

Borealisation of an Arctic marine ecosystem during the Last Interglacial

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Article

Keywords:

Posted Date: September 23rd, 2026

DOI: <https://doi.org/10.21203/rs.3.rs-11006391/v1>

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Additional Declarations: There is **NO** Competing Interest.

Abstract

The Arctic is warming at a rate four times the global average, threatening and overturning marine ecosystems. Here, we present a shotgun metagenomic sedimentary ancient DNA record revealing major reorganisation of an Arctic ecosystem west of Svalbard in response to the transition into the Last Interglacial (LIG), a warm period between 128 and 116 thousand years ago and an analogue for future warming. We document invasion of temperate phytoplankton communities (i.e. 'borealisation') into the Arctic, evidenced by increased cosmopolitan *Gephyrocapsa* coccolithophores, which contrasted diatom-based glacial systems. This shift was preceded by the proliferation of a highly diverse phytoplankton community enriched in smaller eukaryotes and potentially harmful algal bloom taxa. Given the important role of phytoplankton composition in the drawdown of atmospheric carbon dioxide, we consider the impact of the observed changes on the biological carbon pump. Marine megafauna, including whales and fishes lacking strict Arctic distributions, also increased at the start of the interglacial, showing borealisation extended to higher trophic levels. Our LIG data indicate substantial increase of inflow of Atlantic water into the Arctic, i.e. Atlantification, likely transporting heat and salt along with Atlantic organisms, and potentially reducing the Arctic's capacity to sequester atmospheric CO₂ under warmer climate conditions.

Main text

The Arctic has warmed nearly four times faster than the rest of the globe since 1979¹. The West Spitsbergen Current (WSC), which is the main source of heat to the higher polar latitudes, funnels warm North Atlantic water along the western margin of Svalbard and into the Arctic Ocean via the Fram Strait² (Fig. 1). Between 1997 and 2024, the Atlantic water core in the Fram Strait warmed by more than half a degree Celsius³, the velocity of oceanographic currents doubled⁴, and sea ice coverage decreased⁵. Collectively, these changes have been termed 'Atlantification' of the Arctic⁶. This Atlantification facilitates northward expansion of more temperate species into Arctic ecosystems, a phenomenon known as 'borealisation'⁷. Arctic marine ecosystems influence a range of complex biogeochemical cycles including the biological carbon pump, which refers to the production and export of particulate organic carbon from organisms in the surface to the deep ocean⁸. The biological carbon pump in the Atlantic sector of the Arctic Ocean contributes to some of the strongest carbon dioxide drawdown globally⁹. Despite the importance of understanding how Arctic marine ecosystems will respond to continued global warming, future predictions are still highly uncertain^{10,11}, in part due to a lack of long-term ecosystem records documenting biodiversity responses to similar warming in the past.

Palaeoenvironmental archives such as marine sediments can extend past records beyond the instrumental and satellite era¹². Marine Isotope Stage (MIS) 5e, also known as the Last Interglacial (LIG), was a warm period between 128 and 116 thousand years ago (ka) where global temperatures were up to 2°C above pre-industrial baselines¹³, making it a critical analogue for near-future climate scenarios¹⁴. Circum-polar air temperatures were approximately 4–5°C above pre-industrial levels¹⁵ and accompanied

by higher global sea levels, smaller ice volumes¹⁶ and a possibly seasonally ice-free central Arctic Ocean¹⁷, which is predicted to occur before 2050¹⁸. Further, the LIG is a crucial interval for data-model intercomparisons to constrain impacts of cryosphere changes on local and global climate¹⁹.

Palaeoceanographic evidence from the eastern Fram Strait indicates open ocean and warmer conditions during the LIG e.g.²⁰. However, little is known about marine biodiversity during this time beyond a select few groups (e.g. dinocysts²⁰, planktic foraminifera²¹, and calcareous nannofossils²²) that preserve in the relatively sparse fossil record. Sedimentary ancient DNA (sedaDNA) is a powerful technique to detect Arctic marine organisms that cannot not be accessed by standard micropaleontological approaches^{23–27}. For example, a metabarcoding study targeting a diatom specific *rbcL* gene recovered diatom DNA from eastern Fram Strait sediments dating back 30,000 years²⁸. This is particularly valuable in the eastern Fram Strait where diatoms, a key functional group of marine primary producers, rarely preserve in sediments older than the Holocene².

International Ocean Discovery Program (IODP) Expedition 403 targeted highly expanded sediment packages in the eastern Fram Strait, deposited over the past ~ 5.5 million years² and recording glacial-interglacial variability over the last million years²². At Site U1621, the LIG has been identified between 26.15–27.86 m based on geophysical parameters of the sediment, oxygen isotopes and microfossil assemblages (Gebhardt, De Schepper et al., submitted to Nature Communications). The placement of LIG in U1621 corresponds to a calcareous nannofossil abundance peak²² as well as the presence of Atlantic water inflow indicator dinoflagellate cysts²⁹. Here we present a sedimentary ancient DNA shotgun metagenomic record from Site U1621, in the path of the WSC along the western margin of Svalbard (Fig. 1). Our study is the first to track ecosystem-level change into and out of the LIG in the Arctic.

Results and discussion

Diatom- to haptophyte community switch at the glacial-interglacial transition

Our 40 sedaDNA samples cover an ~ 83 kyr period from 153 to 70 ka, spanning the latter half of the MIS 6 glacial and the entire MIS 5 interglacial with a resolution of ~ 2 kyr (Supplementary data 1). A total of 476,557 reads were retrieved from shotgun sequencing and were assigned to 3,078 eukaryotic taxa after subtracting the genera detected in negative controls (Supplementary data 2). The eukaryotic signal is dominated by marine primary producers, major sequesters of atmospheric CO₂, with most reads assigned to the haptophytes (295,128 reads; ~60%) or the diatoms (Bacillariophyta) (112,118 reads; ~23%) (Fig. 2). The diatoms show large genus level diversity (n = 54), with *Thalassiosira* (26,594 reads; 23.7%) the most abundant genus (Fig. 3). Conversely, the Haptophyta reads are overwhelmingly

dominated by a single genus of calcifying phytoplankton, the coccolithophore *Gephyrocapsa* (281,153 reads, ~ 95%).

Our data reveal a shift in dominant primary producer communities from diatoms in the MIS 6 glacial to haptophytes during the later phase of the LIG from 121–115 ka (Fig. 2, Fig. 5f). This transition is the most significant community turnover in our record and is supported by a stratigraphically constrained hierarchical cluster analysis (Fig. 2a) and a strong negative linear relationship between the two phyla ($\beta = -0.79 \pm 0.03$ standard error, $p = 2.45e-24$, $R^2 = 0.94$; Figure S5). Two further pulses of haptophyte dominance are visible later in the record from 104–100 ka and 84–78 ka and correspond respectively to the warmer substages MIS 5c and 5a. Periods of haptophyte dominance are anticorrelated with the pennate to centric diatom ratio, proposed as a potential sea ice proxy²⁸, and thus consistent with an interpretation of diatom-rich ‘cold’ communities and haptophyte-dominant ‘warm’ periods.

The detection of diatom assemblages from the *sedaDNA* is significant because Arctic sediments are notorious for poor diatom microfossil preservation beyond the Holocene^{28,30}. At Site U1621, only unidentifiable diatom fragments and some heavily silicified *Paralia sulcata* valves were found in our study interval²⁹. In contrast, the major haptophyte group detected with the *sedaDNA*, the coccolithophores, is present in the fossil record at this site²². The trend in the coccolithophore signal in the *sedaDNA* agrees with the MIS 5 nannofossil assemblages, which exhibit high abundances, low diversity and dominance of *Gephyrocapsa* species, with a high representation of *G. huxleyi*²². Together with a peak in calcite as inferred from X-ray fluorescence and diffraction analyses (Fig. 5d-e and S6), our DNA data show multiple lines of evidence for an expansion in coccolithophore dominance during the LIG.

