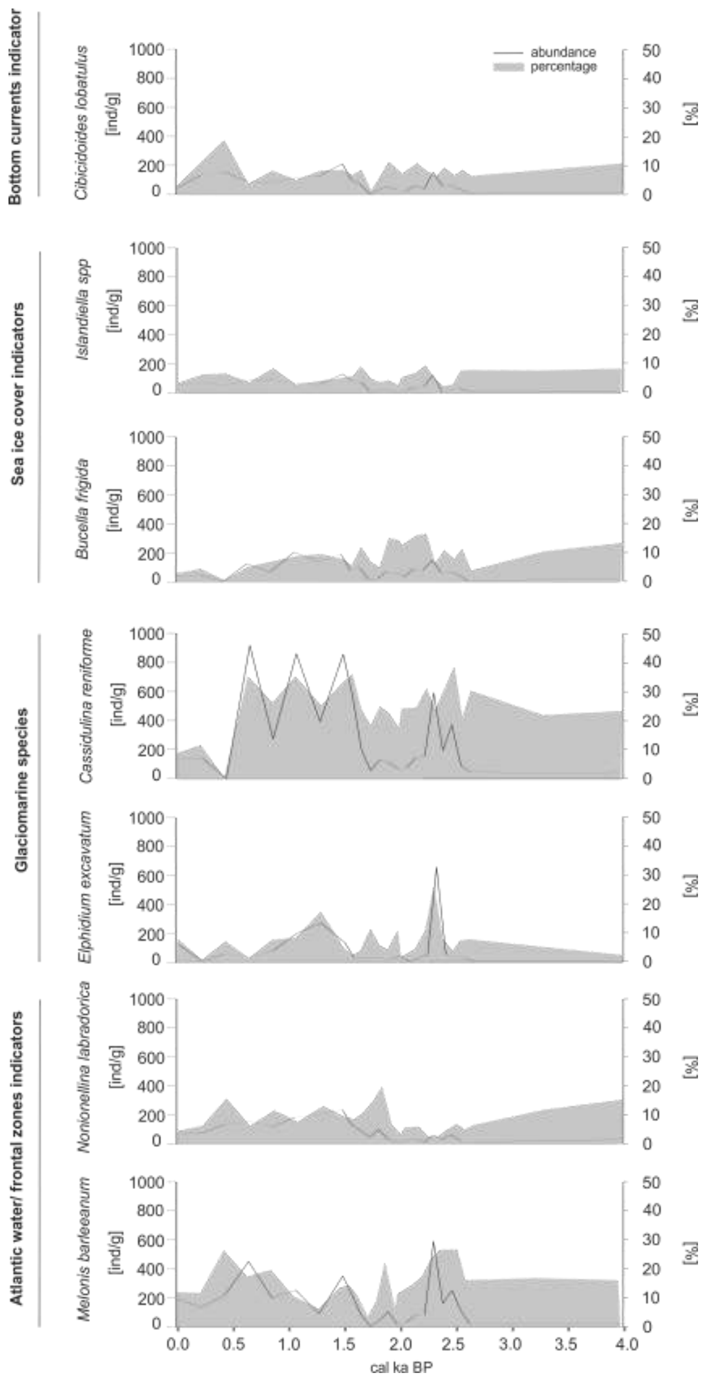

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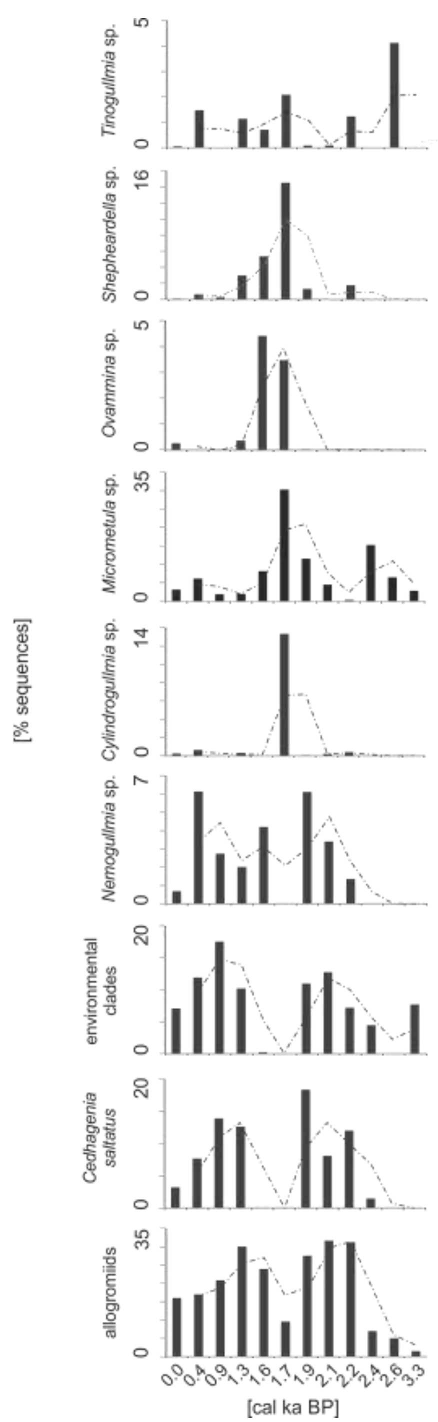

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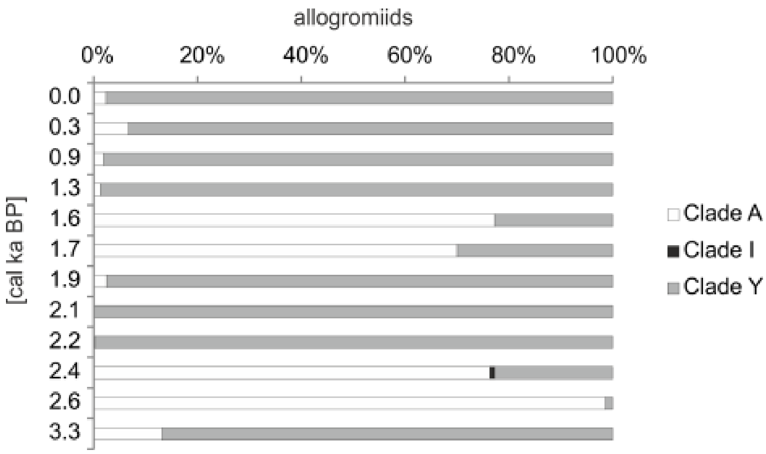

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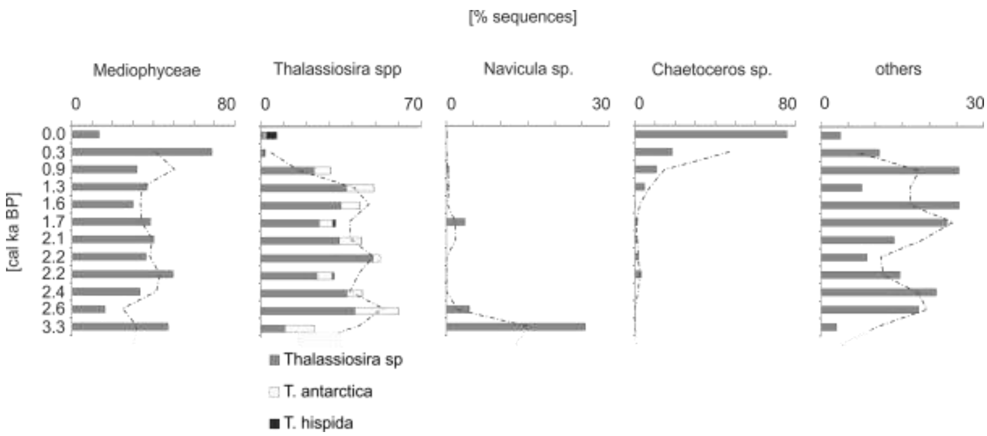

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Sediment depth [cm]	Material (shells)	Raw AMS ^{14}C	Calibrated years BP ± 2σ	Cal. a BP used in age model
2.5	*Nuculana pernula*	107.38 ± 0.33 pMC	-	-
5.5	*Yoldiella lenticula*	290 ± 30 BP	-	-
14.5	*Turitella erosa*	2020 ± 30 BP	1356-1555	1500
43.5	*Yoldiella solituda*	3010 ± 50 BP	2484-2787	2700
52.5	*Yoldiella lenticula*	7545 ± 35 BP	7803-7989	7890