Pleistocene benthic foraminifers in the Arctic Ocean: implications for sea-ice and circulation history

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Abstract

Three sediment cores from the Northwind, Mendeleev, and Lomonosov Ridges distributed across the western Arctic Ocean were investigated for foraminiferal composition with a focus on benthic assemblages. This investigation provides insights into middle to late Pleistocene history of paleoceanographic and sea-ice conditions on multi-millennial time scales. Calcareous foraminiferal abundances and assemblage composition show stratigraphically consistent development, including glacial-interglacial variability and long-term evolution of foraminiferal assemblages. Major long-term changes occurred at the end of the Mid-Pleistocene Transition (estimated ca. 0.7-0.8 Ma) and later near the bottom of Marine Isotope Stage 7 (ca. 0.25 Ma) and near the top of MIS 5 (ca. 0.1 Ma). These changes include notably a diminishing role of phytodetritus-related species, such as *Epistominella exigua*, at the expense of oligotrophic species adapted to live under persistent sea ice, presumably indicating an overall expansion of year-round ice cover in the Arctic during the Pleistocene. The pronounced MPT shift from mostly seasonal to perennial sea ice was coeval, and possibly related to a growth of North American ice sheets and the beginning of glacially-controlled sedimentation in the western Arctic Ocean. The ca. 0.25 Ma transition, interpreted as another step in sea-ice expansion, also co-occurs with signs of ice-sheet expansion in both North America and, especially, Eurasia. The apparent synchronicity of major steps in sea-ice and glaciation histories necessitates a more in-depth investigation of feedbacks involved and broader linkages beyond the Arctic region. The ca. 0.1 Ma change in foraminiferal assemblages marks a consistent stratigraphic event, expressed notably in a proliferation of the cosmopolitan species *Oridorsalis tener*, although its paleoenvironmental significance is not yet fully understood.

1. Introduction

Sea ice plays a principal role in the regulation of the Arctic climate system that shows an increasing vulnerability to the ongoing climate change. The effects of a warming planet are disproportionately felt in the Arctic, where snow and ice dominate the landscape, and even small temperature increases can cause major changes via the surface temperature and albedo feedbacks (e.g., Holland & Bitz, 2003; Bekryaev et al., 2010; Miller et al., 2010). The Arctic Ocean also plays a substantial role in freshwater inputs to the North Atlantic (Peterson et al., 2006) and, thus, the formation of the North Atlantic Deep Water, a critical component of global thermohaline circulation (e.g., Aagaard and Carmack, 1994). Recently, Arctic sea ice has decreased in thickness and volume (Rothrock et al., 2003; Lindsay and Zhang, 2005; Laxon et al., 2013), in concert with a progressive loss of summer sea-ice extent (Comiso et al., 2008; Stroeve et al., 2011). The projected loss of perennial sea ice, while unprecedented for the observational period, is not novel in the context of the geologic history (e.g., Polyak et al., 2010). A better understanding of the interplay between factors affecting paleo-sea-ice can lead to more accurate model predictions of changes we can expect in the near future (e.g., Polyak et al., 2010, and references therein).

Sea ice is a major factor controlling sedimentary environments in the Arctic Ocean, including biological, geochemical, and lithological characteristics, which could be therefore used as proxies for paleo-sea-ice reconstructions (e.g., Polyak et al., 2010; Stein et al., 2012). However, the development of such proxies and their application to the Arctic sedimentary record is impeded by their limited availability due to low biological productivity, low sedimentation rates, and diagenetic losses, as well as poor knowledge of related modern processes. Analyses on

benthic microfossil assemblages provide one way of addressing paleo-sea-ice conditions through their dependence on sea-ice controlled food inputs to sea floor (e.g., Wollenburg and Kuhnt, 2000; Scott et al., 2008; Polyak et al., 2013). This approach is especially valuable due to its relevance to comprehending the potentially severe impact of sea-ice reduction on the Arctic Ocean biota (e.g., Harada, 2016, and references therein), where effects on the deep-sea communities are not understood. Proxy reconstructions utilizing microfossils have been recently developed for Pleistocene records containing relatively abundant and well-preserved calcareous microfossils such as benthic foraminifers (Polyak et al., 2013) and ostracodes (Cronin et al., 2013). However, the most complete record extending to an estimated ~1.5 Ma age was constrained only to one site on the Northwind Ridge, ~800 km north of Alaska. This, along with complex benthic community responses to changing ice conditions, indicates the need for further investigation of microfaunal assemblages in Arctic sedimentary records.

This paper addresses the distribution of benthic foraminifers, and their potential as paleo-sea-ice proxies, in sediment cores across the western Arctic Ocean. Sites analyzed are representative for the Beaufort Gyre, a major circulation feature controlling the transportation of sea ice throughout the western Arctic and its subsequent export into the North Atlantic (e.g., Proshutinsky et al., 2002). Stratigraphic focus will be on the late to middle Pleistocene record extending to ~0.5 Ma, the time of pronounced glacial-interglacial cycles in the Northern Hemisphere. This interval in western Arctic Ocean sediments generally contains considerable amounts of calcareous fossils (such as foraminifers and ostracodes), which are mostly absent in the older sediments.

2. Oceanographic and Stratigraphic Context

Sediment cores used in this study were collected from the Northwind Ridge (NR), Mendelev Ridge (MR), and Lomonosov Ridge off Greenland (LR) in the western Arctic Ocean (Fig. 1). Surface circulation in this basin is primarily controlled by the anticyclonic Beaufort Gyre, whereas, the Pacific and Atlantic inputs contribute to the halocline and deeper intermediate waters, respectively (e.g., Rudels et al., 1994; Jones, 2001). Sites from the Northwind and Mendelev ridges are located in the area of most dramatic modern retreat in summer sea-ice extent and associated changes in oceanic circulation and biogeochemical environments (Stroeve et al., 2011; Morison et al., 2012; Harada, 2016), which make it especially important for paleoceanographic research.

Overall sedimentation rates in the central Arctic Ocean are especially low in the western Arctic due, among other factors, to a high concentration of perennial ice cover, which could have been especially thick and solid during glacial periods (Polyak et al., 2009; Stein et al., 2010). Accordingly, sedimentary records from this region may not be suitable for studies with high age resolution (such as submillennial), but they can provide an important insight into the long-term history of Arctic paleoclimate with an orbital-scale resolution (e.g., Adler et al., 2009; Cronin et al., 2013, 2014).

