

Research paper

Distribution of modern benthic foraminiferal assemblages across the Northeast Greenland continental shelf

Joanna Davies^{a,*}, Jeremy Lloyd^b, Christof Pearce^a, Marit-Solveig Seidenkrantz^a^a Department of Geoscience, iClimate Centre and Arctic Research Centre, Aarhus University, Aarhus, Denmark^b Department of Geography, Durham University, Durham, UK

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ABSTRACT

Analysis of benthic foraminifera in surface samples from 23 sites on the Northeast Greenland continental shelf reveal key assemblage differences between sites. Cluster analysis creates two clear geographical faunal assemblage zones: the 1) inner shelf, and 2) mid and outer shelf sites. These assemblages differ significantly, with the inner shelf sites being characterised by a high percentage and concentration of calcareous species, whilst the mid and outer shelf sites are dominated by agglutinated taxa. At almost all sites, the calcareous assemblages are dominated by *Cassidulina neoteretis* and *Cassidulina reniforme*, suggesting that they thrive across the shelf. *Stetsonia horvathi*, *Oridorsalis tener*, as well as *Glomulina oculis* and other miliolid species are found to be key calcareous species at many sites in the inner shelf zone, but they are rare-to-absent on the mid and outer shelf. Canonical correspondence analysis shows that September sea-ice cover and bottom water oxygen content are positively correlated with benthic foraminiferal assemblages at inner shelf sites, whereas organic carbon content is correlated with those in the mid and outer shelf. The formation of seasonal sea-ice and the Northeast Water polynya rejects brine into surrounding waters and transports CO₂ to the seafloor, creating a highly corrosive environment for calcium carbonate. These environments are also highly productive, as indicated by the high organic carbon content and low bottom water oxygen content. The oxidation of this organic material creates CO₂. We propose that these processes are key drivers in the dissolution of calcareous tests. In contrast, extensive sea-ice, high bottom water oxygen content and low primary productivity in the glacier-proximal region facilitates carbonate preservation.

1. Introduction

Benthic foraminifera are responsive to variations in environmental conditions; thus, their fossil assemblages, preserved in marine sediments, provide a tool to examine past changes in ocean circulation, glacier proximity, sea-ice conditions, and nutrient availability in the Arctic and elsewhere, when instrumental data does not exist. Yet, the use of benthic foraminifera for paleo-reconstructions relies on a solid understanding of the environmental and habitat preferences of different species. Consequently, regional analysis of modern benthic foraminiferal communities and corresponding environmental conditions are required to assist with building robust paleo-environmental reconstructions.

The Northeast Greenland (NEG) continental shelf (Fig. 1) is characterised by the interaction of Arctic and Atlantic Ocean currents, sea-ice, and marine-terminating glaciers. The effects of anthropogenic climate

change are particularly visible in the region with the thinning and break-up of ice shelves fronting marine-terminating glaciers (Khan et al., 2014; Mouginit et al., 2015) and sea-ice declining in thickness and extent (Kwok, 2018; Stroeve and Notz, 2018). Whilst numerous studies have used foraminiferal communities to reconstruct past environmental conditions in this area (Davies et al., 2022; Hansen et al., 2022; Jackson et al., 2022; Lloyd et al., 2023; Pados-Dibattista et al., 2022; Rasmussen et al., 2022; Syring et al., 2020a; Zehnich et al., 2020), the number of studies of modern foraminiferal assemblages are far fewer and based solely on samples collected in the spring and summer of the early 1990s (Ahrens et al., 1997; Mackensen et al., 2000; Newton and Rowe, 1995). These studies only analysed the living fauna and thus largely reflect the assemblages living at the time of collection, rather than those integrated across the entire year as seen in the dead or total assemblage (Ahrens et al., 1997; Mackensen et al., 2000; Newton and Rowe, 1995). Since then, major environmental changes, driven by anthropogenic climate

* Corresponding author.

E-mail address: joannadavies@geo.au.dk (J. Davies).<https://doi.org/10.1016/j.marmicro.2023.102273>

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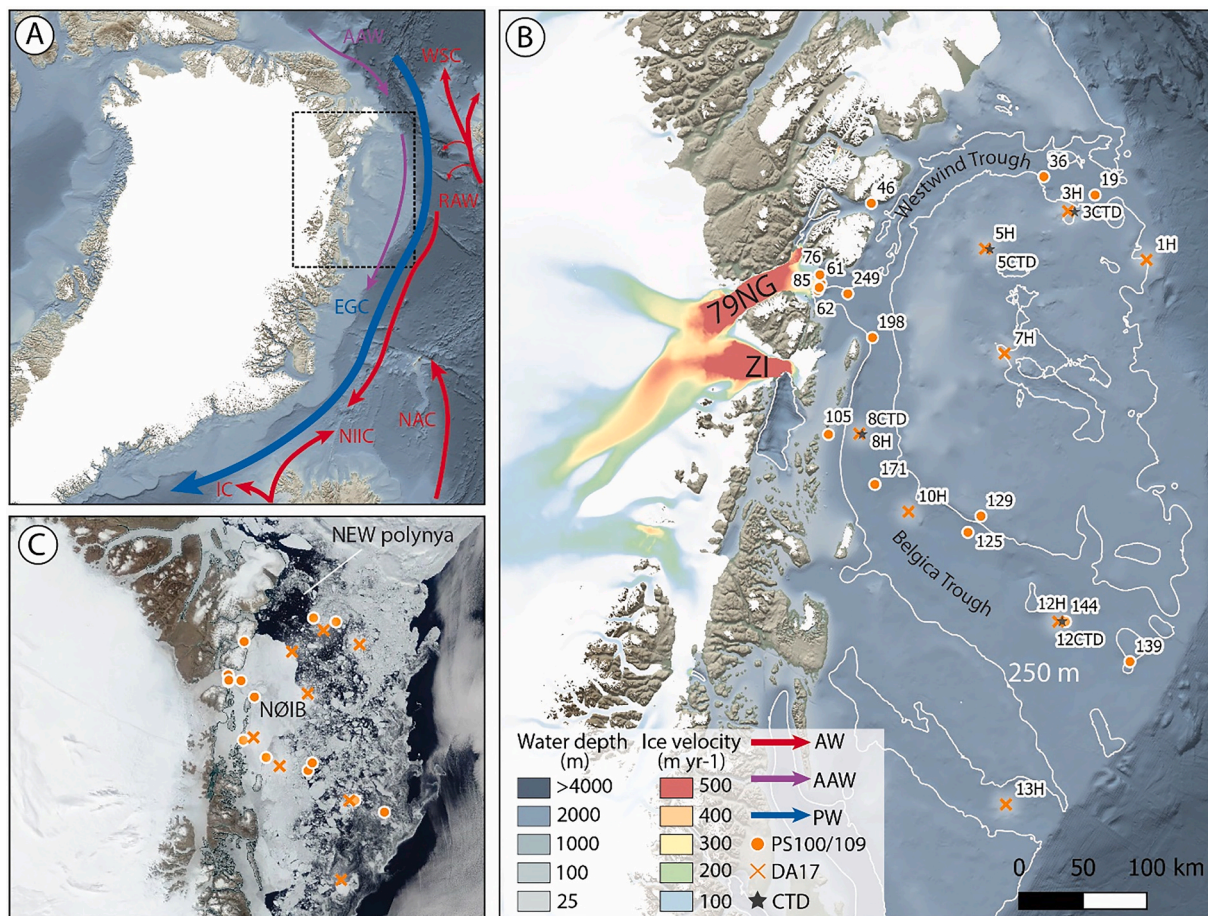


Fig. 1. A) Overview map of the study site, showing the ocean currents and water masses affecting Northeast Greenland including Return Atlantic Water (RAW), West Spitsbergen Current (WSC), North Atlantic Current (NAC), Irminger Current (IC), North Icelandic Irminger Current (NIIC) (red), the Polar Water (PW) carried by the East Greenland Current (EGC) (blue) and Arctic Atlantic Water (AAW) (purple). The ocean bathymetry is from [GEOCO Bathymetric Compilation Group \(2023\)](#). B) The Northeast Greenland continental shelf with surface samples presented in this study, collected on PS100/109 (orange circles) and NorthGreen2017 (DA17; orange crosses), respectively. The relative strength of currents is shown by the line thickness. The ice stream velocity data is from Sentinel-SAR data from 2019 to 20 (Nagler et al., 2015) and two marine terminating glaciers are shown: Zachariae Isstrøm (ZI) and Nioghalvfjærdsfjorden glacier (79NG). The 250 m contour line is shown (white). CTD water column profiles are shown for four sites (8CTD, 12CTD, 5CTD and 3CTD). These are marked with black stars. C) The modern sea-ice conditions from 10 July 2016 on the Northeast Greenland continental shelf, including the Norske Øer Ice Barrier (NØIB) and Northeast Water (NEW) polynya. (Satellite images courtesy of the NASA Worldview application, <https://worldview.earthdata.nasa.gov/>). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

change, have taken place: near-surface air temperatures in NEG have risen by about 3 °C (1979–2017) (Turton et al., 2019), and subsurface water has warmed (An et al., 2021) resulting in the collapse of the ice shelf of the Zachariae Isstrøm (ZI) and retreat of the Nioghalvfjærdsfjorden glacier (79NG) (An et al., 2021; Bentley et al., 2023; Khan et al., 2014; Mouginit et al., 2015).

Here, we present a study of benthic foraminiferal assemblages from surface sediment samples collected on the NEG continental shelf in the Autumn of 2016 and 2017. These datasets offer an opportunity to examine regional differences in benthic foraminiferal assemblages over a larger geographical area than investigated in the 1990s (Ahrens et al., 1997) and link these to the environmental conditions that characterise the region. Moreover, as we focus on the total (living plus dead) fauna, the assemblages represent average conditions across a few years and thus provide a different type of information than previous studies. Here, we investigate the impact of sea-ice cover, brine formation, bottom water temperature, salinity and oxygen content on benthic foraminiferal assemblages across the shelf. The comparison of the foraminiferal assemblages to environmental parameters allows us to evaluate the habitat requirements of some key species, which will improve paleo-reconstructions here and elsewhere in the Arctic.