This diatom to haptophyte turnover mirrors modern borealisation of phytoplankton communities associated with Atlantification in the modern Arctic. Over the last decade haptophytes have increased in relative abundance during warm anomalies in the Fram Strait³¹, and have increased in relation to diatoms since the 1970’s in the Bering Sea³². In the Eurasian Arctic, evidence suggests that increasing influxes of North Atlantic water transport the haptophytes *P. pouchetii* and *G. huxleyi* into the Arctic from more temperate regions^{4,33,34}. Over approximately the last three decades, *G. huxleyi* blooms have expanded 5° northwards to 76° N³⁵, corresponding to the latitude of Site U1621. Further, low diatom abundance and the resultant reduced export of biogenic silica to the seafloor have been observed during warm anomalies and associated with the loss of sea ice in the Fram Strait^{36,37}.

Several independent lines of evidence suggest intensified Atlantification during the LIG: haptophyte to diatom ratio, increased calcite precipitation, as well as an increase in smectite (Fig. 5d) which is a proxy of WSC current strength³⁸. Likewise, the absence of ice rafted debris (IRD) from nearby site KH14 (Fig. 1) points toward a warmer, ice-free ocean²⁰.

Intense ecological change at the onset of MIS 5e

The ecological community underwent a major change after the glacial termination (T-II), with the precise timing of the shift varying slightly depending on the statistical method. Split moving window analysis highlights an intense interval of ecological turnover commencing after T-II and continuing into the LIG (~ 129–122 ka; Fig. 2d). Similarly, hierarchical cluster analysis (CONISS) identified ~ 124 ka, during the early LIG, as the most important point of compositional change in the 83 kyr record (Fig. 2a). Further, NMDS ordination (Bray-Curtis, $k = 2$, stress = 0.142) suggests that the ecological community during the early LIG was distinct from that of the later phase (Fig. 4). This separation of the LIG at ~ 122 ka into two phases from 127–123 ka and 121–115 ka is supported statistically by a PERMANOVA ($F = 11.25$ $R^2 = 0.692$ $p = 0.029$). Together, these independent approaches indicate substantial ecological reorganisation between the early and late LIG. This finding is consistent with regional records that suggest the LIG in the Arctic had two distinct phases²⁰ and experienced a delay in warming that lagged peak insolation and atmospheric CO₂^{39,40}.

Our *sedaDNA* data show high diversity of phyla after T-II and into the early phase of the LIG (Fig. 2). The samples between 129–124 ka, which our statistical approaches consistently identify as part of the post-termination and earlier LIG phase, exhibit lower relative abundances of haptophytes and/or diatoms, which are otherwise the dominant functional groups in the record (63.3–64.7% for this period compared to an average of 84.6%). Instead, the post-termination and early LIG community was characterised by increased relative abundances of several non-dominant photic-zone protist groups. These included *Phaeocystis* (9.2–14.9% versus 5.8% on average), a soft-bodied haptophyte common in the Arctic today, Dictyochophyceae (2.2–5.5% versus 1.1%), Chlorophyta (3.0–4.3% versus 2.0%), Pelagophyceae (3.2–3.5% versus 0.9%), Cryptophyceae (2.2–3.7% versus 0.7%), and Bolidophyceae (1.1–2.1% versus 0.5%). At the genus level, largest contributors from these groups are *Florenciella*, *Dictyocha*, *Micromonas*, *Chloroparvula*, *Bathycoccus*, *Aureococcus*, *Teleaulax* and *Triparma* (Figure S7; Table S7). Several of these genera contribute to a pronounced peak in picoeukaryote abundance, the smallest size class of photic zone eukaryotes, between ~ 129–127 ka (Fig. 5h; Figure S8). Further, we detect algal taxa with the potential to form harmful or toxic blooms during this period with increased relative abundance of the diatom *Pseudo-nitzschia* and the prymnesiophyte *Chrysochromulina*, both projected to increase in the Arctic in the near future^{41–43}. These observations highlight the unique value of *sedaDNA* for reconstructing past plankton communities, as many of the taxa identified here are soft-bodied and rarely preserved in traditional microfossil archives in the global ocean.

The ecological traits of the transitory community provide insight into past oceanographic conditions during this interval. Many taxa that increased in relative abundance were small (with higher surface area to volume ratios), motile (possessing a flagellum to facilitate autonomous movement) or mixotrophic (obtain nutrition from both photosynthesis and the consumption of organic matter) (Table S7). Selection of these traits implies an advantage for physiological and ecological flexibility in a dynamic environment characterised by periodic nutrient limitation.

These conditions are consistent with a transitory period between the meltwater and sea ice influenced T-II and the open-water, strongly Atlantic-water influenced peak warmth of the LIG after ~ 125 ka²⁰. As the warm Atlantic water inflow strengthened, episodic freshwater inputs from melting sea ice and the retreating Svalbard-Barents Sea Ice Sheet likely stratified surface waters. This buoyant freshwater layer could reduce vertical mixing and nutrient supply from the deeper Atlantic waters, leading to nutrient limitation in the photic zone^{e.g.44}. Indeed, variable planktic $\delta^{18}\text{O}$ values suggest intermittent meltwater overprints on a warmer background (Fig. 5a). Increased smectite indicates strengthening of the warm Atlantic water inflow (Fig. 5e), while at the same time there are indications of dynamic cryosphere influence from a muted peak in the pennate-to-centric diatom ratios, a tentative proxy for sea ice (Fig. 5g). The IRD record at KH14 suggests that icebergs melted north of our site, providing an additional source of freshwater (Fig. 5c).

We show that this dynamic and geologically brief interval represents an ecological transition between deglacial and peak interglacial conditions. It mirrors processes observed in the modern Arctic, where increasing freshwater inputs have enhanced upper-ocean stratification^{45,46} and favoured smaller phytoplankton size classes^{8,37,47}. The assemblage identified here may therefore provide a useful analogue for future Arctic ecosystems under continued warming.

By 124–122 ka, during the peak warmth of the LIG, sea ice likely disappeared from the study area, and the transitional habitat was lost. The ecosystem shifted towards a more stable state where the coccolithophores became the dominant primary producers in an open and well-mixed surface ocean.

Earliest evidence of boreal megafauna in the Arctic

We detected higher trophic levels, including fishes and marine mammals, in our sedaDNA dataset (Fig. 5), which is similar to results from other shotgun metagenomic studies of polar marine sediments^{24,25,48,49}. Although these taxa were represented by fewer reads than higher-biomass groups such as the phytoplankton, recent evidence demonstrates that even low-abundance DNA signals can provide ecologically meaningful information⁵⁰. To our knowledge, our study provides some of the oldest molecular evidence for these higher-trophic-level organisms in the Arctic, thereby extending the known Arctic fossil record. The only comparable evidence currently known to us is the recovery of a polar bear mandible from a shallow-marine deposit on Svalbard dated to 130–110 ka⁵¹.

We detected two major groups of marine mammals, the cetaceans (1,309 reads) and Carnivora (109 reads). At species level, most cetacean reads were assigned to the common minke whale (*Balaenoptera acutorostrata*; 533 reads) and the northern bottlenose whale (*Hyperoodon ampullatus*; 301 reads). Carnivora reads were dominated by ice associated seals (*Cystophora cristata*, 64 reads; *Phoca groenlandica*, 30 reads).

Fishes were also present in our record, adding to the growing repository of sedaDNA studies capturing this group⁵². We mainly detected the ray-finned fishes (Actinopterygii, 622 reads), dominated by the cod family (*Gadidae*, 223 reads). At species level, *Gadus morhua* (Atlantic cod, 67 reads) and *Pollachius virens* (Atlantic pollock, 25 reads), both temperate Atlantic and economically important species, were the most common.