In addition, and probably in relation to low sedimentation rates, Arctic paleoceanographic studies are hampered by a number of factors affecting both the development of paleoenvironmental proxies and age constraints. However, most Arctic sediment cores demonstrate a clear recurring pattern in biostratigraphic, geochemical, and lithological characteristics, which can be explained by glacial/interglacial changes. These patterns provide an opportunity for tuning these records to the global climatic history (e.g., Jakobsson et al., 2000;

O'Regan et al., 2008; Stein et al., 2010; Polyak et al., 2013), although independent controls for such tuning are yet to be developed. The cyclicity is especially pronounced in the so-called glacial (middle to late) Pleistocene and is expressed notably in interlamination of brown (manganese enriched) interglacial/major interstadial and grayish glacial sediments, commonly with peaks of ice-rafted debris (IRD) related to deglacial iceberg pulses (e.g., coarse sediment peaks in Fig. 2). The correlation of this cyclic stratigraphy, which can be complicated by low and variable sedimentation rates, is aided by sedimentary events, such as IRD peaks with a specific provenance (e.g., Laurentide detrital carbonates forming characteristic pink-white layers; Clark et al., 1980; Polyak et al., 2009; Stein et al., 2010; Cronin et al., 2013). Sediments deemed older than middle Quaternary typically have a less explicit cyclicity, overall low IRD numbers, low Ca and high Mn contents (Polyak et al., 2009, 2013; Sellén et al., 2010; Stein et al., 2010). We note that although the employed age model for Quaternary Arctic stratigraphy is still tentative, the correlation based on sedimentary cycles and event markers is fairly robust within the western Arctic Ocean, especially in the middle to late Pleistocene (Polyak et al., 2009; Sellén et al., 2010; Stein et al., 2010; Cronin et al., 2014).

Biostratigraphic research in the central Arctic Ocean is complicated by a limited stratigraphic range and irregular occurrences of microfossils, which may be related primarily to unfavorable conditions such as suppressed biological production during glaciations and/or dissolution. A relatively complete record of calcareous foraminifera preserved in interglacial/interstadial intervals typically extends to no older than Marine Isotope Stage (MIS) 7 (ca. 0.25 Ma), even less in the eastern Arctic (e.g., Poore et al., 1993; Jakobsson et al., 2001; Adler et al., 2009; Sellén et al., 2010). Recent studies of better preserved fossiliferous records in the western Arctic Ocean provide insight into longer-term paleoceanographic history covering

nearly all of the middle Quaternary (e.g., Fig. 2; Cronin et al., 2013) or in some cases extending into older strata (Hanslik, 2011; Polyak et al., 2013). We capitalize on these records to develop an integrated picture of benthic foraminiferal change in the western Arctic for the last several glacial cycles that were especially pronounced in the Northern Hemisphere.

3. Material and Methods

3.1 Core material

The calcareous microfossils in the three sediment cores chosen for this study (Table 1; Fig. 1) provide a more complete record for the middle to late Pleistocene than those in most Arctic Ocean cores (Mullen and McNeil, 1995; Hanslik, 2011; Cronin et al., 2013; Polyak et al., 2013). The core sites are geographically distributed across the western Arctic and are located on oceanic ridges in similar water depths between 800 and 950 m, that is, at the transition from the intermediate Atlantic Water Layer to underlying Polar Deep Water (Rudels et al., 1994). The location on the ridges ensures that these cores were not affected by slumping/turbidite deposition. Some winnowing effects have been inferred for the upper part of cores JPC6 and P23, but no apparent hiatuses have been reported (Cronin et al., 2013; Polyak et al., 2013). Lithologic, paleomagnetic, and bulk chemical investigations of these cores have been mostly completed and published (Jakobsson et al., 2008; Channell and Xuan, 2009; Polyak et al., 2009, 2013; Cronin et al., 2013; Hanslik et al., 2013). According to the corresponding age models, especially low sedimentation rates of 2-3 mm/ka on average characterize P23, as representative for the inner part of the Beaufort Gyre (Polyak et al., 2009; Stein et al., 2010). Overall higher sedimentation rates characterize the two other cores, reaching up to 1 cm/ka in the upper part of

PC04. Correlation of cores from the Northwind and Mendeleev Ridges, exemplified by P23 and JPC6, has been illustrated in prior papers (Polyak et al., 2009; Cronin et al., 2014). Detailed lithostratigraphic correlation of these cores with the area north of Greenland, including PC04, is more complicated due to a geographic variability in sediment provenance (e.g., Nørgaard-Pedersen et al., 2007), but general stratigraphic features appear to be comparable (Sellén et al., 2010). As the stratigraphy discussed is within the glacial Pleistocene with a strong cyclicity of Arctic sedimentary environments, the prevailing lithological feature is interlamination of glacial and interglacial/major interstadial (collectively, non-glacial) units (e.g., Fig. 2; Jakobsson et al., 2000; O'Regan et al., 2008; Polyak et al., 2009; Stein et al., 2010). The latter typically contain considerable numbers of calcareous microfossils (benthic and planktic foraminifers and ostracodes), which become overall less abundant down-core throughout the middle Quaternary to a complete disappearance in lower strata.

3.2 Sample processing

Foraminifers have been earlier studied in P23 ($>63\ \mu\text{m}$; Polyak et al., 2013) and PC04 ($>125\ \mu\text{m}$ only; Hanslik, 2011); total numbers have also been counted in $>150\ \mu\text{m}$ in JPC6 (Cronin et al., 2013). For a comprehensive characterization of foraminiferal assemblages in all three cores, we have performed detailed counts in $63\text{--}125$ and $>125\ \mu\text{m}$ size fractions in JPC6 and PC04 (the $>125\ \mu\text{m}$ samples in the latter were recounted for consistency of results). In contrast to an earlier study of P23 (Polyak et al., 2013) that paid more attention to the Early Quaternary, this paper focuses on the younger stratigraphy characterized by all three cores. Sample collection and initial processing for this study was done at the Byrd Polar and Climate Research Center (BPCRC) (cores JPC6 and P23) and at Stockholm University (PC04), with

foraminiferal analysis completed at BPCRC. The wet samples were freeze-dried, weighed, and washed over a 63- μm sieve to remove the mud fraction. Dry weights of most samples fell within the range of 5–10 grams (Supplement 1).