2. Regional setting

The study area spans the NEG continental shelf (Fig. 1); an area approximately 300 km wide and characterised by a series of deep troughs, the Belgica Trough (also known as the Norske Trough) and the Westwind Trough (Fig. 1B). These provide pathways for subsurface, warmer water to reach marine-terminating glaciers (Arndt et al., 2015; Lindeman et al., 2020; Schaffer et al., 2020). The region is influenced by a series of currents carrying water masses of different temperatures and salinities. Polar Water (PW; -2 – -1 °C, ≤ 34.5) occupies the uppermost part of the water column and is transported by the East Greenland Current (EGC) southwards, from the Arctic Ocean over the continental shelf (Aagaard and Coachman, 1968; Johannessen, 1986). Beneath the PW lies Atlantic Water (AW); this consists of Arctic Atlantic Water (AAW) and Return Atlantic Water (RAW) (Rudels et al., 2005), together forming the Atlantic Intermediate Water (AIW). The AW originates from further south in the Atlantic Ocean and is transported northwards by the West Spitsbergen Current. Around half of the AW travels toward the Arctic Ocean, where it cools and freshens becoming the AAW before again being carried southwards by the EGC. The remaining AW travels directly from Svalbard toward the Greenland Shelf as the RAW, which is slightly

warmer than the AAW (Schaffer et al., 2017). The two AW components (AAW and RAW) gradually mix, becoming the AIW. Whilst much of the AW is transported southwards, some enters the deep troughs, where it occupies the lower 200 m of the water column (Schaffer et al., 2017). The Westwind Trough is dominated by AAW transported by the eddy flows of the EGC, and Belgica Trough is characterised by comparatively warm and saline RAW (Rudels et al., 2012; Schaffer et al., 2017). This allows access of the AW to marine terminating glaciers to the west (An et al., 2021; Arndt et al., 2015), facilitating melting from below (Schaffer et al., 2020; Schaffer et al., 2017). The sea floor of the shallower areas between the troughs are primarily dominated by PW (Schaffer et al., 2017), except for the deeper basins in the inter-trough areas, where AW is found (Pados-Dibattista et al., 2022).

The Norske Øer Ice Barrier (NØIB) (Fig. 1C) is an expansive area of land-fast ice (200–400 km wide), located at, or close to, the coastline of NEG (Sneed and Hamilton, 2016). It acts as a buttress to marine terminating glaciers: the ZI and 79NG (Fig. 1B; Reeh et al., 2001). Throughout the twentieth century the NØIB has been stable and present year-round, however since 1997 it has disintegrated more regularly during the summer (Sneed and Hamilton, 2016).

The Northeast-Water Polynya (NEW; Fig. 1C) is a key recurring feature in the northern part of the NEG continental shelf, formed by the NØIB, northward flowing North East Greenland Coastal Current and katabatic winds (Schneider and Budéus, 1997). The polynya begins to open in the Spring (April/May) with a normal extent of around 80,000 km² during summer. The polynya is an area of high primary productivity (Budéus and Schneider, 1995; Schneider and Budéus, 1994), which is reflected in the high total organic carbon content (TOC; around 1%) in the sediments below (Syring et al., 2020b). The release of dense brines from sea-ice production can also affect the mixing of the water column (Bäcke et al., 2002; Barber et al., 2001). This brine water is characterised by a high CO₂ content, high salinities, low temperatures and pH (Rasmussen and Thomsen, 2014; Topp and Johnson, 1997).

3. Materials and methods

3.1. Core collection and sampling

In 2016 and 2017, box and multi cores were collected onboard the RV *Polarstern* as part of the PS100 (Kanzow, 2017) and PS109 (Kanzow, 2018) cruises, respectively (Table 1). Cores were collected from depths ranging from 139 to 568 m. Rose Bengal with ethanol was added to surface sediments (0–1 cm) from expeditions PS100/109, and these were sealed and stored at 4 °C until analysis. Haps (small box corer) and Rumohr cores were collected in September 2017 on board RV *Dana* as part of the NorthGreen2017 Expedition (Seidenkrantz et al., 2018); samples designate as DA17. The sediment surface (0–1 cm) from DA17 sites was sampled and frozen at –20 °C. For several of the DA17 sites, a comparison was made between surface samples from Haps cores (stored frozen) and surface samples taken from Rumohr cores (stored at 4 °C) to investigate whether storage (frozen vs. cooled) impacts the preservation of benthic foraminifera (Supplementary Material). A full list of surface samples analysed, the type of core, and the date of collection can be found in Table 1.

3.2. TOC

All samples were freeze-dried (–45 °C; 0.2 mbar) and homogenised prior to analysis for TOC. For DA17 samples, 15–20 mg of this sediment was weighed into silver capsules and 30 µl Silex water was added. The samples (in a micro-titer plate) and a beaker with concentrated HCl was placed in a desiccator and vacuum applied to make the acid boil. The HCl-vapor acidifies the sediment and removes carbonates. After, the samples were gently dried in an oven (60 °C). The capsules were then firmly closed, and samples analysed for TOC on an elemental analyser connected in continuous flow mode to an isotope ratio mass spectrometer (Delta V, Thermo Scientific).

For PS100/109 samples, the freeze-dried sediment (20–30 mg for

Table 1

All surface sample sites and locations used in this study (MUC: multi-corer).

Short Name	Site Name	Date	Instrument Type	Storage	Water depth (m)	Latitude	Longitude
1H	DA17-NG-ST01-09H	13-09-2017	Haps	Frozen	325	79.63112	–6.05978
1R	DA17-NG-ST1-10R	13-09-2017	Rumohr	Fridge	320	79.62973	–6.07042
3H	DA17-NG-ST03-038H	14-09-2017	Haps	Frozen	367	80.051	–8.96907
3CTD	DA17-NG-ST03-025CTD	14-09-2017	CTD	NA	381	80.04307	–8.87413
5H	DA17-NG-ST05-050H	15-09-2017	Haps	Frozen	205	79.8266	–12.48918
5CTD	DA17-NG-ST05-053CTD	15-09-2019	CTD	NA	233	79.8232	–12.46278
7H	DA17-NG-ST07-078H	16-09-2017	Haps	Frozen	377	79.06875	–11.92265
7R	DA17-NG-ST07-070R	16-09-2017	Rumohr	Fridge	377	79.017172	–11.8986
8H	DA17-NG-ST08-094H	17-09-2017	Haps	Frozen	534	78.49987	–17.30212
8R	DA17-NG-ST08-090R	17-09-2017	Rumohr	Fridge	595	78.50002	–17.3072
8CTD	DA17-NG-ST08-084CTD	17-09-2017	CTD	NA	599	78.49437	–17.35017
10H	DA17-NG-ST10-112H	18-09-2017	Haps	Frozen	504	77.95065	–15.50752
10R	DA17-NG-ST10-109R	18-09-2017	Rumohr	Fridge	504	77.94967	–15.4939
12H	DA17-NG-ST12-138H	19-09-2017	Haps	Frozen	398	77.12797	–10.66585
12R	DA17-NG-ST12-134R	19-09-2017	Rumohr	Fridge	500	77.12505	–10.6632
12CTD	DA17-NG-ST12-127CTD	19-09-2017	CTD	NA	500	77.1297	–10.6757
13H	DA17-NG-ST13-154H	20-09-2017	Haps	Frozen	379	75.84705	–12.59233
19	PS109-19	17-09-2017	MUC	Fridge	315	80.1477	–7.94908
36	PS109-36	19-09-2017	MUC	Fridge	310	80.31762	–10.02898
46	PS109-46	20-09-2017	MUC	Fridge	205	80.15435	–17.36053
61	PS109-61	22-09-2017	MUC	Fridge	162	79.55655	–19.22082
62	PS109-62	22-09-2017	MUC	Fridge	301	79.50667	–19.32192
76	PS109-76	24-09-2017	MUC	Fridge	365	79.62012	–19.29162
85	PS109-85	25-09-2017	MUC	Fridge	156	79.5285	–19.28157
105	PS109-105	28-09-2017	MUC	Fridge	440	78.4816	–18.55728
125	PS109-125	03-10-2017	MUC	Fridge	388	77.7996	–13.63402
129	PS109-129	03-10-2017	MUC	Fridge	139	77.91283	–13.17372
139	PS109-139	04-10-2017	MUC	Fridge	354	76.79842	–8.65753
144	PS100-144	13-08-2016	Box	Fridge	494	77.12633	–10.56883
171	PS100-171	17-08-2016	Box	Fridge	542	78.1405	–16.83417
198	PS100-198	25-08-2016	Box	Fridge	391	79.19117	–17.107
249	PS100-249	18-09-2016	Box	Fridge	310	79.49717	–18.14

Total Carbon (TC) and 40–50 mg for total Inorganic Carbon (TIC)) was ball-milled and added to ceramic boats before being combusted (1000–1500 °C). For TIC, 40% orthophosphoric acid was first added to remove the organic carbon component. The gas produced during combustion was detected by a Non-Dispersive Infrared detector. TOC was calculated by taking the difference between the measured TIC and TC values.

3.3. Foraminifera

The frozen sediment samples from the NorthGreen2017 Expedition were thawed at room temperature prior to laboratory treatment. For all samples, the wet sediment was weighed and sieved. All fauna >63 µm were subsequently analysed. Samples were immediately counted wet, in deionised water on picking trays, and the foraminiferal species identified according to Feyling-Hanssen (1964) and Feyling-Hanssen et al. (1971). For comparison, after wet picking, some samples were subsequently dried in the counting trays, and then recounted dry whilst in the same tray. Results indicated that there was no significant difference (two tailed *t*-test, $p > 0.05$) between these two methodologies. A comparison was also made between frozen and cooled samples for some sites, to ascertain the differences between the preservation of calcareous foraminifera. These results indicate that frozen samples result in a better preservation of foraminifera, so these were used for all analyses. The results of these methodology and storage tests can be found in the Supplementary Material.

A Rose Bengal solution with 30% ethanol, buffered with sodium hydrogen carbonate, was added to the PS100/109 samples during the cruise; this was not done for samples collected on the DA17 cruise. As the PS100/109 samples were Rose Bengal stained, stained (living) and unstained (dead) specimens were counted separately. However, as the samples from the DA17 were not stained, the counts of living and dead tests for PS100/109 were added and used as total assemblage in the further analyses for all samples. The analyses of the total foraminiferal

assemblages for PS100/109 and DA17 were compared with environmental parameters to understand the key environmental controls over foraminiferal assemblages. Total assemblages provide an integrated signal and are a better representation of what we find in the fossil record; hence they are more useful for paleoenvironmental reconstructions.

Benthic foraminiferal species were identified and counted using a binocular microscope, and at least 300 specimens (agglutinated and calcareous combined) were counted, with the exception of three samples (12H, 7H, 10H) where between 127 and 189 specimens were found. For presentation purposes, all Miliolid species except *Glomulina oculis*, were combined (i.e., *Triloculina trihedra*, *Quinqueloculina* sp., *Miliolinella chuckchiensis*, *Miliolinella subrotunda*), while *Nonionella fragilis* and *Nonionella iridea* were combined and listed as *Nonionella iridea* (images shown in Supplementary Material). Species percentages were calculated based on the total assemblages. For indicator species, we also calculated their percentage in relation to total calcareous and total agglutinated tests, separately. Indicator species are defined as those most abundant in the samples, and that have distinguishable environmental preferences. A list of indicator species can be found in the Supplementary Material. Concentrations of benthic foraminifera (agglutinated, calcareous and combined agglutinated and calcareous) were calculated as the number of specimens/g wet sediment for samples from NorthGreen2017 (DA17) and with respect to an approximate volume (no. specimens/ml) for PS100/109 samples, as these samples were not weighed but instead the volume of each sample is approximated (10 ml).