Both the cetaceans and the ray-finned fishes peak at the inception of the LIG (Fig. 5i and 5j), coinciding with the first major phytoplankton shift in the record. The species composition of the marine megafauna community during the interglacial shows the signature of borealisation in the eastern Fram Strait included higher trophic levels. For example, marine mammal detections were dominated by the *Balaenoptera*, a group currently present in acoustic surveys of the eastern Fram Strait and expected to increase with Atlantification⁵³. The *Balaenoptera* have also been implicated in a modern regime shift off the coast of Greenland⁵⁴. As for the ray-finned fishes, most species-level assignments were to temperate taxa. Borealisation of fish communities has been linked to recent warming in the modern Arctic⁵⁵ and sedaDNA detections of Atlantic fish species in Icelandic marine sediments have been shown to correlate positively with sea surface temperatures over the past three millennia⁵⁰. Our results suggest similar patterns during the LIG that warrant further attention with more quantitative or targeted methods of detecting fishes such as hybridisation bait capture^{56,57}.

Interestingly, ice associated seals were mainly detected in one sample at ~ 87 ka during the colder substage MIS 5b (vertical dotted grey line, Fig. 5). This corresponds with notable increase in pennate compared to centric diatoms, including the increased relative abundance of sea ice associated genera *Haslea*, *Nitzschia* and *Attheya*, suggesting enhanced sea ice coverage at this time.

Implications for the biological carbon pump

The borealisation of the marine phytoplankton community has downstream consequences for the export of carbon to the seafloor via the 'biological carbon pump' and thus the ocean's ability to sequester atmospheric carbon dioxide over geological timescales⁵⁸. These processes are particularly important to consider given our study site is part of a marine region with the most intense absorption of anthropogenic carbon globally⁵⁹.

It has been predicted that the efficiency of the biological carbon pump in the Arctic will decline under future warming as the shift to smaller plankton heralds a transition from a carbon export system to a retention system⁸. Diatoms are large, silicified phytoplankton known to sink quickly and drive efficient export of carbon from the surface ocean to the seafloor in the Fram Strait, Arctic³⁶. On the other hand, coccolithophores and other smaller photic zone eukaryotes tend to sink more slowly, promoting greater remineralisation in the upper water column and supposedly less export of carbon to the deep ocean^{60–62}. In this context, our results, which show a shift from larger diatoms to smaller coccolithophores, imply the efficiency of the biological carbon pump was reduced at the LIG in the Eastern Fram Strait. On top of

this, the process of producing the calcium carbonate coccolith exoskeleton can partially offset the drawdown of atmospheric CO₂ otherwise achieved by photosynthesis, further weakening the coccolithophore carbon pump⁶³.

However, recently the prevailing paradigm that smaller eukaryotes are less efficient exporters of carbon to the deep ocean has been challenged^{64,65}. For example, Bachy et al.⁶⁶ highlight the previously underestimated contribution by the picoeukaryote *Micromonas* to deep sea export in the Fram Strait, while Weiß et al.⁴⁹ suggested *Phaeocystis* blooms in the Southern Ocean drew down enough carbon to cause a reduction in global atmospheric carbon dioxide during the Antarctic Cold Reversal. Further, Le Moigne et al.⁶⁷ found similar carbon export efficiencies between diatoms, coccolithophores and *Phaeocystis* communities in the Atlantic sector of the Arctic Ocean, with the highest overall efficiency attributed to a monospecific ice edge bloom of *P. pouchetii*. At lower latitudes across the Atlantic, González-Lanchas et al.⁶⁸ found that smaller-sized – but fast-growing – coccolithophores drove the dominant carbon contribution to the sediments. By contrast, Fram Strait observations have also showed that sea ice meltwater, and resulting stratification, slows the biological carbon pump⁵⁹.

Conclusions

Ancient DNA preserved in sediments revealed borealisation of an Arctic marine ecosystem in response to the warming, and associated Atlantification, at the penultimate glacial transition. Our study unveils new insight into biodiversity across multiple trophic levels from a region with a scarcity of continuous fossil records.

We detect major ecological turnover including a transition away from a diatom dominated glacial system to the rise of a community dominated by cosmopolitan *Gephyrocapsa* coccolithophores, marking an increase in the influence of warmer North Atlantic inflow during the later phase of the LIG. This ecological change, coupled with a reduced ability of warmer surface waters to absorb atmospheric CO₂, suggests diminished efficiency of ocean carbon sequestration during the LIG. However, better understanding of organic carbon burial and carbon export by different marine functional groups is required in both the modern Arctic and in the sedimentary record to fully resolve uncertainties.

We also find evidence for a diverse marine assemblage enriched in smaller eukaryotes, mixotrophs and potentially harmful algal bloom-forming taxa that we associate with a stratified water column from increased meltwater input during the earlier phase of the interglacial. The shift in the plankton community at the glacial-interglacial transition occurred in concert with an increase in marine megafauna detections, composed predominately of whales and fishes with Atlantic or non-obligate polar distributions. Together, these findings demonstrate that past Arctic warming triggered extensive biodiversity turnover, providing a valuable analogue for ongoing ecosystem change in the rapidly warming Arctic.

Methods

Sample material

Hole U1621C was retrieved with an Advanced Piston Corer in July 2024 on IODP Expedition 403 on the *RV JOIDES Resolution* in a water depth of 1,636 m (Fig. 1). The sediments were drilled at the Bellsund Drift at 76° 31.3152 N, 012° 44.3552 E, a highly expanded depocenter in the southeastern Fram Strait that developed under the influence of the northward flow of the West Spitsbergen Current ²⁹. Shipboard biostratigraphy, palaeomagnetism, and correlation of magnetic susceptibility from Hole U1621A and Hole U1621B with a nearby record from KH-14 ²⁰ suggested the approximate location of our target interval, MIS 5e, was ~ 26 m below the seafloor. To target this period and its temporal context, 40 samples of ~ 2–3 cm³ were taken from a depth between ~ 19–33 m from Hole U1621C for *sedaDNA* analysis using strict clean protocols outlined in section 8 of the Expedition 403 Methods ⁶⁹ (Table S1). These samples came from the ten core sections between 4H1 and 5H3. The recovered sediment in this interval was primarily siliclastic silty clay ²⁹. Controls were taken alongside *sedaDNA* samples to track potential contamination (see Figure S4 for results of the biological controls). Air controls were taken in the clean room while sampling was underway. Drilling fluid was laced with a chemical tracer, perfluorodecalin (PFD), to assess whether the drill fluid had penetrated the core interior (results presented in Table S6). A sample of drill fluid was also taken for DNA analysis. All *sedaDNA* samples were frozen immediately at – 20°C and subsequently shipped frozen to nipaluna/Hobart, Australia, for analysis in the ancient DNA lab at the Institute for Marine and Antarctic Studies (IMAS).

SedaDNA extraction and shotgun metagenomics

~ 0.25 g of wet sediment was subsampled for *sedaDNA* extraction using a silica-based protocol optimised for retrieving short DNA fragments ⁷⁰. Samples and negative controls from shipboard subsampling were extracted in six batches, each with an extraction blank control (EBC). Shotgun metagenomic libraries were prepared from 20 µL of *sedaDNA* extract using standard methods to create indexed, double-stranded libraries ^{57,71–73}. Magnetic beads were used to size select fragments of DNA < 500 bp ⁷³. The indexed samples including controls were pooled equimolar at 25.9 nM in 44 µL. The libraries were sequenced on a Standard Illumina NovaSeq S1 Flow Cell (200 cycles) at the Garvan Institute of Medical Research, Kinghorn Centre for Clinical Genomics (Darlinghurst, Australia).