This study covers samples from the entire occurrence range of calcareous foraminifers in cores PC04 and JPC6 (Hanslik, 2011; Cronin et al., 2013) and the correlative stratigraphic interval in P23 corresponding roughly to the late to middle Quaternary, ca. 0.8 Ma (Polyak et al., 2013) (Fig. 3). Typically, one-centimeter thick samples were taken at an average 2 or 4-cm interval in cores JPC6, P23, and the upper Pleistocene section of PC04, and with 8-cm spacing in the lower part of this core. The resulting age resolution is estimated to vary from ca. 2–4 to 10–15 ka per sample. Regardless of average resolution, we aimed to represent all of the apparent lithostratigraphic units by at least one-two samples (for the thinnest units). We also aimed to analyze samples at higher stratigraphic frequency from interglacial/interstadial intervals, where foraminifers are generally more abundant, than from foraminiferal-poor or barren glacial intervals. Overall, although insufficient for detailed paleoclimatic studies, this material appears to provide relevant information on the long-term development of the Arctic Ocean in the Pleistocene.

Total numbers of both planktic and benthic foraminifers were counted in the $>150\ \mu\text{m}$ size fraction. Individual benthic species were counted at somewhat sparser intervals in the 63–125 μm and $>125\ \mu\text{m}$ fractions. Investigation down to at least 63 μm size is essential as many of the diagnostic deep-sea species, especially in polar oceans, are not retained in larger size fractions (e.g., Lagoe, 1977; Schröder et al., 1987). More than 90% of foraminiferal tests found underneath permanent ice cover are $<125\ \mu\text{m}$ in size (Scott and Vilks, 1991; Wollenburg and Mackensen, 1998), suggesting a significant loss of assemblage information when only the larger

size fractions are considered. Counts in the size fraction >125 μm , however, may be still useful for comparison with other studies (e.g., Ishman and Foley, 1996; Osterman et al., 1999).

Approximately 250-300 foraminifera were identified in each sample counted, mostly to the species level. To ensure data compatibility, identifications were compared to multiple publications on Arctic foraminifera (e.g., Green, 1960; Lagoe, 1977; Scott and Vilks, 1991; Wollenburg, 1992; Ishman and Foley, 1996; McNeil, 1997; Scott et al., 2008), the Arctic foraminiferal collection at the Canadian Geological Survey (Calgary, Canada), and type specimens located in the Cushman Collection at the Smithsonian Institution (Washington, D.C., USA). Taxonomic notes in Polyak et al. (2013, suppl.) are also applicable to this study.

The Shannon-Wiener diversity index was calculated using the PAST software package (PAleontology STatistics; Hammer et al., 2001). A Q-mode cluster analysis was performed using census data and input into Systat 13 (detailed explanation given in 3.2 below).

3.3 Foraminifera proxy application

Foraminiferal assemblages in Arctic Ocean sediments can potentially indicate the conditions of sea ice, which largely control the supply of food from the ocean surface to sea floor (e.g., Hoste et al., 2007; Vanreusel et al., 2000). Polyak et al. (2013) proposed to use two distinctly different ecological groups of benthic foraminifera, so-called polar and phytodetrital species, as proxies of mostly perennial or seasonal sea-ice regime, respectively. In core P23, the stratigraphically longest foraminiferal record from the central Arctic Ocean, these groups occur at distinctly different intervals corresponding to paleoenvironments with enhanced vs. reduced sea-ice and glacial impact (Polyak et al., 2013). The polar species are predominated by *Stetsonia horvathi* and *Bolivina arctica*, signature small-sized Arctic foraminifers (Green, 1960; Herman,

1973; Lagoe, 1977). Outside the Arctic, *S. horvathi* characteristically co-occurs with the presence of polar waters either in modern environments (Cornelius and Gooday, 2004) or in glacial Pleistocene intervals (Pawlowski, 1991; Osterman, 1992; Collins et al., 1996), and is typically absent in other ocean regions based on studies of size fraction >63 μm or smaller (e.g., Kurbjeweit et al., 2000; Hayward et al., 2003; Phipps et al., 2012). A notable exception is the finding of *S. horvathi* (listed as *S. arctica*) in deposits of the Bengal Fan predominated by suspended load (Scott and Leger, 1990). *Bolivina arctica*, which is not found in modern environments, has been reported from glacial intervals in the North Atlantic (Collins et al., 1996). We infer that the primary factor controlling the occurrence of these and related species is probably low and unstable organic flux to the seafloor, a common characteristic of sea-ice-dominated areas (Stein and Macdonald, 2004). This pattern is supported by the distribution of *S. horvathi* in modern Arctic sediments (Wollenburg and Kuhnt, 2000; Husum et al., 2015), while the ecology of *B. arctica* has to be reconstructed from paleorecords. In contrast to polar foraminifers, phytodetrital species, such as *Epistominella exigua*, typify areas with strong seasonal pulses of fresh organic matter (e.g., Gooday, 1988; Smart et al., 1994; Thomas et al., 1996). In the Arctic this depositional environment occurs at the Marginal Ice Zone (MIZ) due to primary production blooms during ice melt (e.g., Hoste et al., 2007; Perrette et al., 2010). Consistent with this pattern, *E. exigua* in modern sediments is found in the Arctic only at the MIZ close to Fram Strait (e.g., Wollenburg and Mackensen, 1998; Wollenburg and Kuhnt, 2000). Similar environments are inferred for the intervals with *E. exigua* in sediment cores (Rasmussen et al., 2007; Polyak et al., 2013). It is likely that some of the polar species are also capable of feeding on phytodetritus (Cornelius and Gooday, 2004) and may thus occupy transitional habitats between strictly perennial sea ice and MIZ environments. In particular,

Epistominella arctica is a common species in the Arctic Ocean, but also has affinity to areas with high seasonal production (Pawlowski, 1991; Wollenburg and Mackensen, 1998; Cornelius and Gooday, 2004). An affinity of this species to both low-productivity environments and phytoplankton blooms attests to the transitional ecological strategy of this species (Wollenburg and Kuhnt, 2000). Some species occurring in minor proportions, such as *Valvulineria arctica*, have also been reported as characteristic for the Arctic Ocean, where they co-occur with the polar species in both modern and Quaternary sediments (Green, 1960; Lagoe, 1977; Poore et al., 1994; Polyak et al., 2013), and thus may be related to perennial or transitional sea-ice environments.

For evaluating species diversity we utilize a commonly used Shannon-Weiner $H(S)$ index that incorporates a measure of evenness and number of species and is defined as $H = -\sum p_i \ln(p_i)$, where p_i is the proportion of the i^{th} species (Shannon, 1948; Buzas and Gibson, 1969). Previous application of diversity indices to the foraminiferal record in P23 gave mixed results because of considerably different assemblages in the early Quaternary and younger stratigraphy (Polyak et al., 2013). In this study we deal with a more consistent foraminiferal composition that provides better material for using the diversity information.