Two measures of diversity are included in the analysis: the number of species present and the Shannon diversity index. The Shannon diversity index accounts for the number of species living in a community, together with their relative abundances, or evenness (Shannon, 1948).

3.4. Environmental variables

Environmental variables (bottom water temperature, bottom water salinity, bottom water oxygen, and water depth) were recorded at each

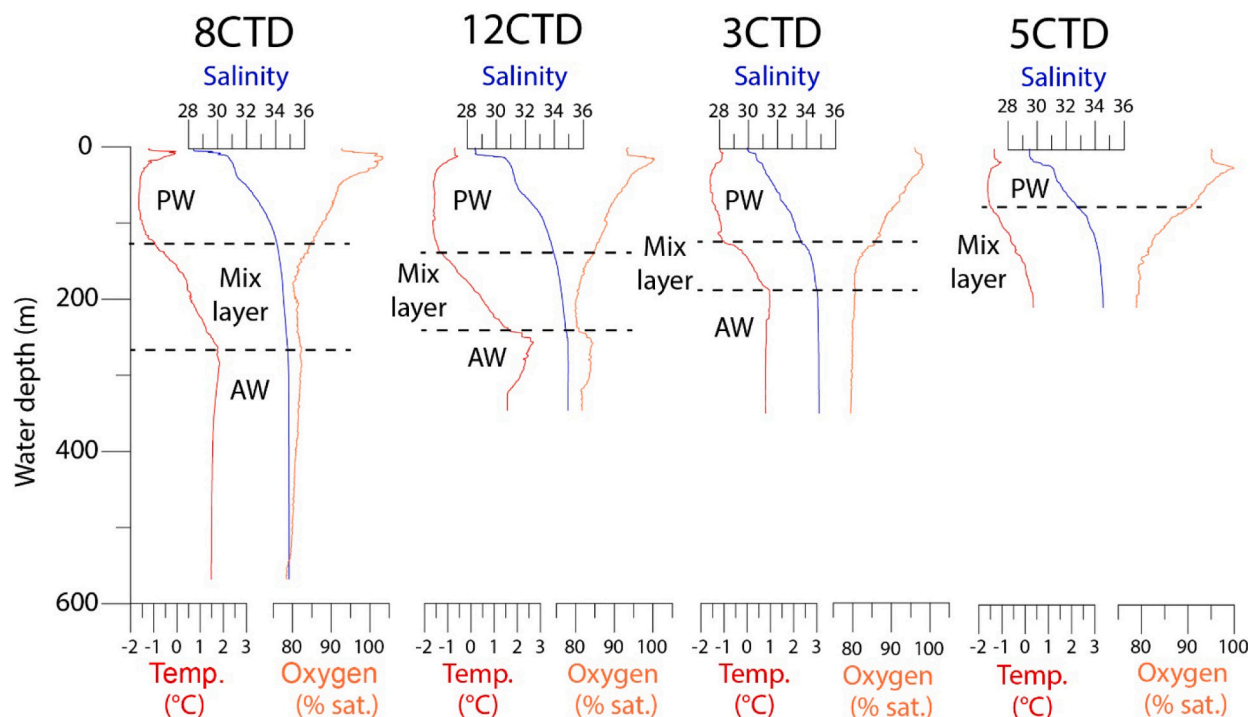


Fig. 2. Examples of water column CTD profiles on depth showing temperature (red), salinity (blue) and oxygen (orange) for three selected sites across the Northeast Greenland shelf. 8CTD (left) located close to the coastline, 12CTD from the outer Belgica Trough, 3CTD from the outer Westwind Trough and 5CTD (right), which has PW at the bottom of the water column. The water masses, Atlantic Water (AW) and Polar Water (PW), as referenced in the text, are shown. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

site during the cruises using a Seabird CTD (Conductivity, Temperature, Depth). The four examples are provided in Table 1 and Fig. 2. September sea-ice concentration data was extracted from Nimbus-7 SMMR and DMSP SSM/I-SSMIS Passive Microwave Dataset and was averaged over a five-year time period (DiGirolamo et al., 2022).

3.5. Data analysis

All statistical analysis was undertaken using the PAST v3. software (Hammer et al., 2001). Prior to statistical analysis, the six environmental variables (bottom water temperature, bottom water salinity, bottom water oxygen, water depth, September sea-ice cover, TOC) were normalised using a Box-Cox transformation ($\lambda = 0.0743$). A principle component analysis (PCA) was then undertaken on the environmental parameters.

Benthic foraminiferal species present with at least 2% abundance in at least one sample were included in the data analysis. A hierarchical clustering was undertaken using the unweighted pair-group average (UPGMA) and Bray-Curtis similarity index used. This analysis divides the sites into zones and subzones, based on their benthic foraminiferal assemblages.

Links between environmental variables and benthic foraminiferal assemblage data was investigated using a canonical correspondence analysis (CCA), which extracts synthetic environmental gradients. This was undertaken on species with at least 2% abundance in one sample and the normalised environmental data. The eigen analysis algorithm follows that in Legendre and Legendre, 1998, using scaling type 1.

4. Results

4.1. Water column characteristics

Water column profiles from four selected sites on the inner (8CTD) and outer (12CTD) shelf area in Belgica Trough, on the outer shelf in Westwind Trough (3CTD) and from a shallower inter-trough bank (5CTD), highlight differences in the water column characteristics between these areas (Fig. 2). The stratified water column is visible at all sites, with lower temperatures and salinities in the upper part of the water column. The shift from colder, polar waters in the upper part of the water column to warmer Atlantic-sourced waters begins at around 125 m, 130 m, 125 m and 75 m for sites 8CTD, 12CTD, 3CTD and 5CTD

respectively (Fig. 2). Whilst the water column is slightly stratified at site 5CTD, the bottom water conditions are colder than the other sites. The AW at site 12CTD is generally warmer ($\sim 2^\circ\text{C}$), compared to $\sim 1.5^\circ\text{C}$ and $\sim 1^\circ\text{C}$ at sites 8CTD and 3CTD, respectively. The salinities are generally higher at sites 8CTD and 12CTD, compared to 3CTD. Similarly, the range in temperatures are similar for sites 8CTD and 12CTD, but lower at site 3CTD.

4.2. Environmental conditions

The environmental parameters that characterise the 23 sites in this study (sea-ice cover, water depth, bottom water temperature, bottom water salinity, bottom water oxygen and TOC) are summarised in Table 2. These are used to ascertain the governing environmental conditions driving the pattern of benthic foraminiferal assemblages across the NEG continental shelf.

Bottom water temperatures, taken from the CTDs at each site, range from -1.07 to 1.72°C . Salinities range from 34 to 35 psu across the shelf; those sites with lower bottom water temperatures are also characterised by lower bottom water salinities. The bottom water oxygen saturation ranges from 78.3% to 88.7%. The water depth ranges from 139 to 568 m across sites. Samples 45, 61, 85, 5H and 129 are all located at water depth shallower than 250 m, which is too shallow to be within the main AW (Fig. 2) that flows through the deeper troughs at depths below ca. 250 m (Schaffer et al., 2017). These sites are also characterised by comparably lower bottom water temperatures and salinities, which suggest that they are within the influence of Polar Water, which is found above the AW, or are influenced by the mixing zone between the AW and PW (Fig. 2) (Schaffer et al., 2017).

September sea-ice cover (2012–2017 average) varies across the shelf, ranging from 18.3% to 81.5%. Generally, the sea-ice cover is lower at sites from the outer and mid parts of the shelf, compared to those situated close to the coastline. The TOC content in surface sediments varies between 0.6% to 1.8% across the shelf.

PCA provides an overview of the variability of the environmental conditions that characterise the NEG continental shelf. Axes 1 and 2 of the PCA explain 58% and 35.3% of the variance, respectively (Fig. 3). Water depth and temperature are positively correlated with each other and have the highest positive loading on Axis 1. September sea-ice cover has the highest loading on Axis 2 and is negatively correlated with Axis 1. TOC has a slight positive loading on Axis one and negative on Axis 2.

Table 2
Environmental variables that characterise the 23 sites in this study.

Site	Core site depth (m)	CTD max depth (m)	Bottom water Temp ($^\circ\text{C}$)	Bottom water Salinity	Surface sediment TOC (%)	Bottom water Oxygen (%) saturation)	Sept sea-ice cover 2012–2017 average (%)
1H	325	316	0.66	34.84	0.88	80.23	49.33
3H	367	350	0.78	34.85	1.12	79.39	52.27
5H	205	210	0.35	34.55	1.13	78.91	57.27
7H	377	360	0.87	34.8	1.79	80.34	52.67
8H	534	568	1.49	34.94	0.76	78.5	64.07
10H	504	484	1.49	34.94	0.96	78.29	50.53
12H	398	346	1.57	34.94	1.02	81.74	23.87
13H	379	397	1.58	34.94	0.78	82.96	18.13
19	315	324	0.69	34.85	0.61	83.69	59.67
36	310	306	0.8	34.86	0.61	83.76	60.47
46	205	199	0.81	34.61	0.45	83.84	70.07
61	162	162	0.34	34.41	0.34	84.79	81.53
62	301	300	1.72	34.86	0.21	85.95	81.53
76	365	344	1.72	34.91	0.13	85.58	81.53
85	156	156	0.27	34.32	0.16	85.93	81.53
105	440	425	1.53	34.92	0.42	84.75	74.4
125	388	381	1.49	34.93	0.44	85.27	46.2
129	139	144	-1.07	33.96	0.25	88.69	46.87
139	354	349	1.56	34.93	0.52	87	22.4
144	494	463	1.42	34.94	0.86	88.27	31.73
171	542	510	1.49	34.94	0.59	85.42	69.13
198	391	385	1.51	34.94	0.59	86.38	80.13
249	310	299	0.99	34.71	0.03	85.33	81.53

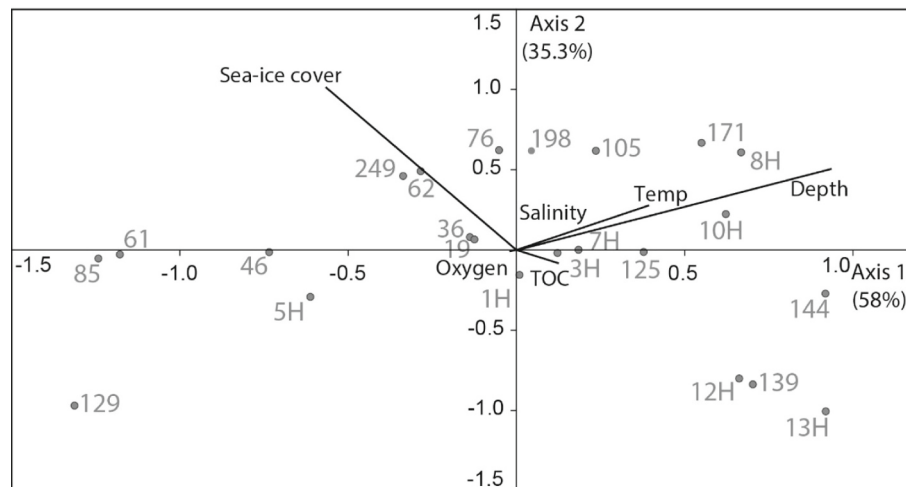


Fig. 3. PCA for environmental variables (black lines) that characterise sites (grey) on the Northeast Greenland continental shelf. The variance explained by each axis is shown in brackets.