Bioinformatic processing

Raw sequences were processed using the University of Tasmania (UTAS) Menzies Genomics cluster rosalind, which is part of the Tasmanian Partnership for Advanced Computing. Quality of raw and filtered data was checked using FastQC (version 0.11.9) and MultiQC ⁷⁴. Raw data were demultiplexed and forward and reverse reads collapsed using Adapterremoval2 ⁷⁵. Low complexity and duplicate reads

were removed with Komplexity (version 0.3.6)⁷⁶ and Dedupe⁷⁷, respectively. Taxonomy was assigned by aligning the filtered reads against the non-redundant, curated genomic NCBI RefSeq database for protozoa, mitochondria and plastids (<https://www.ncbi.nlm.nih.gov/refseq>) using the MEGAN alignment tool (MALT)⁷⁸, which has been shown to perform well for short, fragmented DNA⁷⁹. The resulting 'blastn' files were converted to 'rma6' format for further processing in MEGAN6⁸⁰, where subtractive filtering was performed at genus level, except for the coccolithophore *Emiliana*. For the latter, one read ('CCCTTCGTCCATGTTGACGTCGATCACCTGCGCG') was detected in an EBC (EBC45). The read was blasted against the NCBI nucleotide database, which confirmed that this read had been misassigned, likely due to its shortness (34 base pairs, as opposed to reads in samples with high detections of *Emiliana* that were on average > 41 bp). The sequence was also not detected in any of the samples or remaining controls (after searching in all blastn files), confirming a spurious misassignment rather than contamination. We note that the RefSeq NCBI database uses outdated nomenclature for the genus *Emiliana*, which contains the species *E. huxleyi*. In this study, we have renamed *Emiliana huxleyi* reads to the currently accepted classification *Gephyrocapsa huxleyi*. Read counts of all eukaryotes were exported for downstream analysis.

Ancient damage pattern analysis

Damage analysis (Figure S9) was performed on different taxonomic groups using the program HOPS (<https://github.com/rhuebler/HOPS>). 'RunSummary.txt' files were downloaded from the 'ancient' and 'default' output directories and 'Percent damage' was calculated by finding the proportion of 'ancient' reads of the total reads⁵⁷.

Statistics

Relative abundances were calculated by standardising phylum counts within each sample prior to community composition analyses. Constrained Incremental Sum of Squares (CONISS) analysis was conducted on phylum relative abundance data in RStudio (version 2025.09.0, "Cucumberleaf Sunflower") using the *vegan* (version 2.6-8) and *rioja* packages. Shannon diversity was calculated separately on rarefied assemblages (875 reads per sample) to minimise the influence of unequal sequencing depth on diversity estimates. The rarefaction threshold was selected based on the second-lowest sequencing depth among samples. Sample 35 (Table S1) was excluded from the rarefied dataset due to an anomalously low read count (106 reads). Assemblage turnover through the sediment sequence was assessed using a split moving-window analysis implemented in R. Bray-Curtis dissimilarities were calculated using functions from the *vegan* package, while data handling and visualisation were performed using packages from the *tidyverse* and *ggplot2*. The analysis was performed on phylum relative abundance data using adjacent moving windows of eight samples ($k = 8$). For each window position, the mean relative abundance of each phylum was calculated and Bray-Curtis dissimilarity between paired windows was used as a differentiation index, with higher values indicating greater

compositional change between successive intervals. To assess statistical significance, sample order was randomly permuted 999 times and the split moving-window analysis repeated for each permutation. The 99th percentile of the maximum differentiation index obtained from the permuted datasets was used as a conservative significance threshold, accounting for multiple comparisons across the sequence. Differentiation-index values exceeding this threshold were interpreted as significant episodes of community turnover. A locally weighted regression (LOESS) smoother was applied to the differentiation-index series to visualise long-term trends in assemblage change. Linear regression analysis of Haptophyta and Bacillariaceae (diatoms) relative abundances was performed in base R. Plots were created using the package *ggplot2* (version 3.5.2) and edited for style in Inkscape (version 1.3.2).

The hierarchical donut chart was constructed using genus-level diatom mean relative abundance data across all samples. Genera were classified as centric or pennate diatoms based on established taxonomic assignments. A hierarchical donut chart was produced in R using *ggplot2*, with inner sectors scaled according to mean genus abundance and an outer annotation ring denoting centric and pennate taxa. Genera were grouped into pennates or centrics and ordered by decreasing abundance within each group, with labels shown only for the ten most abundant genera.

Non-metric multidimensional scaling (NMDS) was used to visualize patterns in community composition between samples using the *vegan* package in R. The community matrix was subset to the taxa columns and taxa with zero abundance across all samples were removed. One sample with anomalously low read counts was removed from the final NMDS because it was an outlier (sample 35, see Table S1). NMDS ordination was performed with the *metaMDS* function using Bray-Curtis dissimilarities and two dimensions ($k = 2$). The robustness of the solution was assessed using the final stress value where values < 0.2 are deemed acceptable for ecological interpretation⁸¹. A random seed was set (`set.seed(123)`) to ensure reproducibility.

Geophysical properties of the sediment: magnetic susceptibility

See cruise methods⁶⁹.

Geophysical properties of the sediment: X-ray fluorescence (XRF) analysis

All U1621 XRF Core Scanner data were collected, at MARUM, University of Bremen every 1 cm down-core over a 1 cm² area with down-core slit size of 12 mm using generator settings of 10, 30 and 50 kV, a current of 0.5, 0.6 and 0.5 mA respectively, and a sampling time of 6 seconds directly at the split core surface of the archive half with XRF Core Scanner III (AVAATECH Serial No. 12). The split core surface

was covered with a 4 micron thin Ultralene foil to avoid contamination of the XRF measurement unit and desiccation of the sediment. Intervals with gaps, cracks, or disturbed sediment surface were skipped. The here reported data have been acquired by a SGX Sortech Silicon Drift Detector (Model SiriusSD® D65133Be-INF with 133eV X-ray resolution), the Topaz-X High-Resolution Digital MCA, and an Oxford Instruments 100W Neptune X-Ray tube with rhodium (Rh) target material. Raw data spectra were processed by the analysis of X-ray spectra by Iterative Least square software (WIN AXIL) package from Canberra Eurisys. Routine quality checks were performed on the data, and 15 elements were deemed suitable for interpretation. These were: Ba at 50 kV, Br, Rb, Sr, Zr, Pb at 30 kV and Al, Si, P, S, K, Ca, Ti, Mn, Fe at 10 kV. Due to varying grain size, pore size and water content throughout the core sections, we present element ratios rather than individual elemental intensities.

Age-depth models

The age-depth model for Site U1621 is based on visual correlation of the magnetic susceptibility spliced record of U1621 (on m CCSF-A, splice in ²⁹) to the U1623 magnetic susceptibility time series (Gebhardt, De Schepper et al., submitted to Nature Communications) using PyAnalySeries (version 5.29) (Supplementary data 1). The age-depth model for U1623 is based on oxygen isotope stratigraphy, tuned to the LR04 benthic isotope stack⁸². Our resulting sample resolution was ~ 2 ka, with each centimetre horizon representing an average of ~ 63 years of sediment accumulation.

We also made a correlation to the more northerly CAGE19-3-KH14 last interglacial sediment record²⁰, to ensure that the timing of paleoceanographic changes are directly based on the same reference. Tie points between KH14 and U1623 (Supplementary data 1) were selected based on visual correlation of the combined KH14 magnetic susceptibility and XRF log(Ca/Ti) record to the U1623 magnetic susceptibility and XRF log(Ca/Ti) time series (Gebhardt, De Schepper et al., submitted to Nature Communications) using PyAnalySeries (version 5.29). This exercise resulted in an updated and refined age model of the Steinsland et al.²⁰ age model for KH14.