A Q-mode cluster analysis (using Euclidean distances and Ward's linkage parameters, following Mello and Buzas, 1968) was used to facilitate the identification of foraminiferal assemblage zones (subzones). The analysis was performed on census data from the $>63 \mu\text{m}$ size fraction for each core using species which represent $\geq 2\%$ of any sample. Relative abundances were transformed using the equation:

$$2\arcsin\sqrt{p}$$

where p = abundance, and input into Systat 13 for analysis. Cluster analyses performed on each core separately produced more meaningful results than all core samples analyzed together, as suggested by a comparison with sedimentological characteristics, foraminiferal abundances, and distribution of ecologically-significant taxa (described in Section 4). This pattern probably results from a geographic variance in taxa composition and/or different stratigraphic ranges of calcareous microfauna in individual cores. Census data with the resulting dendrograms and downcore cluster distributions, as well as indices characterizing individual taxa contribution (occurrence, constancy, and assemblage zone fidelity) can be found in the supplementary information (Supplements 2-6). We note that, while providing some guidance, a formal approach such as cluster analysis is hardly sufficient for characterizing the paleoecological meaning of changes in foraminiferal composition, especially in stratigraphically complex (e.g., condensed and patchy) Arctic Ocean records. For example, the clusters derived cannot capture intermittent occurrence of taxa as typical for environments controlled by glacial-interglacial cyclicity. For a more comprehensive interpretation, we aimed to use a broader context, including foraminiferal abundances, distribution of species deemed significant for paleo-sea-ice conditions, and attendant sedimentary stratigraphy.

Foraminiferal abundances, although controlled by sedimentary and diagenetic factors in addition to productivity, may add complementary paleoenvironmental information to assemblage data. For a comprehensive coverage, we consider the planktic and benthic abundances along with their ratio in the $>150\ \mu\text{m}$ size in all samples analyzed, and benthic abundances in a wider size range of $>63\ \mu\text{m}$ and $>125\ \mu\text{m}$ in samples with detailed counts.

4. Results

4.1. Foraminiferal assemblages

We aimed to assign Assemblage Zones (AZs) to core intervals characterized by one prevailing biofacies identified by means of cluster analysis. While the defined AZs may not be identical in different cores, their succession has an overall similar pattern at all three sites, with several step changes in the composition of foraminiferal abundances and assemblages (Figs. 3–4). The analyzed record in P23 encompasses a transition between AZ 2 and 1 identified in Polyak et al. (2013) based on a pronounced turnover from predominantly phytodetrital (*E. exigua*, *Eponides weddellensis*) to polar (*S. horvathi*, *B. arctica*) foraminiferal species, respectively. The turnover corresponds to a marked lithostratigraphic transition estimated to approximate the early/middle Pleistocene boundary, ca. 0.7–0.8 Ma, with sedimentary cyclicity especially explicit above this boundary. A similar change in foraminiferal composition appears also in the lower part of PC04 (e.g., high contents of *E. exigua*; Fig. 4). In this paper we cover only AZ1 and the top of AZ2 not exceeding the correlative range of calcareous microfauna recovered in PC04 (Figs. 3–4), which is sufficient to represent the transition between the AZs. In addition to phytodetrital species, AZ2 in P23 is characterized by the presence of extinct species of foraminifers and ostracodes (Polyak et al., 2013; Cronin et al., 2014). Not surprisingly, extinct foraminiferal species, such as *Cibicidoides* spp., are readily identified by formal criteria as characteristic for AZ2 in P23 (Supplement 6). At least one of these species, *Cibicidoides circumcarinatus* (McNeil) or a closely related non-keeled form, is also identified in the lower ~50 cm of PC04 (*Cibicidoides* spp. of Hanslik (2011)), corroborating correlation of this interval to the upper part of AZ2. We note that its boundary with AZ1 in this core is not resolved by cluster analysis (Fig. 4), possibly because only the very top of AZ2 has been recovered

Changes in foraminiferal composition in AZ1, which is the main focus of this study, were difficult to identify clearly in P23 alone due to its compressed stratigraphy, but the addition of the two other cores provided more detail. These changes show a similar pattern in the three cores, with two apparent steps corroborated by cluster analysis results. We designate the units separated by these boundaries as Assemblage Zones (Subzones) AZ1a, 1b, and 1c. The AZ1c/1b boundary in all three cores falls near the bottom of lithostratigraphic unit estimated as MIS 7, ca. 0.25 Ma (Fig. 4). The difference between these subzones is expressed notably in the composition of interglacial assemblages, where *E. arctica* replaces *E. exigua* as one of the major species (Figs 2–4). This pattern is corroborated by high constancy and/or fidelity values for *E. exigua*, typically along with *Elphidium* spp. in AZ1c. Corresponding values for *E. arctica* in AZ1b are mostly not as high, probably in relation to its intermittent occurrence peaks. Another characteristic species of AZ1b-a is *V. arctica*, whose content generally increases up-core. The AZ1c/1b transition co-occurs with the appearance of high abundance peaks of both planktic and benthic faunas (Figs. 3–4). Species diversity is generally higher in AZ1b-a, with H(S) values around 2 as compared to mostly around 1.5 in AZ1c. In addition to foraminiferal changes, AZ1b-a are generally characterized by the occurrence of sea-ice dependent ostracode *Acetabulostoma arcticum* (Cronin et al., 2013, 2014).

AZ1b/1a boundary is clearly identified by cluster analysis in the upper part of JPC6 and PC04 corresponding to the upper part of MIS 5, ca. 0.1 Ma (Fig. 4). Similar changes in foraminiferal composition are also seen in P23, where formal cluster identification of AZ1a is complicated by a small number of samples due to a compressed stratigraphy of this part of the record. Foraminiferal composition of AZ1a has characteristically elevated numbers of *Bulimina*

aculeata (in the lower part of the AZ) and *Oridorsalis tener*, especially high in >125 µm size fraction. These species only sporadically occur in the older strata.

We note that the identified AZs are used to discriminate major ecological groups (biofacies) rather than simply for correlation purposes, and are therefore broader than biostratigraphic subdivisions used by Hanslik (2011). A more detailed downcore distribution of major species, including their occurrence in glacial/nonglacial layers, is exemplified by core JPC6 investigated with the best stratigraphic resolution except for compressed MIS 1–4 (Fig. 2). This distribution indicates high contents of *B. arctica*, *E. arctica*, and *E. exigua* mostly in non-glacial or immediately adjacent intervals, with only *S. horvathi* consistently having maximal percentages in glacial layers. These patterns cannot be seen as clearly in the two other cores due to a more compressed record in P23 and insufficient sampling resolution in PC04.