Bottom water oxygen has a very low negative loading on both Axis 1 and 2, and salinity has a slight positive loading on Axis 1 and 2.

4.3. Foraminifera

A total of 52 calcareous and 23 agglutinated foraminiferal species (total 75) were identified in our samples (Figs. 10, 11, 12 and 13). A full list of the species identified can be found in the Supplementary Material, including author names and year of original description.

4.3.1. Cluster analysis

Cluster analysis, undertaken on the benthic foraminiferal assemblages for all sites, divides the samples into two faunal zones (FZ) and three subzones (Fig. 4). Subzones were only identified if they encompass at least two sites. A cluster analysis of the benthic foraminiferal species (present in abundances of at least 2% in at least one sample) was also undertaken; this is shown in the Supplementary Material.

4.3.2. Faunal Zone 1

Faunal Zone 1 (FZ1) is made up of sites located on the inner shelf, characterised by extensive sea-ice cover and all located within 100 km of the marine terminating glaciers of the Northeast Greenland Ice Stream (Fig. 1C). However, site 125 is a locational anomaly, being located in the middle section of the Belgica Trough (Fig. 4B).

FZ1 consists of 11 samples, primarily dominated by calcareous species (average 83.5%) and with a high concentration of benthic foraminifera in general (Fig. 5). The calcareous specimens are well-preserved (Fig. 12, e.g. images 1–10). The most common calcareous species across all sites in this zone are *Cassidulina neoteretis* and *Cassidulina reniforme*. Other dominant species are *Stetsonia horvathi*, as well as *G. oculus* and other miliolid species (see methodology), in particular *T. trihedra* and *Quinqueloculina* sp. However, *G. oculus* is noticeably absent or only present in very low abundances at sites 171, 125 and 46. *Nonionella iridea* is abundant in FZ1, present at every site, but lower at sites 249 and 85.

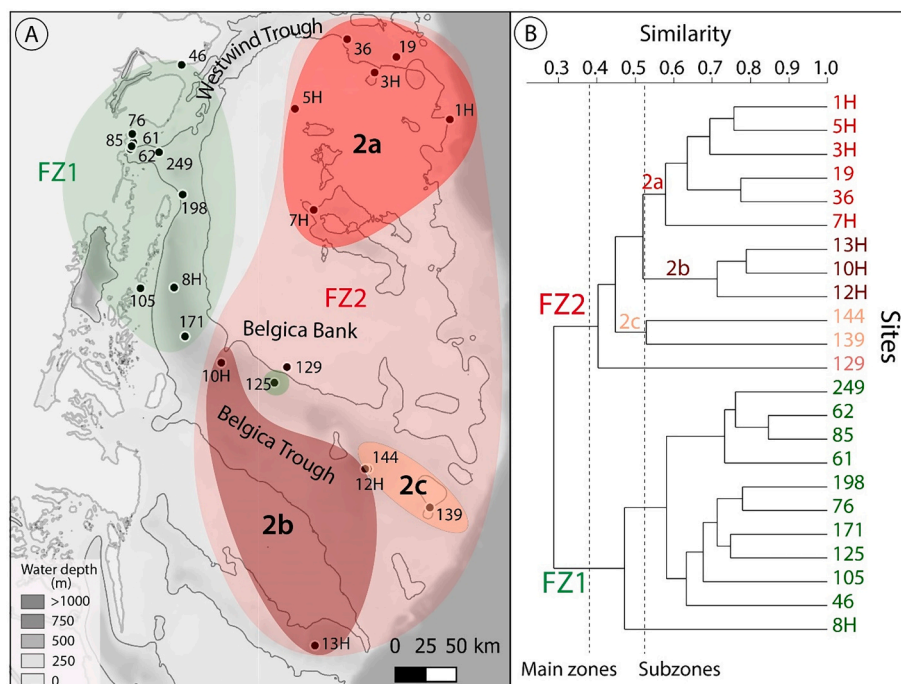


Fig. 4. A) Map showing the main (light-coloured) and sub (dark-coloured) faunal zones from the cluster analysis: FZ1 (green) and FZ2 (red) with subzones 2a, 2b and 2c shown in bold. Indicator species for FZ1 are *G. oculus*, miliolids, *S. horvathi*, *O. tener*, *N. iridea*, *C. reniforme* and *C. neoteretis* and for FZ2 are *P. bipolaris*, *T. torquata*, *A. glomerata*, *C. neoteretis* and *C. reniforme*. The 250 m depth contour line is shown in dark grey. Sites are coloured when there are at least 2 sites in the faunal (sub)zone. B) Cluster analysis based on sites with benthic foraminiferal species present in abundances >2% in at least one sample. The main locational faunal zones (FZ) and subzones are marked and coloured based on clusters and subclusters: FZ1 (red) and FZ2 (green). For the full site name and location see Table 1. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

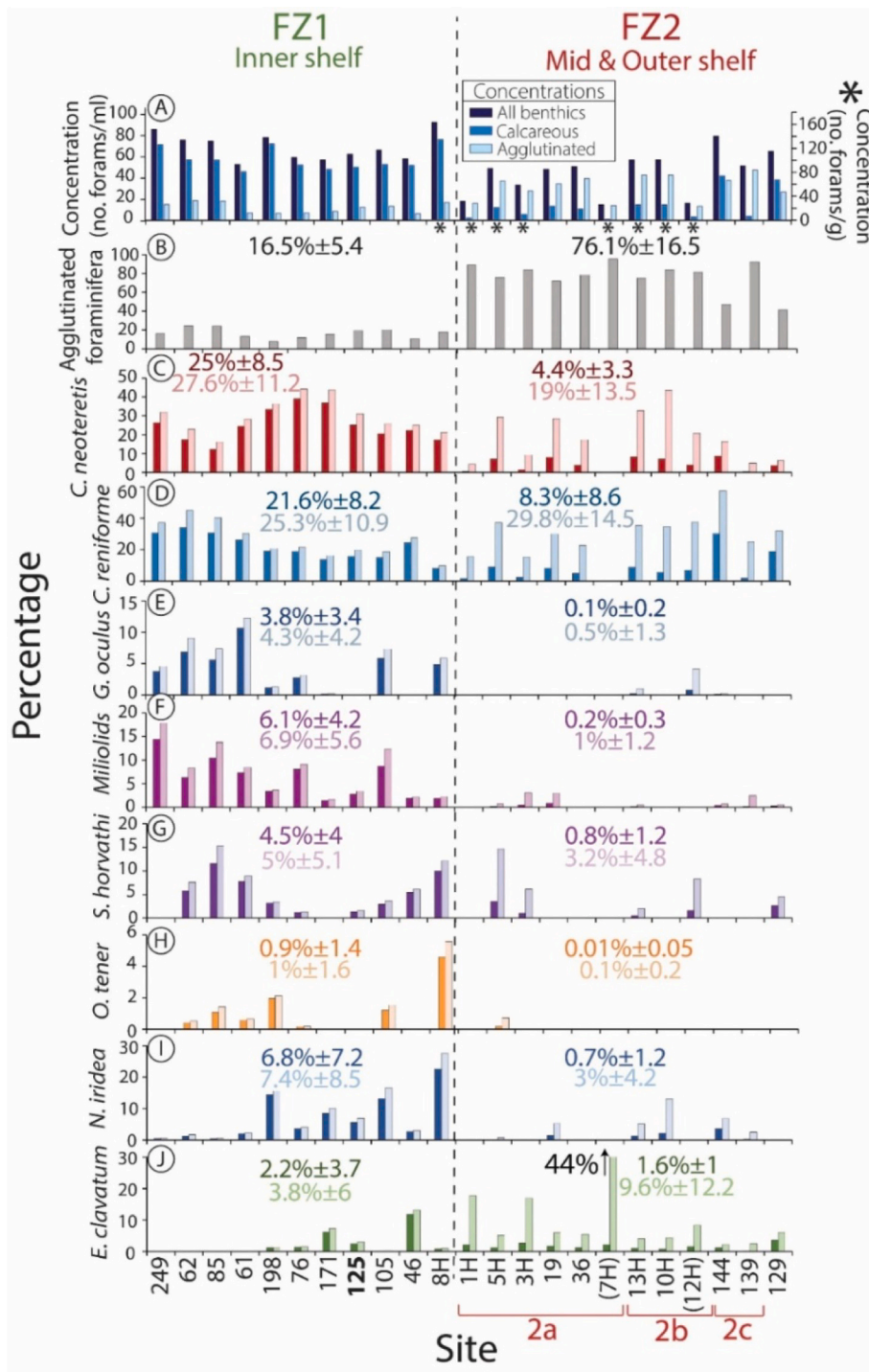


Fig. 5. A) Foraminiferal concentrations as no./gram sediment (DA17 samples; marked with an *) or no./ml of sediment (PS100/109 samples) of the total foraminiferal fauna (both calcareous and agglutinated) (dark blue); calcareous (blue) and agglutinated specimens (light blue). B) The percentage of the agglutinated specimens of the total benthic foraminiferal assemblage. C-J) The relative frequency of key calcareous benthic foraminiferal species as a percentage of the total benthic assemblages in each sample (dark; both calcareous and agglutinated species) and of calcareous species alone (light). The average abundance for each species and zone is shown, together with the standard deviation. Sites with low numbers of calcareous foraminifera (<30 tests) are highlighted between brackets (). The locational anomaly (site 125) is in bold. Subzones are marked at the bottom. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Elphidium clavatum is noticeably absent-to-rare at all sites in FZ1, apart from sites 46, 125 and 171 where it slightly more abundant. *Oridorsalis tener* is present in relatively high abundances at many of the sites in FZ1, however, it is completely absent from sites 46, 125, 171 and 249. It is noticeably present in much higher abundances at site 8H than any of the other sites across the NEG continental shelf (Figs. 3 and 4).

The dominant agglutinated species are *Textularia earlandi*, *Portatocammina bipolaris*, and *Lagenammina difflugiformis* (Fig. 7; 21.8%, 15.8% and 14.5% average abundance of the agglutinated assemblage, respectively). *Textularia torquata* is present in low abundances, at almost all sites in this zone, apart from site 46 where it is slightly more abundant (Figs. 7 and 8).