Stable isotope analysis

Samples collected every 10 cm were dried and sieved at Kerala University. Stable carbon and oxygen isotopes ($\delta^{13}\text{C}$ and $\delta^{18}\text{O}$) of the planktic foraminifer *Neoglobobulimina pachyderma* were measured with a Thermo Fisher Scientific MAT 263 mass spectrometer with an automated Kiel I device at the Alfred Wegener Institute in Bremerhaven. For the measurements, on average eight (between four and ten) specimens of *N. pachyderma* were handpicked from the 125–250 μm size fraction and measured. Raw data were referenced to an internal Solnhofen limestone standard and converted to VPDB (Vienna Pee Dee Belemnite) notation using NBS19⁸³; all reported carbonate isotope data are given in per mill (‰) relative to the VPDB standard. Individual measurements with carbonate contents below or above the analytical threshold were excluded from further processing, similarly those samples that yielded more

than one expansion during measurements. The external reproducibility of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ was assessed with the internal laboratory Solnhofen limestone standard over a period of one year and was better than 0.04‰ for $\delta^{13}\text{C}$ and 0.08‰ for $\delta^{18}\text{O}$. Stable isotope measurements were submitted to Pangaea, doi generation currently pending.

Identification of the peak glacial (MIS 6), termination (T-II), and interglacial marine isotope stages

A consistent pattern in geophysical parameters was discovered for each glacial–interglacial transition at the nearby Site U1623, where for each succession of termination and peak interglacial over the last ~ 1 million years, the magnetic susceptibility and log(Ca/Ti) record show a characteristic pattern (Gebhardt, De Schepper et al., submitted to Nature Communications). Simplified for our studied interval, the peak glacial (MIS 6) is characterised by a maximum in log(Ca/Ti), Termination 2 (T-II) by stable, low magnetic susceptibility values, and the peak interglacial (here MIS 5e) by stable, low magnetic susceptibility values combined with a maximum in log(Ca/Ti). The planktic oxygen isotope data (see above) provides more information: the peak glacial is characterised by the heaviest values and T-II shows strong variability, likely reflecting freshwater imprint due to ice sheet melt. MIS 5e has consistent light isotope values, and although less clear compared to MIS 5e, also MIS 5c and MIS 5a show lighter values compared to the MIS 5b and MIS 5d (Fig. 5).

X-ray diffraction (XRD) analysis

Analysis by XRD was used to determine bulk mineralogic composition and quantify mineralogic environmental proxies such as calcite and smectite. We freeze-dried the samples, gently disaggregated them and ground in a McCrone mill for 10 min to obtain an average particle size of ~ 1 μm . We dried the resulting slurry at 45°C and spiked it with corundum (CR-1, Baikowski) as an internal standard to a final concentration of 20.0 wt%. We collected diffractograms using a Bruker D8 Advance diffractometer in Bragg-Brentano geometry with Cu K α radiation ($\lambda = 1.5406 \text{ \AA}$; 40 kV, 40 mA), primary and secondary Soller slits of 2.5°, divergence and antiscatter slits of 0.3°, a detector slit of 0.2°, and a Vortex detector (Hitachi). We collected diffractograms from 5–90°2 θ with a step size of 0.026°2 θ and counting time of 8 s per step, while samples were spun at 20 rpm. We used the BGMN code for Rietveld analysis implemented within PROFEX software⁸⁴ to refine the mineral quantities. Clay minerals were quantified as mineral groups, including swelling clay minerals (both discrete smectites and mixed-layer species with a smectite component), chlorite, kaolinite, and di- and trioctahedral mica. We refer to the sum of these mineral groups as total clay minerals.

We conducted Rietveld refinement of the bulk diffractograms to estimate mineral proportions in the whole sediment, rather than only in a < 2 μm fraction. We chose this approach because some clay minerals such as kaolinite and chlorite might occur as particles > 2 μm in diameter and can be partly

excluded during clay fractionation. We extracted the $< 2 \mu\text{m}$ fraction from a few samples and analysed air-dried and after glycolation to identify the types of swelling clays. These analyses confirmed two expandable components: a discrete smectite phase and an mixed-layer illite-smectite phase (not shown). In the Rietveld refinement, the discrete smectite component, most directly comparable to the smectite phase reported by Lucchi et al.³⁸, was described using an Fe-rich smectite model (nontronite), with the layer-to-layer distance constrained to $> 14.5 \text{ \AA}$, consistent with two interlayer water sheets. We modelled the mixed-layer illite-smectite component by an Al-rich smectite model (montmorillonite) with one interlayer water sheet and a broad layer-to-layer distance constrained between $11.5\text{--}13.5 \text{ \AA}$. These models were used as quantitative proxies for two distinguishable expandable clay populations, not as compositional representatives. To estimate WSC strength in a way comparable to Lucchi et al.³⁸ and to avoid dilution by the interglacial increase in calcite associated with calcite forming organisms, we expressed the discrete smectite abundance relative to the total clay minerals.

Declarations

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information. The online version contains supplementary information at [doi]

Data availability

Raw shotgun metagenomic reads will be made available through NCBI SRA.

All other data will be uploaded to the Pangaea database.

Code availability

The sedaDNA data processing pipeline, statistical analyses and figures code will be made available on GitHub.

Funding

This research was supported by an Australian & New Zealand International Scientific Drilling Consortium (ANZIC) Post Cruise Analytical Funding Grant. Expedition 403 and the JRSO were funded via NSF grant OCE 1326927. AGL acknowledges the Beatriz Galindo fellowship BG24/00019 and PID2025-171543NB-

C33, funded by the Spanish Ministry of Science, Innovation, and Universities, and project NE/ Z000300/1 funded by IODP UK-NERC. MB acknowledges the project PID2021-126495NB-C33 and PID2025-171543NB-C33 funded by the Spanish Ministry of Science, Innovation, and Universities. LT acknowledges support from the CNRS International Research Project OSIRIS, France-Australia collaboration. ZG is funded by the MOPGA Visiting Fellowship programme (Campus France, dossier no.186807Z). SJ and ZG were supported by the geochemistry–mineralogy platform of ISTerre (Grenoble, France), partially funded by a grant from Labex OSUG2020 (investissements d’avenir ANR10-LABX56). This manuscript is a contribution to the Italian PRA2023 AWARE (Arctic Meltwater Pulses Under Past Global Warm Conditions) project.

Author contributions:

LD – Conceptualisation, Methodology, Formal Analysis, Investigation, Drafting/Preparation – first draft, Visualisation, Funding Acquisition. SDS – Conceptualisation, Methodology, Investigation, Review & Editing, Funding Acquisition. AG-L – Investigation, Visualisation, Review & Editing. CG – Investigation, Review & Editing. MB – Formal analysis, Review & Editing. KH – Investigation, Review & Editing. TC – Formal Analysis, Review & Editing. AKMW – Review & Editing. KS – Conceptualisation, Project Administration. TR – Conceptualisation, Project Administration, Funding Acquisition. RL – Conceptualisation, Project Administration, Funding Acquisition. AF – Investigation, Review & Editing. JM – Investigation. IM – Review & Editing. SJ – Investigation, Formal Analysis. ZG – Investigation, Review & Editing. LT – Conceptualisation, Review & Editing, Supervision. SAV – Investigation. JT – Conceptualisation, Methodology, Review & Edition, Supervision. LA – Conceptualisation, Methodology, Review & Editing, Supervision. TN – Conceptualisation, Methodology, Review & Editing, Supervision.

Acknowledgements

We acknowledge the use of the high performance computing facilities provided by Digital Research Services, IT Services at the University of Tasmania.

This research used data acquired at the XRF Core Scanners Lab at the MARUM – Centre for Marine Environmental Sciences, University of Bremen, Germany.

We acknowledge and thank all the crew and technicians on the *RV JOIDES Resolution*, especially those on the final expedition, for their hard work and expertise that has been the foundation of countless scientific discoveries for generations. Sample preparation and characterization for mineralogic analyses has been performed at the geochemistry-mineralogy platform of ISTerre (Grenoble, France).