4.2. Foraminiferal abundances

The range of calcareous microfossils in core JPC6 extends to ~240 cm estimated to underlie MIS 13 (Figs. 2–3). The calcareous record in PC04 is longer stratigraphically, extending into the lower Quaternary by correlation with a more complete record from P23 (Figs. 3–4). Below this level, both foraminifers and ostracodes are abundant in P23, but are absent in correlative strata from other cores investigated (Polyak et al., 2013; Cronin et al., 2014).

Downcore changes in foraminiferal abundance patterns are generally consistent in the records under study despite differences in absolute numbers between the cores, with overall lower numbers in core P23 (Fig. 3). In the bottom part of the stratigraphy discussed, below the estimated lower/middle Quaternary boundary (MIS 19 and older), numbers of both benthic and planktic foraminifers are mostly low in both P23 and PC04, with relatively elevated numbers of

>63 μm benthics in the latter. Especially low values characterize the overlying interval containing a distinct IRD layer corresponding to estimated MIS 16 (Fig. 2). Further up-core, starting from an estimated MIS 13, foraminiferal abundances become higher overall (Fig. 3). This trend is especially conspicuous in all three cores for larger-size benthic specimens (>150 μm), with >63 μm numbers also increasing markedly in P23. A peak of planktic foraminifers at estimated MIS 11 has a peculiar composition with predominating subpolar species *Turborotalita egelida* and therefore makes a distinct stratigraphic marker (Fig. 3). The highest abundances of both planktic and benthic foraminifers along with consistently high planktic to benthic ratios are reached in non-glacial (brown) lithostratigraphic units in the upper part of the record, above estimated ca. 0.25 ka (MIS 7) (Figs. 2, 4). This pattern does not apply to larger-sized benthic foraminifers (>125 μm), which have a more even downcore distribution (JPC6) or maximal abundances between MIS 13 and 7 (PC04 and P23). Their absolute numbers, however, are too low to have a considerable effect on the total >63 μm numbers.

4.3. Distribution of key species

For a more thorough understanding of key foraminiferal species expected to indicate sea-ice conditions in the stratigraphic range under study (*S. horvathi*, *B. arctica*, *E. arctica*, and *E. exigua*), their contents were compared to total benthic foraminiferal abundances and diversity (Fig. 5). Despite a considerable scatter, probably resulting from a combination of samples from different parts of the western Arctic region and different stratigraphic levels, major differences in the distribution patterns of these species are clearly discernible. Relationship of the diversity index to total abundances is not straightforward as highest abundances correspond to intermediate diversity values. Relationship of individual species to the diversity index changes

from mostly negative in *S. horvathi* (highest percentages at low H(S) of 1–1.5) to more positive in *E. arctica* and *E. exigua* (highest percentages at H(S) of 1.5–2). Relationship to total abundances looks more complex. A relatively positive trend is revealed by *E. arctica*, while *S. horvathi* and *E. exigua*, representing more extreme perennial-ice and ice-marginal environments, both have highest percentages at very low abundances. However, scatterplots for these two species also show a noticeable difference in the position of maximal abundances, which correspond to around 10-20% of *S. horvathi*, but extremely low numbers to complete absence of *E. exigua*. This pattern suggests different controls on the distribution of the two species.

5. Discussion

5.1. Foraminifera as sea-ice indicators

The foraminiferal distribution in cores under study can be interpreted in terms of sea-ice conditions inferred from both modern and Quaternary data (e.g., Wollenburg and Mackensen, 1998; Wollenburg and Kuhnt, 2000; Polyak et al., 2013). The overall pattern of foraminiferal assemblages (taphocoenoses) in relation to sea-ice conditions in the Arctic Ocean is discussed below and summarized in Fig. 6.

Highest contents of *S. horvathi*, a species that consistently co-occurs with sea ice or other oligotrophic environments (e.g., Wollenburg and Kuhnt, 2000; Scott and Leger, 1990), correspond in our data to lower total abundances and diversity (Fig. 5), which are expected to be low under perennial sea ice and, thus, low organic production. This notion is corroborated by a co-occurrence of *S. horvathi* peaks with glacial lithofacies in the Pleistocene record as exemplified by JPC6 (Fig. 2). We, therefore, infer that among the leading Arctic species, *S.*

horvathi is likely the most adapted to life under perennial sea ice, although it can also live under transient seasonal sea-ice environments (Husum et al., 2015). In comparison, the downcore pattern of another apparently polar species, *B. arctica*, shows more common occurrence in non-glacial intervals, which suggests that it may prefer more moderate environments in terms of sea-ice regime. The modern distribution of this species is not known as it is usually rare in sediments younger than estimated MIS 5.

Even more moderate (intermediate) sea-ice conditions can be inferred for *E. arctica* that shows peaks in the interglacials, especially in the upper Pleistocene, co-occurring with high diversity and abundance values (Figs. 4–5). This pattern is consistent with a broader geographic distribution of *E. arctica* (or a closely related form) in surface and downcore sediments (Pawlowski, 1991; Cornelius and Gooday, 2004). An association with phytodetrital food and mild sea-ice conditions has been suggested for *E. arctica* based on its distribution in surficial Arctic sediments (Wollenburg and Kuhnt, 2000). This type of condition may be represented by multiple leads and/or ice thinning in a warming climate, which facilitates sub-ice phytoplankton blooms (Arrigo et al., 2014). The primarily sea-ice diatom composition of such blooms differs from a more diverse phytoplankton assemblage at the ice margin (e.g., Gosselin et al., 1997; Arrigo et al., 2014). This distinction may contribute to a change in benthic assemblages from the ice margin to ice-covered waters, along with decreasing food availability.

The known phytodetrital species *E. exigua* has highest percentages in the older interglacials (below MIS 7) with an affinity to higher diversity but low abundances (Fig. 5). This pattern can be understood, if we consider that foraminiferal abundances can be controlled not only by productivity, but also by sediment dilution and calcite dissolution. Dilution is unlikely to be an issue in low-deposition Arctic Ocean settings, except for possibly deglacial events (e.g.,

Polyak et al., 2009), but dissolution can be very strong, especially near the sea-ice margin (Steinsund and Hald, 1994; Scott et al., 2008; Husum and Hald, 2012). Reduction of sea-ice cover and associated migration of MIZ during interglacials likely lead to enhanced dissolution of calcareous fossils in Arctic Ocean sediments (Matthiessen et al., 2001; Wollenburg et al., 2001). This factor can explain a negative relationship between *E. exigua* and total abundances.