The Shannon index is a measure of diversity within communities, taking into account the relative abundance of species together with the evenness of their distribution; higher values represent higher diversity. Within FZ1 the Shannon diversity index ranges from 2.3 to 2.5. The species richness, or the number of species present, in FZ1 ranges from 28 to 44 (Fig. 9).

4.3.3. Faunal Zone 2

Faunal zone 2 (FZ2) is made up of sites on the outer and mid parts of the NEG continental shelf, including the Belgica and Westwind troughs. These sites are all located at least 150 km from the coastline, a significant distance from the terminus of marine terminating glaciers. This

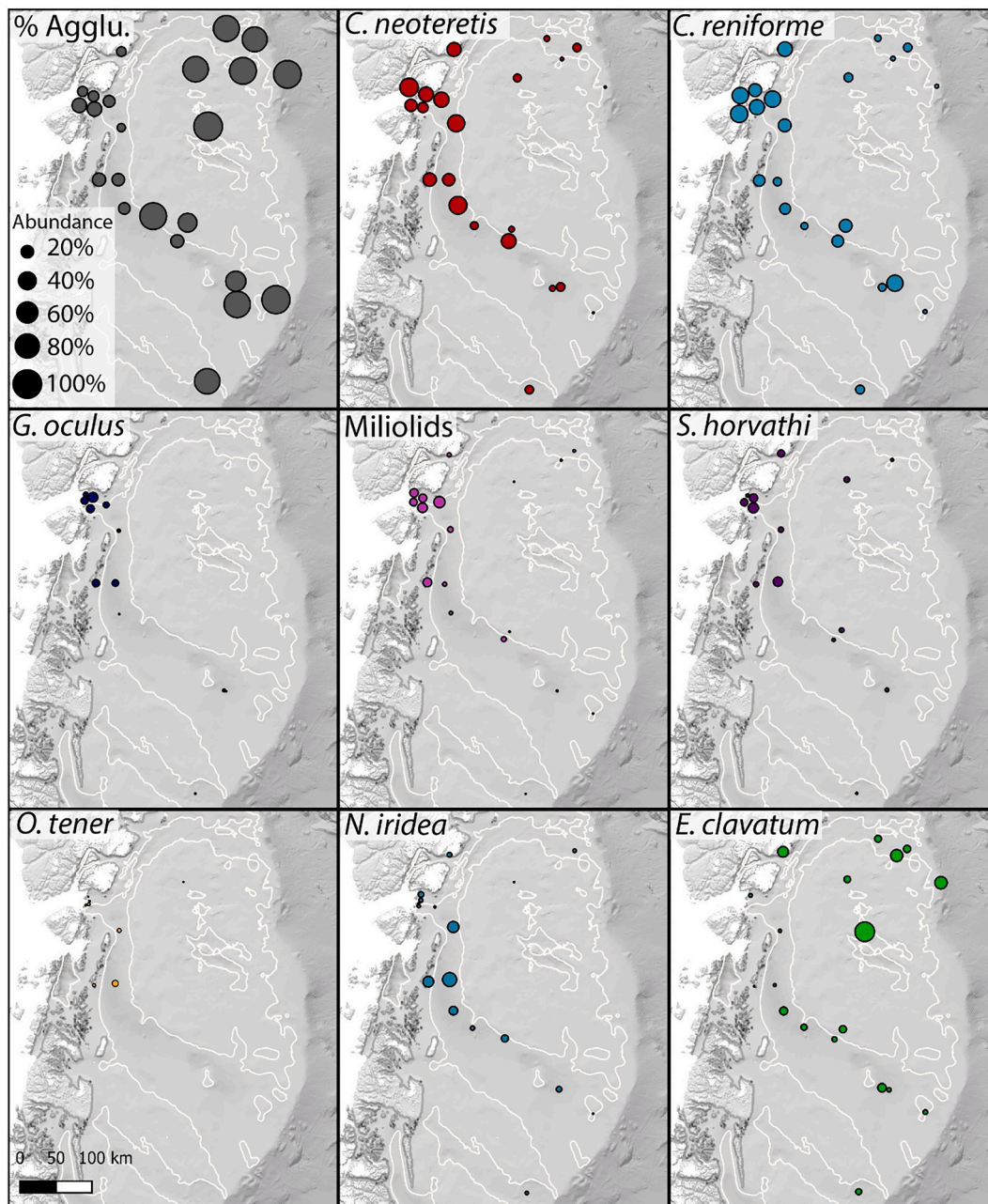


Fig. 6. Map showing the percentages of agglutinated species (grey) and of indicator calcareous benthic foraminiferal species across the Northeast Greenland continental shelf: *C. neoteretis* (red), *C. reniforme* (blue), *G. oculus* (dark blue), other miliolids (pink), *S. horvathi* (purple), *O. tener* (orange), *N. iridea* (blue) and *E. clavatum* (green). Abundances of the calcareous species are calculated as a percentage of the total calcareous species in the assemblage, and the percentage agglutinated species is calculated based on the total benthic assemblage (calcareous and agglutinated species combined). The size of the circle depicts the percentage abundance (see key). The 250 m contour line is shown (white line). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

area is characterised by more seasonal sea-ice and open water, and it spans much of the NEW polynya (Fig. 1C).

FZ2 contains 12 sites and assemblages are dominated by agglutinated species (76.1% on average) (Figs. 5 and 6). The concentration of benthic foraminifera is generally lower than in FZ1, particularly in the calcareous fraction. The calcareous foraminifera in FZ2 were generally not as well preserved as those in FZ1, and subject to visible dissolution (Fig. 12, compare Image 11 and 12). Sites 1H, 7H and 12H have noticeably lower overall concentrations of all benthic foraminiferal species than other sites. These sites are located on the outermost continental shelf (1H,12H) and in the mid-part of the continental shelf (site 7H).

Like FZ1, the calcareous fraction of FZ2 sites is mainly dominated by *C. neoteretis* (4.4%) and *C. reniforme* (8.3%) (Fig. 5 and 6). An exception is site 7H, where these two species are absent. However, the low number of calcareous tests in this sample (<30) makes it difficult for conclusions to be drawn with any certainty. *Elphidium clavatum* (44%) dominates the calcareous fraction at 7H, together with *Melonis barleeanus* (11%) and *Stainforthia concava* (22%). *Elphidium clavatum* is more abundant in the Westwind Trough and inter-trough areas than in the Belgica Trough (Fig. 6). The miliolid species at FZ2 sites, including *G. oculus*, are present in much lower abundances than most of the sites in FZ1. Specifically, *G. oculus* is present only at two sites in FZ2 (sites 13H and 12H). *Oridorsalis tener* is noticeably absent at sites in this zone, apart from a low

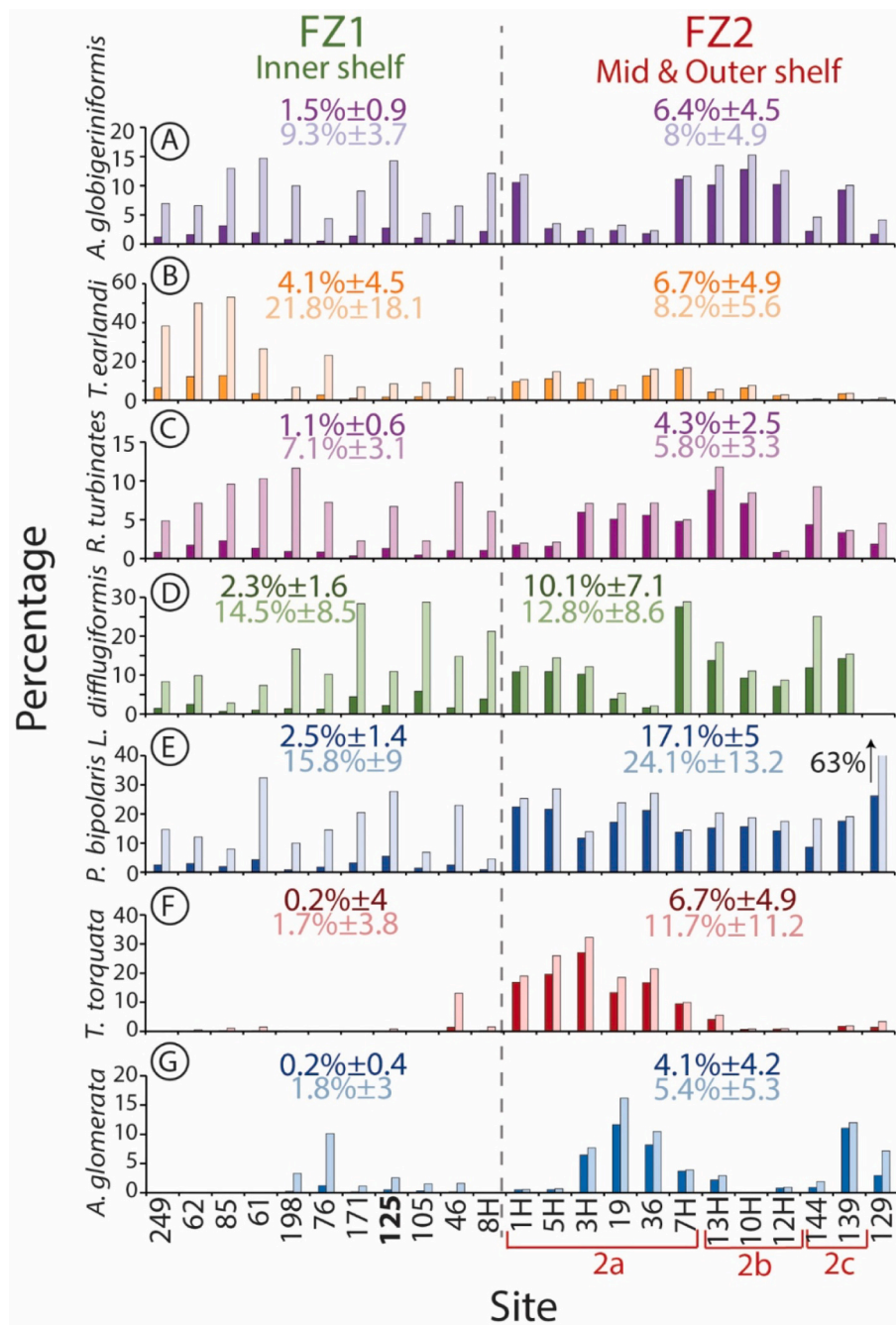


Fig. 7. A-G) Relative frequency of key agglutinated benthic foraminiferal species in the faunal zones, shown as a percentage of total benthic assemblages (dark; both calcareous and agglutinated species) and of agglutinated specimens only (light). The average abundance for each species and zone is shown, together with the standard deviation. The locational anomaly (site 125) is shown in bold. Subzones are marked at the bottom. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

abundance at site 5H. Similarly, *N. iridea* is present at lower abundances and at fewer sites in this zone, when compared to FZ1. This species is also more abundant in the Belgica Trough compared to the Westwind Trough (Fig. 6).