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Figures

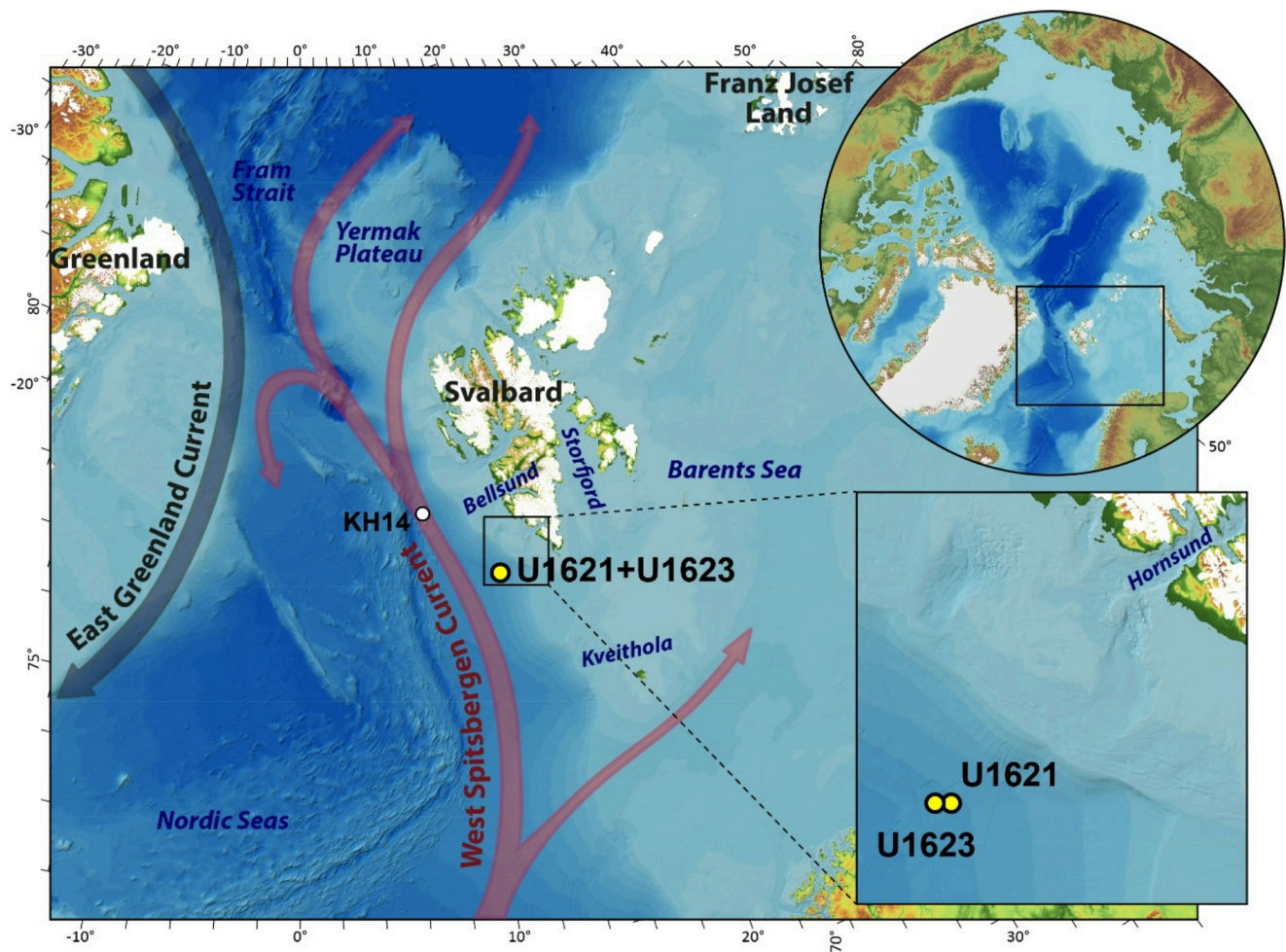


Figure 1

Map showing the location of IODP Sites U1621 U1623 in the eastern Fram Strait, Arctic. Also shown is the location of core site KH14 discussed in the text. The red arrows represent the northward flow of the West Spitsbergen Current (WSC), a branch of the Atlantic Meridional Overturning Circulation (AMOC) that transports heat and salt into the Arctic Ocean.

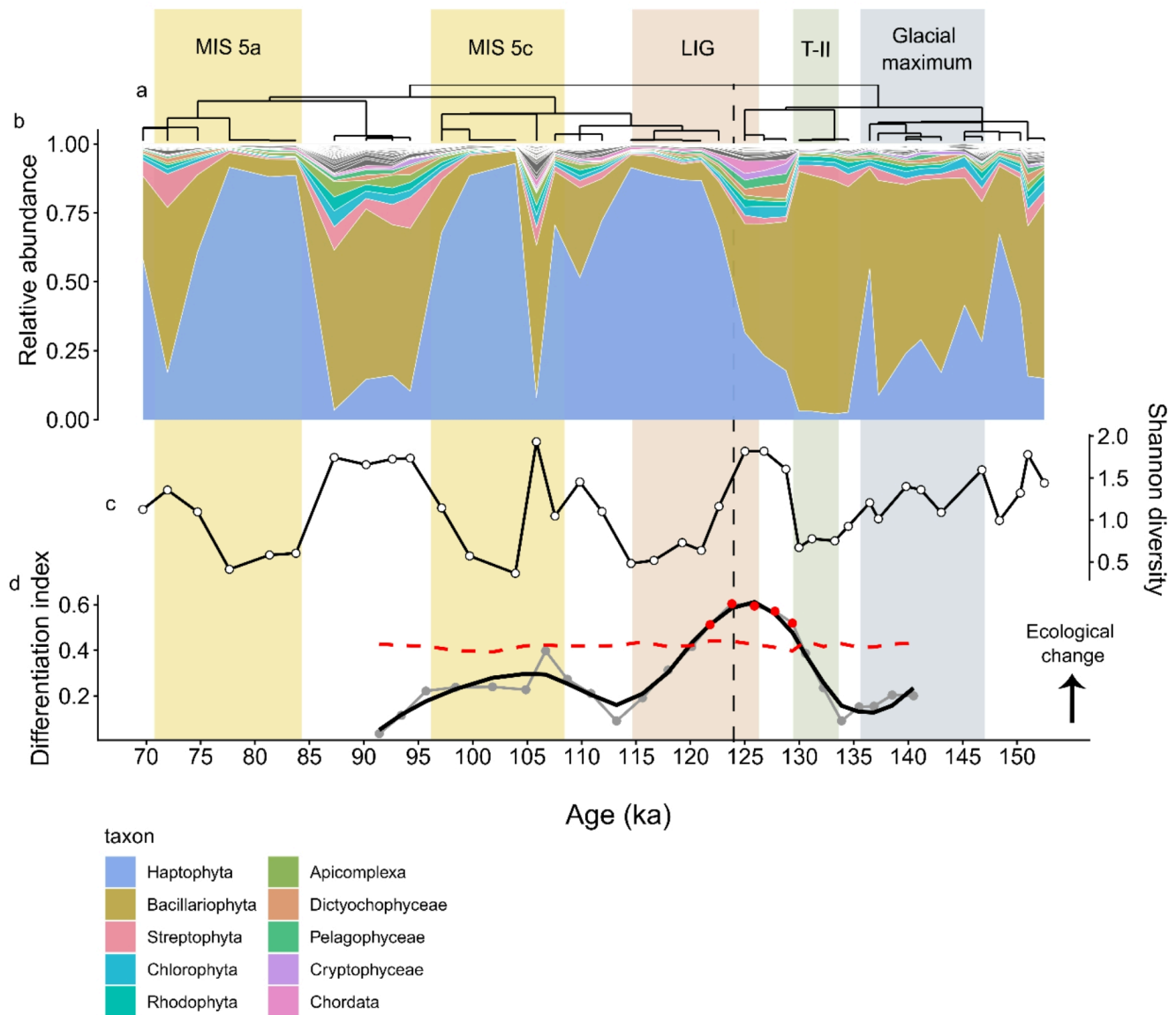


Figure 2

Eukaryotic phylum-level community dynamics reconstructed from sedimentary ancient DNA (sedaDNA) at IODP Site U1621, Bellsund Drift. Vertical shaded polygons denote the MIS 6 glacial maximum, T-II (glacial termination) and the LIG (peak interglacial), as defined by Gebhardt, De Schepper et al. (in prep). (a) Constrained Incremental Sum of Squares (CONISS) cluster analysis of phylum relative abundance data; vertical dashed line indicates zonation boundary. (b) Relative abundance of eukaryotic phyla through time; colours represent the ten most abundant phyla based on mean relative abundance, with remaining phyla in grey shades. (c) Shannon diversity calculated from rarefied assemblages (875 reads per sample). (d) Split moving-window analysis of community turnover based on Bray-Curtis dissimilarity ($k = 8$). The grey line and points represent the differentiation index (compositional turnover between adjacent windows), the black line shows a LOESS-smoothed trend, the red dashed line indicates the permutation-