We note that differences in water depth, not encountered in the data under study, may provide an additional control on benthic biofacies (e.g., Polyak, 1990; Wollenburg and Mackensen, 1998; Osterman et al., 1999). For example, the numbers of *E. exigua* decrease with increasing water depth at the same stratigraphic intervals (Poore et al., 1994). In contrast, *S. horvathi* becomes more abundant at greater depths both in downcore and surface sediments, along with overall lower diversities (Polyak, 1990; Poore et al., 1994; Wollenburg and Mackensen, 1998). These patterns might be related to lesser amounts of labile organic matter reaching greater depths and/or higher sedimentary fluxes in deep basins, which further diminish the food content.

5.2. Stratigraphic and paleoenvironmental changes

As demonstrated in earlier studies (Poore et al., 1994; Polyak et al., 2004; Adler et al., 2009; Cronin et al., 2013, 2014), total foraminiferal abundances, both benthic and planktic, are clearly higher in the interglacials or major interstadials, with especially high numbers starting from MIS 7, presumably due to better preservation of calcareous material (see more details below). Overall, higher interglacial abundances make sense as biological production increases with diminishing ice cover (e.g., Arrigo et al., 2014; Harada, 2016). However, this pattern may be complicated by dissolution of calcareous tests, which could be strongest during the warmest

conditions accompanied by MIZ retreat into the Arctic (e.g., Matthiessen et al., 2001; Wollenburg et al., 2001). The glacial-interglacial differences are also expressed in benthic assemblage composition, as schematically illustrated in Fig. 6. Glacial intervals with low foraminiferal abundances are overwhelmed by oligotrophic polar species, typically predominated by *S. horvathi*, as exemplified by JPC6 (Fig. 2). The shift to interglacial/major interstadial intervals marked by increased abundances is characterized by higher content of transitional species, notably *E. arctica*, presumably indicating moderate sea-ice coverage with intermittent phytodetritus pulses. Low-abundance taphocoenoses with peak percentages of *E. exigua* are interpreted as MIZ-proximal environments during interglacial culminations.

In addition to glacial-interglacial variability, an underlying long-term change in foraminiferal assemblages has been identified since early studies in the central Arctic Ocean (O'Neill, 1981; Scott et al., 1989; Ishman et al., 1996), but its paleoenvironmental significance was poorly understood. More insight can be now provided with mounting data on smaller size fractions and a better understanding of environmental controls on foraminiferal assemblages. Major downcore changes in benthic assemblages and abundance patterns have the same succession in the cores under study (Figs. 3–4). The foraminiferal turnover at the AZ2/1 boundary, described from P23 and attributed to a shift from mostly seasonal to mostly perennial sea ice (Polyak et al., 2013), is also seen in PC04 located downstream from the Beaufort Gyre towards the exit from the Arctic Ocean via the straits of the Canadian Archipelago or the Fram Strait, depending on the circulation (Fig. 1; Dyke et al., 1997; Proshutinsky et al., 2002). This geographic distribution indicates that the expansion of sea ice at the early to middle Pleistocene transition affected a large part, if not the entirety of the western Arctic, although the details of this change in sea-ice regime are not yet understood. The reason for highly localized preservation

of calcareous microfauna at this stratigraphic level remains unclear. The three cores under study were obtained from similar water depths overlain by waters with similar properties (transition from the Atlantic Layer to Upper Polar Deep Water), nevertheless, only in P23 and PC04 does the calcareous microfauna extend to the AZ2/1 boundary. If this enhanced preservation was affected by a stronger than present admixture of Pacific water via the Bering Strait, as suggested by Polyak et al. (2013), then this water had to shortcut the western Arctic bypassing the Mendeleev Ridge.

Calcareous microfauna in JPC6 appear starting from estimated MIS 13, consistent with its resumption in the two other cores after a prominent sandy interval, where biota may have been suppressed by high glacial inputs (Figs. 2–4; Polyak et al., 2013). In general, except for core P23 and to some extent PC04, calcareous fossils in the central Arctic Ocean have not been reported in any considerable amounts from sediments older than MIS 11–13 (Cronin et al., 2013, 2014) or a correlative level in the age models used by earlier authors (Herman, 1970; Scott et al., 1989; Clark et al., 1990). This transition is not accompanied by changes in microfaunal assemblages, as exemplified by cores P23 and PC04 (Fig. 4), or any considerable change in sedimentation patterns. The likely cause for this increase in abundance is improved calcium carbonate preservation that could be related to either a change in bottom water circulation or reduced import of organic matter to the sea floor (e.g., Steinsund and Hald, 1994; Rasmussen and Thomsen, 2014). It is notable that older sediments in a number of cores from the central Arctic Ocean lacking calcareous microfossils have been shown to contain agglutinated foraminifers (Scott et al., 1989; Evans, 1998; Cronin et al., 2008), another likely indication of calcareous test dissolution (Alve and Murray, 1995; Rasmussen and Thomsen, 2014).

Despite a consistent occurrence of calcareous fossils at least during interglacials starting from MIS 13, their abundances are still relatively low and foraminifers are commonly etched by dissolution until MIS 7, except for a typically distinct peak of both benthic and planktic foraminifers at estimated MIS 11 (Fig. 3). Respective interglacial foraminiferal assemblages below MIS 7 have relatively high percentages of *E. exigua*, presumably indicative of intermittent seasonal-ice conditions and MIZ proximity. A characteristic presence of shallow water *Elphidium* spp. in AZ1c indirectly corroborates intermittent sea-ice cover as an indicator of sea-ice transport from continental margins that requires seasonally open water. Surprisingly, *E. exigua* has low content in estimated MIS 11, despite its unusual, potentially subpolar planktonic fauna predominated by *T. egelida* (Cronin et al., 2013).