The agglutinated assemblage is diverse and dominated by *Ammonoglobigerina globigeriniformis*, *Adercotryma glomerata*, *L. difflugiformis*, *P. bipolaris*, *Recurviroides turbinatus* and *T. torquata* (Fig. 7 and 8). The two subzones differ slightly in their agglutinated fauna: subzone 2a has higher abundances of *A. glomerata* and *T. torquata* (Fig. 7), these sites are located in the Westwind Trough and the inter-trough area (Fig. 8).

Within FZ2 the Shannon diversity index ranges from 2.2 to 2.7. The species richness in FZ2 ranges from 15 to 34, with the lowest numbers occurring at site 7H (15 species) and 10H (17 species) respectively (Fig. 9).

4.4. Link between environmental variables and benthic foraminiferal assemblages

Axis I and Axis II of the CCA, performed on the benthic foraminiferal species and the six environmental variables, explain 55.7% and 18.6% of the total variation in the benthic foraminiferal data (eigenvalues of 0.41 and 0.12; Fig. 14), respectively. The faunal zones, defined using cluster analysis, are shown in red (FZ2) and green (FZ1). Samples in FZ1 (green) are negatively correlated with CCA Axis I and sites in FZ2 (red) are, in general, positively correlated with CCA Axis I. The exception are sites 144 and 129 which are slightly negatively correlated with Axis I. CCA Axis I is negatively correlated with September sea-ice cover and bottom water oxygen, whilst TOC is positively correlated with Axis I (i.e. FZ2). Axis II is positively correlated with water depth and bottom water temperature and salinity. Broadly, sites in subzone 2a (red) are

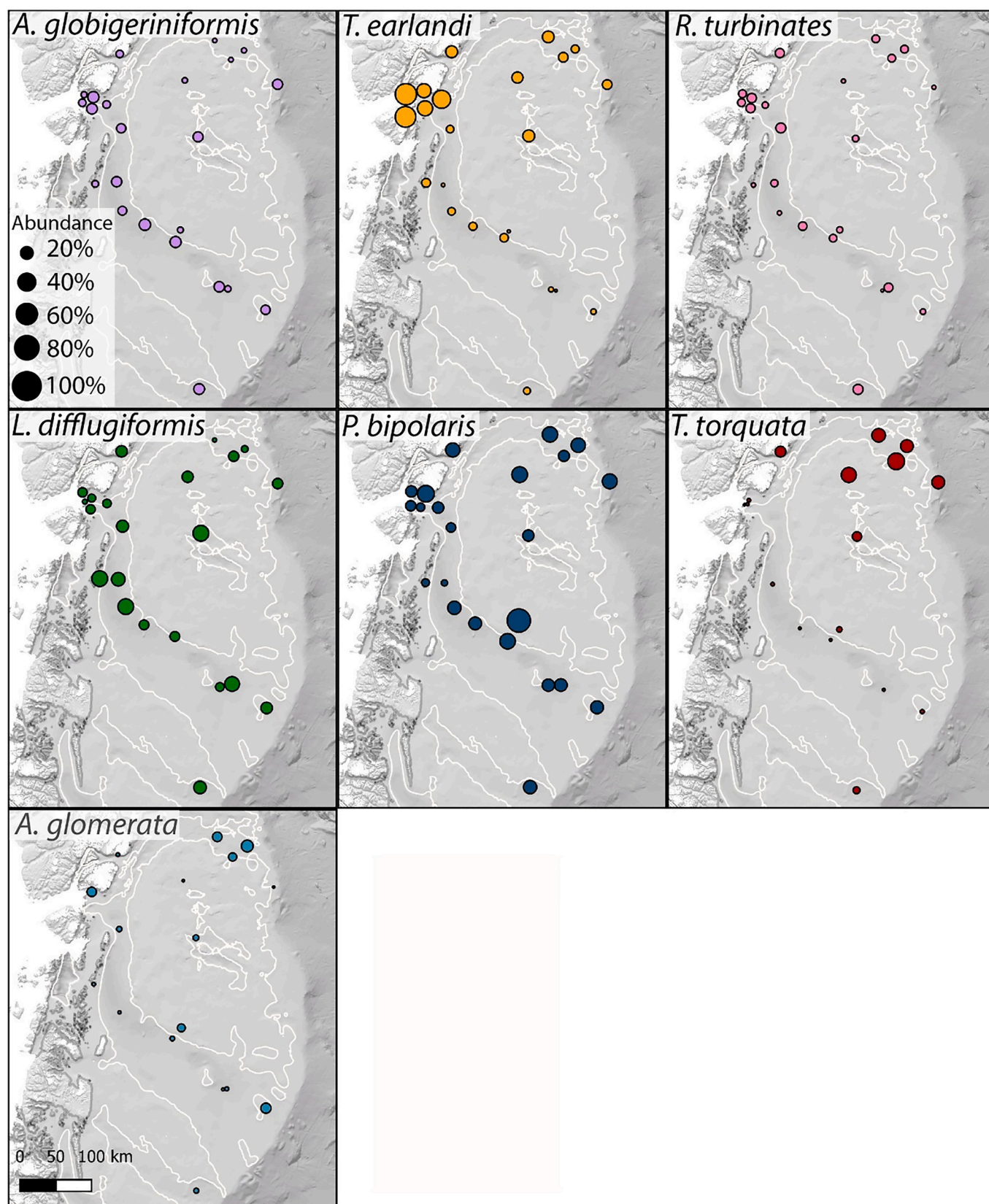


Fig. 8. Map showing the percentages of indicator agglutinated benthic foraminiferal species across the Northeast Greenland continental shelf: *A. globigeriniformis* (light purple), *T. earlandi* (orange), *R. turbinates* (pink), *L. difflugiformis* (green), *P. bipolaris* (dark blue), *T. torquata* (red), *A. glomerata* (light blue). Abundances of the agglutinated species are calculated as a percentage of the total agglutinated species in the assemblage. The size of the circle depicts the percentage abundance (see key). The 250 m contour line is shown (white line). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

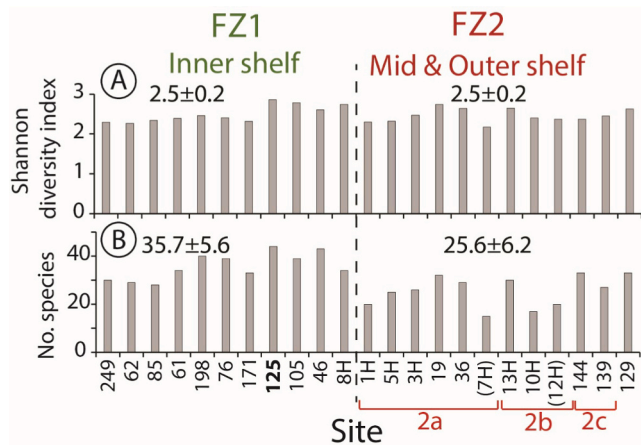


Fig. 9. Histograms showing measures of diversity. A) The Shannon diversity index and B) the number of species in each sample. The average value is shown for each faunal zone, together with the standard deviation. The locational anomaly (site 125) is shown in bold. Subzones are marked at the bottom. Sites with low numbers of calcareous foraminifera (<30 tests) are highlighted between brackets ().

negatively associated with Axis II and sites in subzone 2b and 2c (light red and dark red) are positively associated. The CCA indicates that, in general, agglutinated species have positive loadings along Axis I and calcareous species have negative loadings.

5. Discussion

5.1. Calcareous/agglutinated foraminifera ratio

The ratio between agglutinated and calcareous species in this study represents a major difference between the inner shelf sites (FZ1) and those on the mid and outer shelf (FZ2). Across the NEG continental shelf, the percentage of agglutinated foraminifera varies from 8% to 95%. The lowest values are found on the inner shelf in FZ1 (average 16.5%), and much higher values characterise FZ2 (76.1% in average), in the mid and outer shelf region. This difference is not only controlled by variations in calcareous foraminiferal concentrations, as the concentrations of agglutinated foraminifera in the sediment samples in FZ2 are significantly higher than in FZ1. Furthermore, many of the calcareous specimens present in FZ2 are poorly preserved, suggesting harsh and acidic conditions in this region (Fig. 12, images 11 vs 12). There are key differences in the environmental variables between these FZs, specifically sea-ice cover, TOC and bottom water characteristics, suggesting that these may be controlling the agglutinated/calcareous ratios of benthic foraminifera.

A faunal assemblage dominated by agglutinated species is indicative of harsh environmental conditions, in which agglutinated species are more adaptable than calcareous species, or of acidic conditions, where calcareous tests are dissolved or poorly preserved (Murray and Alve, 1999; Steinsund and Hald, 1994). Previously, the percentage of agglutinated species has been linked to cold, corrosive bottom water (Aksu, 1983; Jennings and Helgadottir, 1994), changing sedimentation rates (Korsun and Hald, 1998; Lloyd et al., 2007; Loubere and Gary, 1990), oxygen-depleted environments (Jennings and Helgadottir, 1994), high organic material content and productivity (Alve, 1990; Walter and Burton, 1990), and sea-ice formation which reduces bottom water ventilation and can cause brine formation which results in corrosive conditions (Aksu, 1983; Lloyd et al., 2007; Rasmussen and Thomsen, 2014; Seidenkrantz et al., 2007; Seidenkrantz, 2013).

Preliminary ^{210}Pb data from seven short Rumohr cores across the NEG continental shelf indicate that there is no consistent pattern in sedimentation rates across the continental shelf (unpublished data).

Thus we argue that one or more of the other aforementioned reasons is driving the distribution of agglutinated and calcareous benthic foraminiferal assemblages in NEG.

5.1.1. Sea-ice cover and polynya activity

When sea-ice forms, salt is ejected into the surrounding surface waters, creating large amounts of dense water, leading to strongly stratified bottom water masses, reduced ventilation and a corrosive environment (Haarpaintner et al., 2001; Schauer, 1995; Seidenkrantz et al., 2007; Weeks and Ackley, 1986). Another characteristic of areas influenced by sea-ice formation is high primary productivity and export of organic material (Schewe and Soltwedel, 2003; Vancoppenolle et al., 2013). The decay of this organic matter produces CO_2 and can lead to acidic conditions and thus the dissolution of calcareous foraminifera (de Vernal et al., 1992, 2020; Jennings and Helgadottir, 1994; Steinsund and Hald, 1994), visible in the poorly preserved specimens at many of these sites (e.g., Fig. 12, images 11 vs 12).

Sites in FZ2 are characterised by less extensive September sea-ice cover, higher TOC and lower bottom water oxygen content than FZ1, and in the CCA these three variables correlate negatively (sea-ice and oxygen) and positively (TOC) with the foraminiferal assemblage of FZ2 respectively (Fig. 14). This suggests that the formation of seasonal sea-ice, which creates a highly productive and corrosive environment, may be driving the dissolution of calcareous tests, and thus the dominance of agglutinated taxa in the assemblages at sites in this zone (Fig. 15). This is consistent with the calcareous tests found in FZ2, which often have visible signs of dissolution when compared to those in FZ1, which are well preserved (Fig. 12).