derived significance threshold (99th percentile of the maximum differentiation index from 999 randomisations), and red points identify intervals of statistically significant community turnover.

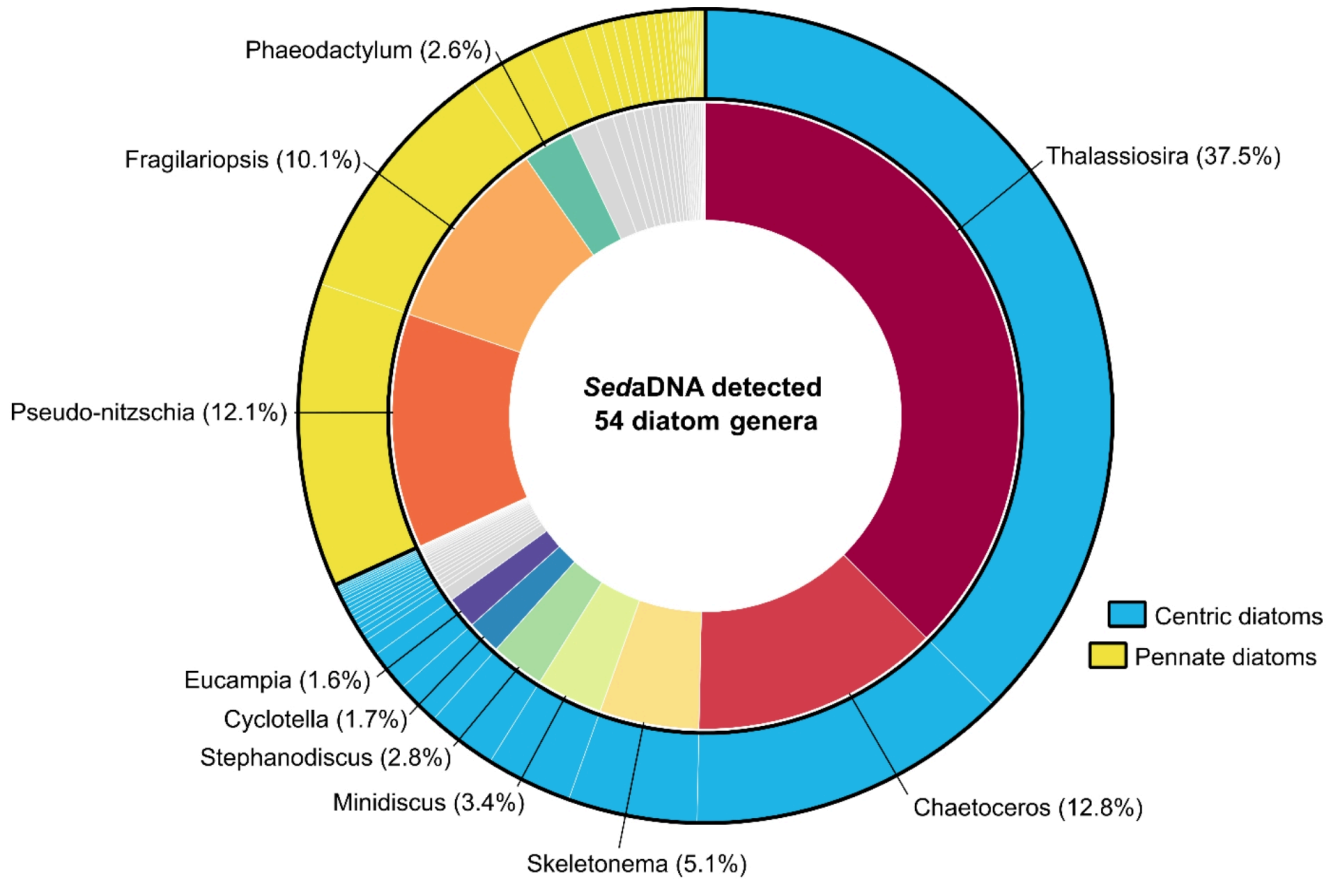


Figure 3

Hierarchical donut chart summarising diatom diversity recovered from sedimentary ancient DNA (sedaDNA) in Arctic marine sediments spanning 153–70 ka. Inner sectors represent individual genera and are scaled according to their mean relative abundance across all samples; only the top ten most abundant genera labelled. The outer ring distinguishes centric (blue) and pennate (yellow) diatoms. A total of 54 genera were detected, revealing substantial diversity within this functionally important group of phytoplankton that has remained largely undocumented in Arctic sediment archives older than the Holocene owing to the poor preservation and post-depositional dissolution of siliceous frustules. The relative abundance of centric and pennate taxa provides a broad ecological indicator of changing sea-ice influence, as pennate diatoms are commonly associated with sea-ice and marginal ice-zone environments, whereas many centric taxa are characteristic of pelagic open-water productivity.