The AZ1c/1b transition, the most pronounced change in microfauna after the AZ2/1 boundary, is identified at the stratigraphic level estimated as the lower part of MIS 7 (Figs. 3–4) (Hanslik, 2011; Cronin et al., 2013; Polyak et al., 2013), although the exact MIS boundaries are yet to be constrained. The replacement of *E. exigua* by *E. arctica* as a leading interglacial species, accompanied by *V. arctica* that has a similar stratigraphic distribution, indicates that ice-free summers likely occurred more rarely after this transition, even at peak interglacials. This conclusion is corroborated by the concurrent, consistent presence of *A. arcticum*, an ostracode related to perennial sea ice (Cronin et al., 2010) (Fig. 4). The only younger interval with a considerable increase in *E. exigua* content is estimated to occur near the bottom of MIS 5 in the current age model, and probably marks the last interglacial culmination (Jakobsson et al., 2001; Polyak et al., 2004; Hanslik, 2011). We note, however, that due to the larger size of *E. exigua* relative to polar species (*S. horvathi*, *E. arctica*, etc.) its percentages may be lower in >63 µm data (e.g., Figs. 2, 4).

The AZ1c/1b change is also characterized by increased foraminiferal numbers, expressed notably in higher interglacial abundance peaks of well-preserved planktic and small-size benthic foraminifers along with higher P/B ratios above this transition. Planktic tests are known to be more susceptible to dissolution than benthic (e.g., Corliss and Honjo, 1981; Murray, 1989). Small benthic tests may also be disadvantaged in terms of preservational potential due to their thinner walls and shallower habitats in sediment, and thus, more exposure to oxidative environments (e.g., Sexton and Wilson, 2009). Higher P/B ratios can indicate better preservation as well, but could also be caused by lower food fluxes to the seafloor. A somewhat counterintuitive overall increase in species diversity in AZ1b-a relative to AZ1c may be partially related to elevated interglacial/major interstadial foraminiferal numbers; however, the highest abundances correspond to only moderately high H(S) values of 1.5–2 (Fig. 5), possibly biased by dissolution during the times of maximal sea-ice retreat.

The paleoenvironmental signal of the AZ1b/1a transition appears to be complex. While peaks of *E. arctica* persist above this boundary, along with relatively high occurrences of *V. arctica*, the content of *S. horvathi* and *B. arctica* decreases to a nearly complete disappearance of the latter. *Oridorsalis tener*, a species characteristic of AZ1a, has a cosmopolitan deep-sea distribution that includes the Arctic Ocean (e.g., Wollenburg and Mackensen, 1998; Osterman et al., 1999), whereas *B. aculeata* that peaks in the lower part of this AZ is not known from the modern Arctic. While the full meaning of these changes is yet to be understood, we suggest that they may be related to adaptations of benthic fauna to life under perennial ice and/or additional sources of nutrition delivered by ice, such as partially labile terrestrial organic matter (e.g., Stein and Macdonald, 2004). Regardless of their paleoecological signature, the conspicuous changes at the AZ1b/1a boundary, expressed both in >63µm and >125µm size fractions, provide a useful

stratigraphic marker throughout the Arctic Ocean (e.g., Ishman et al., 1996; Polyak et al., 2004; Cronin et al., 2014). The age of the *B. aculeata* maximum, which is water-depth dependent and can be expressed as a double peak in some cores, has been estimated as MIS 5a (Adler et al., 2009; Cronin et al., 2013, 2014), consistent with a correlative *B. aculeata* peak in Baffin Bay dated to MIS 5a (Fillon and Duplessy, 1980).

The overall trend in the abundance of calcareous microfauna in Arctic Ocean records, other than glacial-interglacial variability, suggests an enhanced preservation at younger stratigraphic levels, with two apparent step changes at around MIS 13 and 7, discussed above (e.g., Fig. 3). This stepwise pattern is indicative more of syndepositional dissolution in older strata rather than postdepositional diagenetic alteration that would likely result in a more uniform downcore pattern. This inference makes sense in the context of a slow burial of particles deposited on the Arctic Ocean floor due to overall low sedimentation rates, which increases the degree of calcium carbonate dissolution (e.g., Loubere and Gary, 1990). We infer that the progressive decrease in dissolution from lower to upper Quaternary sediments in the Arctic Ocean is related to the expansion of sea ice, which diminished organic fluxes to the seafloor and enhanced water stratification, both factors favorable for carbonate preservation (e.g., Steinsund and Hald, 1994; Rasmussen and Thomsen, 2014). In addition, Clark and Hanson (1983) suggested that inputs of detrital carbonates may have also affected biogenic carbonaceous material. This aspect deserves a more thorough investigation as the amounts of detrital carbonates, mostly dolomites, indeed increase markedly upcore from the bottom of the "glacial" Pleistocene (e.g., Fig. 2; Polyak et al., 2009, 2013; Stein et al., 2010), and at some intervals closely follow variations in foraminiferal numbers (Hanslik et al., 2013).

5.3 Climatic linkages

The expansion of sea ice inferred from foraminiferal turnover at the AZ2/1 boundary co-occurred with a growth of ice sheets in the Amerasian Arctic, as revealed notably in the pronounced rise in IRD (Polyak et al., 2013). The co-occurrence of changes in ice-sheet volume and sea ice suggests causality, but the relationship and feedbacks involved are not well understood. The timing of these changes at the end of the Mid-Pleistocene Transition (MPT) suggests that they were part of a broad, interregional climate reorganization. Unlike this paleoclimatic setting, the timing of the AZ1c/1b transition estimated at ~0.25 Ma is not known for concerted, large-scale paleoclimatic changes. However, this stratigraphic interval in western Arctic cores features a marked increase in the peaks of terrigenous carbonates indicative of iceberg pulses from the Laurentide ice sheet (Polyak et al., 2009; Stein et al., 2010), thus suggesting intensification of glaciations in North America. Inputs from Eurasian glaciations also increased dramatically with the MIS 6 glaciation to follow (e.g., Spielhagen et al., 2004; O'Regan et al., 2008). Thus, similar to the change at the end of the MPT, the next pronounced expansion of perennial sea ice inferred from the AZ1c/1b transition may have been related to ice-sheet growth at the Arctic Ocean periphery. The causal links involved in this relationship have yet to be investigated.

6. Summary

Foraminiferal data from three sediment cores from the Northwind, Mendeleev, and Lomonosov ridges (800–950 m water depth) show mostly consistent stratigraphic changes in abundance and benthic assemblage composition across the western Arctic, where calcareous

preservation allows for longer microfossil records than in the eastern Arctic Ocean. Changes include glacial-interglacial variability and long-term evolution of foraminiferal assemblages. Low-abundance assemblages from middle to late Pleistocene glacial intervals are primarily represented by oligotrophic polar species, typically predominated by *S. horvathi*. Interglacial/major interstadial intervals are characterized by increased abundances and higher content of species, presumably indicating moderate sea-ice coverage with intermittent phytodetritus pulses, notably *E. arctica*. Peak percentages of a phytodetritus species *E. exigua* are interpreted as proximity to the Marginal Ice Zone during interglacial culminations; these taphocoenoses typically have low abundances due to dissolution.