This argument is supported by studies of benthic foraminifera in other areas of the Arctic. Analysis of modern faunas from Svalbard and the Barents Sea indicate that carbonate dissolution can be caused by the presence of CO_2 -rich brine waters and high organic carbon content in the sediment and bottom waters (Hald and Steinsund, 1992; Steinsund and Hald, 1994; Wollenburg and Kuhnt, 2000). In Mikis Fjord, East Greenland, it is argued that seasonal sea-ice breakup is a key process governing the dominance of agglutinated fauna in samples there (Jennings and Helgadottir, 1994). Moreover, a study of modern foraminiferal assemblages in Storfjorden, Svalbard, found a strong dominance of calcareous species at inner fjord stations, with agglutinated species dominating in deep basin and sill stations; the ratio of agglutinated to calcareous species was used as a proxy of sea-ice cover in this instance (Fossile et al., 2020; Nardelli et al., 2022).

Many sites in FZ2 (Subzone 2a: sites 36, 19, 1H, 5H, 7H) are located within, or in close proximity to, the NEW polynya (Fig. 1C), a key feature located to the north of the continental shelf. Similar to areas characterised by seasonal sea-ice formation, polynyas are regions with high brine production, dense water formation (Alve, 1990; Arrigo et al., 2008), and high primary productivity which creates a lower-oxygen environment. Consequently, a faunal assemblage dominated by agglutinated species can be indicative of polynya activity. The high abundance of agglutinated species has been used to infer polynya stability in Svalbard fjords (Rasmussen and Thomsen, 2014) and on the inner NEG shelf (Jackson et al., 2022). Thus, findings from FZ2 support previous suggestions that the calcareous vs. agglutinated benthic foraminiferal ratio can act as a proxy for seasonal sea-ice and polynya activity if other contextual factors are taken into account.

In contrast, NEG sites located on the inner shelf (FZ1) are characterised by a fauna primarily dominated by well-preserved calcareous species (Fig. 12, images 1–10). In this region, the environment is characterised by higher September sea-ice cover, lower TOC concentrations in the sediment and higher bottom water oxygen content. This environment, of near-perennial sea-ice cover and generally strong stratification between the Polar Water at the surface and Atlantic-source subsurface water, results in a limited food supply, high bottom-water salinity, and limits ocean/atm exchange of CO_2 , creating an environment which favours the preservation of calcareous tests (de Vernal et al.,



Fig. 10. Micrographs of the key calcareous species from DA17 samples, the sites are listed next to each species in brackets. 1. *Cassidulina neoteretis* (13H) 2. *Oridorsalis tener* at umbilical (2a) and dorsal (2b) view (8H) 3. *Islandiella norcrossi* (8R), 4. *Cassidulina reniforme* (12H), 5. *Nonionella iridea* (8R) 6. *Nonionellina labradorica* (3H), 7. *Elphidium clavatum* (3R), 8. *Stainforthia concava* (8R), 9. *Elphidium albumbilicatum* (8R), 10. *Cibicides lobatulus*, umbilical (10a) and dorsal (10b) (8R), 11. *Stainforthia feylingi* (12R), 12. *Parafissurina lateralis* (90R), 13. *Buccella frigida*, umbilical (13a) and dorsal (13b) view (12R), 14. *Stetsonia horvathi* (8R), 15. *Astrononion gallowayi* (8R), 16. *Pullenia osloensis*, 17. *Cornispira distincta* (8R), 18. *Glomulina oculus* (8H), 19. *Fissurina* sp. (7R) 20. *Triloculina trihedra* (8R), 21. *Quinqueloculina seminula* (8R), 22. *Melonis barleeanus* (1H).

1992; Schroder-Adams et al., 1990; Fig. 15). Similar patterns have been found elsewhere; on the Axel-Heiberg shelf and Petermann Fjord, calcareous foraminifera dominated at sites under perennial sea-ice (Jennings et al., 2020b; Schroder-Adams et al., 1990), and such inferences have been made for paleo-reconstructions in Baffin Bay (Scott et al., 1989) and the Davis Strait (de Vernal et al., 1992).

The clear pattern of higher abundances of agglutinated foraminifera on the mid and outer shelf (FZ2) in our study supports the use of calcareous vs benthic foraminiferal ratios for reconstructing sea-ice production and polynya activity. However, this is reliant on a multiproxy approach and careful consideration of the environmental

context and regional differences.

5.2. Distribution of key benthic foraminifera species

Whilst the main difference between FZ1 and FZ2 is the ratio and concentration of agglutinated and calcareous foraminifera, the distribution of many benthic foraminiferal species also differs between these zones; these are termed indicator species (listed in the Supplementary Material). The environmental preferences of these indicator species are discussed in more detail in the next section and summarised in Table 3.



Fig. 11. Examples of key agglutinated species from DA17 samples, the sites are listed next to each species in brackets. 1. *Recurvoides turbinatus* (12H), 2. *Lagammina difflugiformis* (3H), 3. *Hormosinella guttifera* (12H), 4. *Trochammina pseudoinflata*, umbilical (4a) and dorsal (4b) view, (8R) 5. *Cribrostomoides subglobosus* (12H), 6. *Adercotryma glomerata* (3R), 7. *Textularia earlandi* (5H), 8. *Ammoglobigerina globigeriniformis*, dorsal (8a) and umbilical (8b) (5H), 9. *Portatrochammina bipolaris*, umbilical (9a) and dorsal (9b) (5H), 10. *Textularia torquata* (5H).

5.2.1. Faunal zone 1 (FZ1): Inner shelf

Faunal assemblages in FZ1 are primarily located in the inner shelf region. This environment is primarily positively correlated with September sea-ice cover and bottom water oxygen content. An overview of key foraminiferal species and their environmental preferences in NEG, and elsewhere, are summarised in Table 3.

FZ1 has the highest overall concentration of benthic foraminiferal species, generally characterised by higher concentrations of calcareous foraminifera than FZ2. Whilst this is likely attributed, in part, to the poor preservation of calcareous foraminifera in FZ2, the overall higher concentrations of benthic foraminifera still imply an environmental preference of these species in glacial proximal environments. The species richness of FZ1, or number of species present, is higher than in FZ2. However, the Shannon diversity index, which accounts for relative

abundance of each species as well as the evenness of their distribution, has the same value for FZ1 and FZ2. However, it must be noted that the calcareous foraminifera have most likely been subjected to dissolution. This means that the diversity calculations may not capture the true diversity value, particularly in FZ2.

Cassidulina neoteretis (average 25%) and *C. reniforme* (average 8.3%) are the most dominant species at sites in FZ1, suggesting that they thrive in the environment off NEG. Elsewhere, *C. neoteretis* has been linked to AW stratified beneath cold and fresh waters (Cage et al., 2021; Jennings and Helgadottir, 1994; Seidenkrantz, 1995; Wollenburg et al., 2004; Jennings et al., 2020a, 2020b), while *C. reniforme* is most commonly linked to Polar Water (Hald and Korsun, 1997; Polyak et al., 2002), although it has also been suggested as an indicator of chilled Atlantic Water (Ślubowska-Woldengen et al., 2007). In NEG, the link between

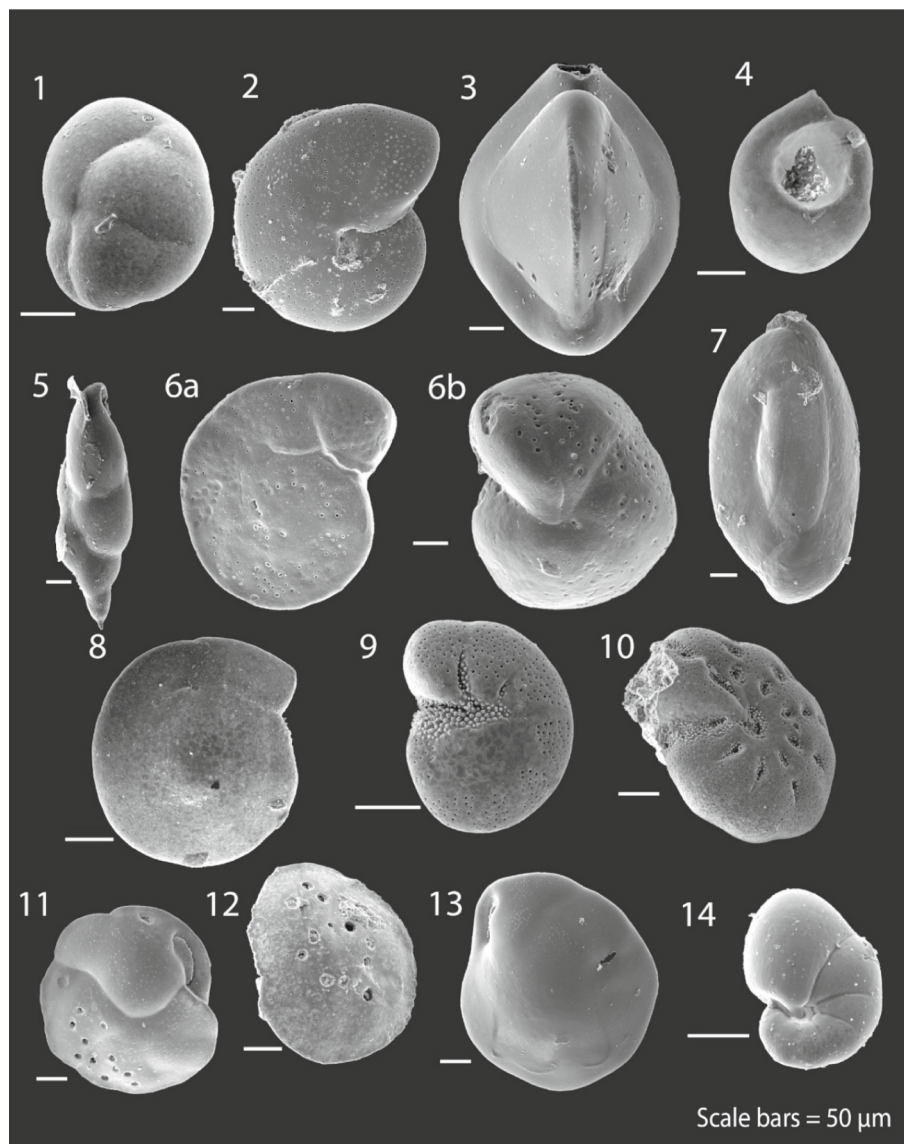


Fig. 12. SEM images of key calcareous benthic foraminifera species: 1. *Cassidulina reniforme* (8H), 2. *Melonis barleeanus* (8H), 3. *Triloculina trihedra* (8H), 4. *Glomulina oculus* (8H), 5. *Stainforthia concava* (8H), 6. *Cibicides lobatulus* umbilical (6a) and dorsal (6b) (7H), 7. *Quinqueloculina seminula* (8H), 8. *Oridorsalis tener* (8H), 9 & 10, *Elphidium clavatum* (8H), 11. *Cassidulina neoteretis* (8H), likely subject to predation, 12. *Cassidulina neoteretis* (10H) (poor preservation example), 13. *Islandiella norcrossi* (8H), 14. *Nonionella iridea* (8H).

these species and bottom water masses is less clear.