NMDS (Bray-Curtis) – Stress = 0.142

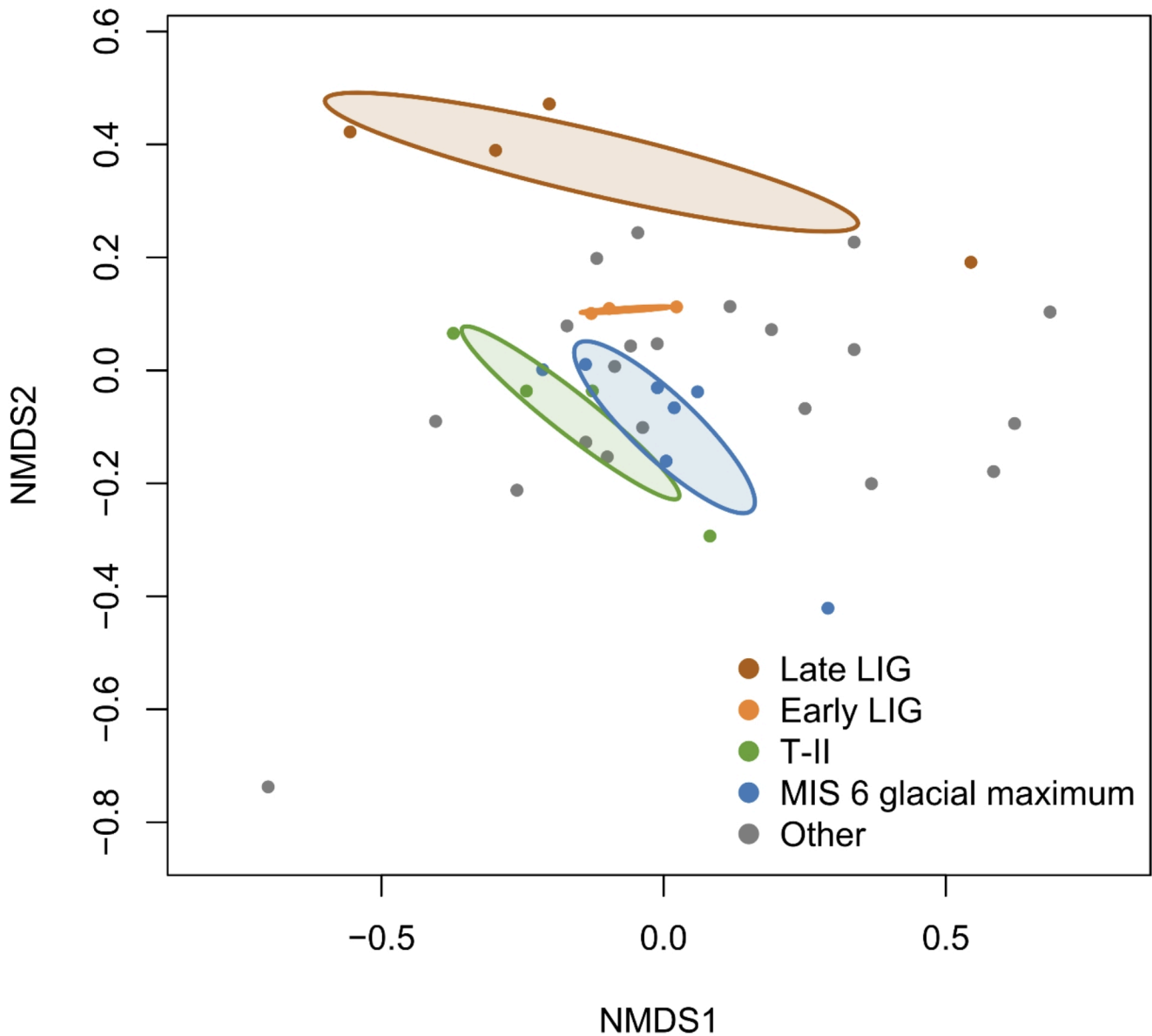


Figure 4

Shifts in eukaryotic assemblages during the MIS 6-MIS 5 transition. Bray-Curtis non-metric multidimensional scaling (NMDS) ordination of all eukaryotic genera ($k = 2$; stress = 0.142). Samples are coloured by stratigraphic interval: MIS 6 glacial maximum (blue), T-II or termination (green), early LIG (orange), late LIG (dark red) and other (grey). Ellipses indicate within-group dispersion around group centroids. A PERMANOVA comparing early and late LIG samples indicates significant differences in assemblage composition ($F = 11.25$ $R^2 = 0.692$ $p = 0.029$).

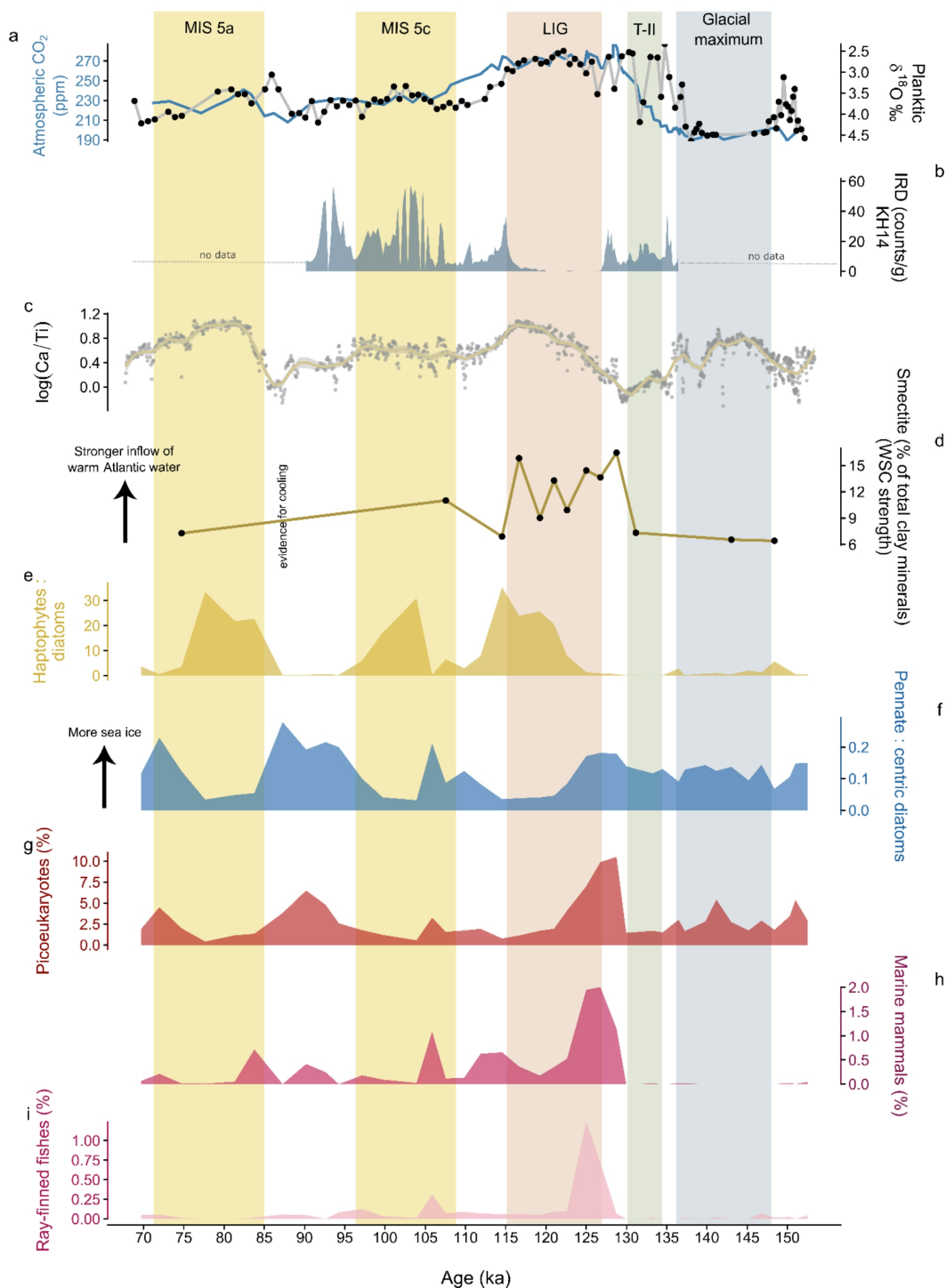


Figure 5

Ecological indicators from sedaDNA compared with regional palaeoenvironmental proxies focusing on the Last Interglacial. Vertical shaded polygons denote the MIS 6 glacial maximum, T-II (glacial termination) and the LIG (peak interglacial), as defined by Gebhardt, De Schepper et al. (in prep) and the MIS 5c and 5a intervals. (a) Atmospheric CO₂ (ppm) reconstructed from the EPICA Dome C ice core record¹ (blue line, left axis) and $\delta^{18}\text{O}$ from planktic *Neoglobobulimina pachyderma* foraminifera (grey line, right axis).

(b) Ice-rafted debris (IRD; counts g⁻¹ sediment) from core KH14². (c) XRF-derived Ca/Ti ratios. (d) The abundance of swelling clays, indicative of the strength of the West Spitsbergen Current. SedaDNA-derived ecological indicators (e-i) are expressed as relative abundance of the total eukaryotic signal. (e) The haptophyte-to-diatom ratio. (f) The pennate-to-centric diatom ratio, interpreted as a proxy for sea-ice conditions. (g) Picoeukaryotes (*Ostreococcus*, *Micromonas*, *Bathycoccus*, *Chloropicon*, *Chloroparvula*, *Picocystis*, *Pelagomonas*, *Aureococcus* and *Triparma*). (h) Marine mammals. (i) Ray-finned fishes.

Supplementary Files

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