Major long-term changes took place at the end of the Mid-Pleistocene Transition (estimated ca. 0.7–0.8 Ma) and later near the bottom of MIS 7 (ca. 0.25 Ma). The MPT change, described earlier from core P23 (Polyak et al., 2013), involves a turnover from assemblage dominated by phytodetritus-feeding foraminifers (i.e., *E. exigua*), with an extinct component, to a polar-type fauna dominated by *S. horvathi* and *B. arctica* (Assemblage Zones 2/1).

Taphocoenoses representing this turnover have only been found at geographically-limited sites at the Northwind Ridge and north of Greenland, whereas elsewhere in the Arctic Ocean calcareous microfossils (foraminifers and ostracodes) appear to have minimal to no preservation in sediments older than MIS 11–13 (~0.5 Ma). The more ubiquitous later Pleistocene faunal transition (AZ 1b/1a) was less profound, yet distinct, and included notably a replacement of the phytodetritus-feeder *E. exigua* by a moderate polar species *E. arctica* in the interglacial intervals, along with the spread of sea-ice related ostracode *A. arcticum*. This boundary also marks the onset of high-abundance interglacial peaks of planktic and small-sized benthic foraminifers, presumably resulting from enhanced preservation.

These changes, interpreted in terms of their relationship to sea-ice conditions based on the foraminiferal distribution in modern and downcore sediments, indicate an overall expansion of year-round ice cover in the Arctic during the Pleistocene. This development was beneficial for polar species adapted to meager and unstable food supply in an ice-covered ocean, and may have also favored calcium carbonate preservation in sediments due to enhanced water stratification and reduced fluxes of reactive organic matter. The MPT shift from mostly seasonal to perennial sea-ice was coeval, and possibly related to a growth of North American ice sheets and the beginning of glacially-controlled sedimentation in the western Arctic Ocean. The ca. 0.25 Ma transition also co-occurs with signs of ice-sheet expansion in both North America and Eurasia, but the broader linkages of this change beyond the Arctic region are not yet understood.

The ca. 0.1 Ma change in foraminiferal assemblages also require further investigation, such as a proliferation of the cosmopolitan species *O. tener* and rare (for the Arctic) *B. aculeata*, along with a somewhat elevated diversity. These features may be related to changes in the food delivery/type in the late Pleistocene and/or better adaptation of benthic fauna to perennial sea-ice cover.

We note that this study addressed the long-term changes in Arctic foraminiferal assemblages as proxies of middle to late Pleistocene sea-ice history on multi-millennial time scales. More detailed studies will require zooming in on specific intervals, such as the identified major transitions, preferably using records that provide higher age resolution. These studies will benefit from using foraminiferal proxies discussed in this paper, potentially with addition of more species for detailing paleoenvironmental changes.

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Table 1. Sediment core information.

Core ID	Latitude	Longitude	Water	Core	References
			depth (m)	length (cm)	
HLY0503-06JPC	78.29	-176.99	800	1210	Polyak et al., 2009; Cronin et al., 2013, 2014
LOMROG07-PC04	86.7	-53.77	811	523	Hanslik, 2011; Cronin et al., 2014
P1-93AR-P23	76.96	-155.07	951	572	Mullen & McNeil, 1995; Polyak et al., 2009, 2013; Cronin et al., 2014

Figure captions

Figure 1. Index map with location of sediment cores under study. Arrows show major surface-water circulation features (from Dyke et al., 1997; TPD - Transpolar Drift, BG - Beaufort Gyre). Brown line – climatological late-20th century summer ice extent (15% concentration), pink line – 2012 summer ice extent (historical minimum). CAA – Canadian Arctic Archipelago; BS and FS – Bering and Fram Straits; NR, MR, and LR – Northwind, Mendeleev, and Lomonosov ridges, respectively.

Figure 2. Combined distribution of lithological (Cronin et al., 2013) and foraminiferal proxies in core HLY0503-JPC6: content of coarse sediment >63 μm , bulk Ca and Mn XRF counts, benthic foraminiferal abundances (>63 and >150 μm) and key species distribution (>63 μm). Core photo is shown on the left; brown units are highlighted by yellow. Estimated Marine Isotope Stages (from Cronin et al., 2013) are shown on the right. PW – major detrital carbonate peaks (pink-white layers).

Figure 3. Foraminiferal abundances in cores under study. BCF/g and PF/g - benthic calcareous and planktic foraminifers per gram sediment, respectively, with size fractions (μm) indicated. P/B - planktic to benthic ratio. Black and gray circles show samples with detailed >63 μm and total >150 μm foraminiferal counts, respectively. Both detailed and total counts in P23 were performed to >500 cm (Polyak et al., 2013); examination of JPC6 for foraminifers >150 μm was performed to 400 cm. Assemblage Zones (AZ) are explained in the Results section. Correlation lines show AZ boundaries (solid lines) and the top of very low abundance interval in AZ1b

(punctured line). Asterisk in AZ1b - planktic peak with *T. egelida*. Approximate estimated Marine Isotope Stages (MIS; from Hanslik, 2011; Cronin et al., 2013; Polyak et al., 2013) are indicated on the right.

Figure 4. Distribution of foraminiferal assemblage zones (AZ) and key benthic species (>63 μm unless otherwise indicated) in cores under study. Also shown are total abundances (BCF/g) and diversity (H(S)). Dark and light gray bars on the right show distribution of extinct species (see Polyak et al., 2013 for more detail) and ostracode *A. arcticum* (from Cronin et al., 2014). Approximate estimated Marine Isotope Stages (MIS; from Hanslik, 2011; Cronin et al., 2013; Polyak et al., 2013) are indicated on the far right. AZ boundaries except for those indicated by (-) are supported by cluster analysis (see Supplement for details).

Figure 5. Scatterplots characterizing benthic foraminiferal assemblages (>63 μm): total abundance vs. diversity, and key species distribution vs. both abundance and diversity. Samples are color-coded by sediment cores.

Figure 6. Conceptual scheme of benthic foraminiferal assemblages (taphocoenoses) as proxies of Arctic sea ice. Assemblages are categorized in relation to sea-ice conditions by characteristic leading species and interpreted abundance patterns. Single or double plus signs indicate relatively low and high abundances, respectively, controlled by relative intensity of test preservation and production as shown below.

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Figure 6