Most sites dominated by *C. neoteretis* are swept by warm and saline bottom waters. However, sites 46, 61 and 85 are characterised by colder ($<1^{\circ}\text{C}$) and lower salinity (<34.5) bottom water, yet the assemblage is dominated by *C. neoteretis*. At other sites, *C. neoteretis* is absent despite relatively high bottom-water temperatures, however, these latter sites are also characterised by overall low concentrations of calcareous foraminifera and dissolution may play a role here. Similarly, sites (171, 125, 249, 62, 198, 105, 76, 8H) with warmer ($>1^{\circ}\text{C}$) and higher salinity (>34.5) bottom water masses have high abundances of *C. reniforme*. Still, *C. reniforme* shows roughly an opposite pattern to *C. neoteretis* within FZ1, suggesting that it is more common at the cooler sites. However, due to the low number of sites that are clearly dominated by Polar Water at the sea floor to test the potential presence of *C. neoteretis* vs. *C. reniforme* in Polar vs. Atlantic waters, these conclusions remain uncertain. Moreover, in a direct comparison between percentage of *C. neoteretis* and temperature there appears to be no clear link between the strength and temperature of the warmer water masses, and the abundance of *C. neoteretis* (Supplementary Material Fig. 5). Thus, we conclude that environmental conditions, other than temperature and salinity, are also impacting the abundance of these species in this region. Further investigation that includes more sites dominated by Polar

bottom water masses is required.

Sites located within 60 km of the glacial termini (249, 62, 85, 61, 198, 105, 8H and 76) and with more extensive sea-ice cover (Fig. 1C), are characterised by the presence of *G. oculus*, which is notably absent or present in low numbers at sites located 100 km from the terminus of glaciers (46, 125, 171) and FZ2 (outer and mid shelf location). This distribution supports the previous suggestion by Jennings et al. (2020a) that *G. oculus* has a preference for very proximal glacier conditions and furthermore it seems to have an affinity to extensive sea-ice cover.

FZ1 is generally characterised by the presence of *S. horvathi*; suggesting a preference for environments characterised by more extensive sea-ice cover, high bottom water oxygen and low primary productivity. This supports previous investigations finding *S. horvathi* associated with colder surface waters and more extensive sea-ice cover (Jennings et al., 2020b; Jennings et al., 2004; Polyak et al., 2002; Wollenburg and Kuhnt, 2000). Furthermore, it has been found to have low trophic requirements, surviving with limited fresh food export to the sea floor (Jennings et al., 2020b; Wollenburg and Kuhnt, 2000; Wollenburg and Mackensen, 1998). In fact, its distribution is suggested to be mainly related to the lowest phytodetritus accumulation values (Wollenburg and Mackensen, 1998). This supports our observation that it is abundant at sites beneath perennial sea-ice with low primary productivity (low TOC) and high

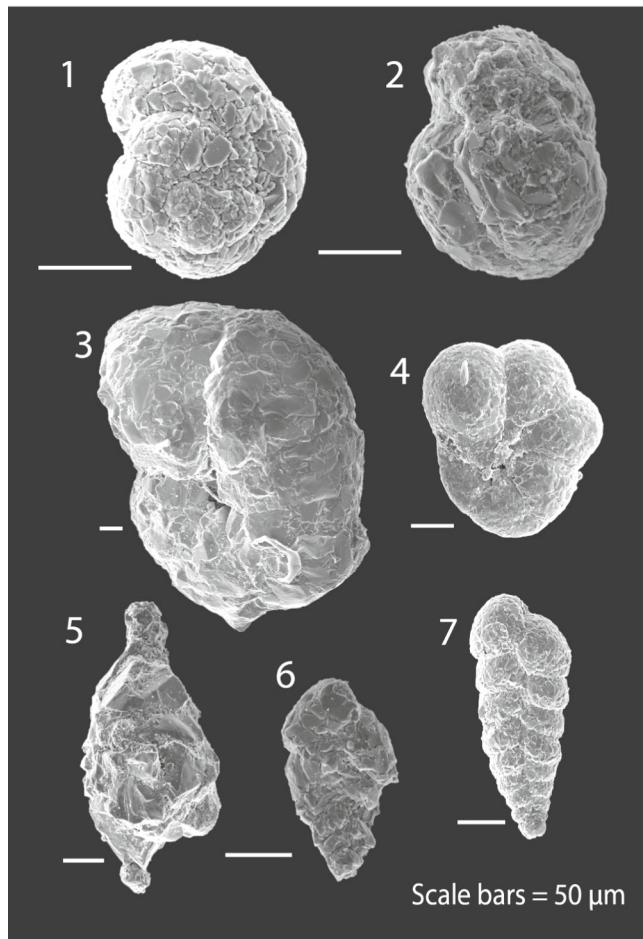


Fig. 13. SEM images of key agglutinated benthic foraminifera species: 1. *Ammoglobigerina globigeriniformis* (8H), 2. *Adercotryma glomerata* (3H), 3. *Cribrostomoides subglobosus* (12H), 4. *Portatrochammina bipolaris* (8H), 5. *Lagenammina difflugiformis* (3H), 6. *Textularia torquata* (3H), 7. *Textularia earlandi* (5H).

bottom water oxygen. However, it is also present at some more distal sites in FZ2 with higher sediment TOC content; thus, it cannot be used exclusively to infer a proximal glacial environment with low primary productivity.

Oridorsalis tener is abundant at many sites in FZ1, which are characterised by extensive sea-ice cover, relative proximity to glaciers, and low TOC content, suggesting tolerance for relatively unproductive environments. Previous studies from the continental slope of Southwest Norway, found *O. tener* living in low TOC environments (Mackensen et al., 1985). In the Arctic Ocean, this species was also dominant at sites from the perennially sea-ice covered Lomonosov Ridge, again characterised as a species adapted to oligotrophic conditions (Husum et al., 2015). This suggests that it can be used as an indicator of low-productivity environments, associated with more extensive sea-ice cover.

The small species *N. iridea* (here *N. iridea* and *N. fragilis* are combined) is also found in relatively high numbers at most sites within this faunal zone. Again, this suggests that it can survive in environments with low organic matter input, as it is negatively correlated with TOC and positively correlated with bottom water oxygen content in the CCA. However, within FZ1 it is more abundant at those sites slightly further away from the glacier margin (8H, 105, 198, 171, 125) and located in the Belgica Trough, which is characterised by stronger Atlantic Water than the Westwind Trough (Schaffer et al., 2017). It must be noted that its small size makes it susceptible to advection by currents, so it may not

always be representative of the sites at which it is found (Jennings et al., 2020b). Elsewhere, it has been described as being an opportunistic species that responds to phytodetritus input (Duffield et al., 2015; Gooday and Hughes, 2002), contrary to our own findings in NEG. However, it is also suggested that it can survive in periods with low food input. In Petermann Fjord, it was found beneath the ice tongue, however no living specimens were found in this environment, suggesting entrainment or advection to the site locations (Jennings et al., 2020b).

When examining the agglutinated fraction of the assemblage, *T. earlandi* is present at all sites in FZ1. This could suggest that this species may have an affinity for environments with extensive sea-ice cover and low primary productivity, however it is also present at all sites in the mid and outer shelf environments so cannot be used as an exclusive indicator for sea-ice or ice-proximal conditions in this region. In Disko Bay it was found to prefer clay and silt rich environments and its abundance is primarily driven by substrates rather than water mass characteristics (Lloyd, 2006). These fine-grained sediments are characteristic of glacial plumes (Hald and Korsun, 1997; Jennings et al., 2020b).

5.2.2. Faunal Zone (FZ2): The mid and outer shelf

FZ2 sites are primarily located in the mid and outer region of the NEG continental shelf, spanning both the Belgica and Westwind troughs as well as the inter-trough area of Belgica Bank (Fig. 3B). The CCA identifies TOC as a key driver, and shows that the benthic foraminiferal data is negatively correlated to September sea-ice cover (Fig. 14).

As with FZ1, FZ2 is dominated by *C. neoteretis* and *C. reniforme*, indicating these are the dominant species of the calcareous assemblage across the NEG continental shelf (see detailed discussion above). *Cassidulina neoteretis* is absent from 7H, despite the CTD data showing the presence of AW at depth. However, at this site the abundance of calcareous species is low in general, with dissolution likely resulting in an unrepresentative calcareous fauna. Again, this implies that other factors, apart from the water masses, are driving the abundance of these species in this region.

Elphidium clavatum is present at all sites in FZ2. Whilst it is present at some sites in FZ1, it is noticeably absent or present in very low numbers at those sites closest to the glacier margins (<60 km) under more extensive sea-ice. This suggests that it does not thrive in areas covered by perennial sea-ice. As these sites are characterised by a high TOC content and low bottom water oxygen content, it suggests that this species may have a preference for highly productive environments, such as polynyas or seasonal sea-ice. In the same region, samples collected in 1993 show that this species dominates polynya proximal locations (Ahrens et al., 1997), supporting our interpretation of this species' environmental preference in NEG. Elsewhere in the Arctic, this species has been described as opportunistic (e.g. Hald et al., 1994; Osterman, 1984) and has been used to infer an unstable glaciomarine environment, characterised by reduced or varying salinity, cool temperatures and high turbidity (Hald and Korsun, 1997), often occurring in high abundances with *C. reniforme* (Hald et al., 1994). Previous observations indicate that this species does not live beneath perennial sea-ice (Jennings et al., 2020b; Vilks, 1980), supporting our findings from NEG.

Of the agglutinated species, *T. torquata* and *A. glomerata* are noticeably more abundant in FZ2, particularly in subzone 2a, located in the inter-trough area (Belgica Bank) and Westwind Trough. This indicates that these species may have a preference for more productive environments, characteristic of polynyas and seasonal sea-ice. *T. torquata*, in particular, is abundant at sites located in close proximity to the NEW polynya (subzone 2a). In previous studies from the Arctic, *A. glomerata* has been associated with Atlantic-sourced waters (Hald and Korsun, 1997; Lloyd, 2006), and glaciomarine environments more generally (Jennings and Helgadottir, 1994; Madsen and Knudsen, 1994; Schaffer and Cole, 1986). It has been suggested that food availability determines the distribution of *T. torquata* (Wollenburg and Kuhnt, 2000), supporting our interpretation that it is linked to primary productivity and

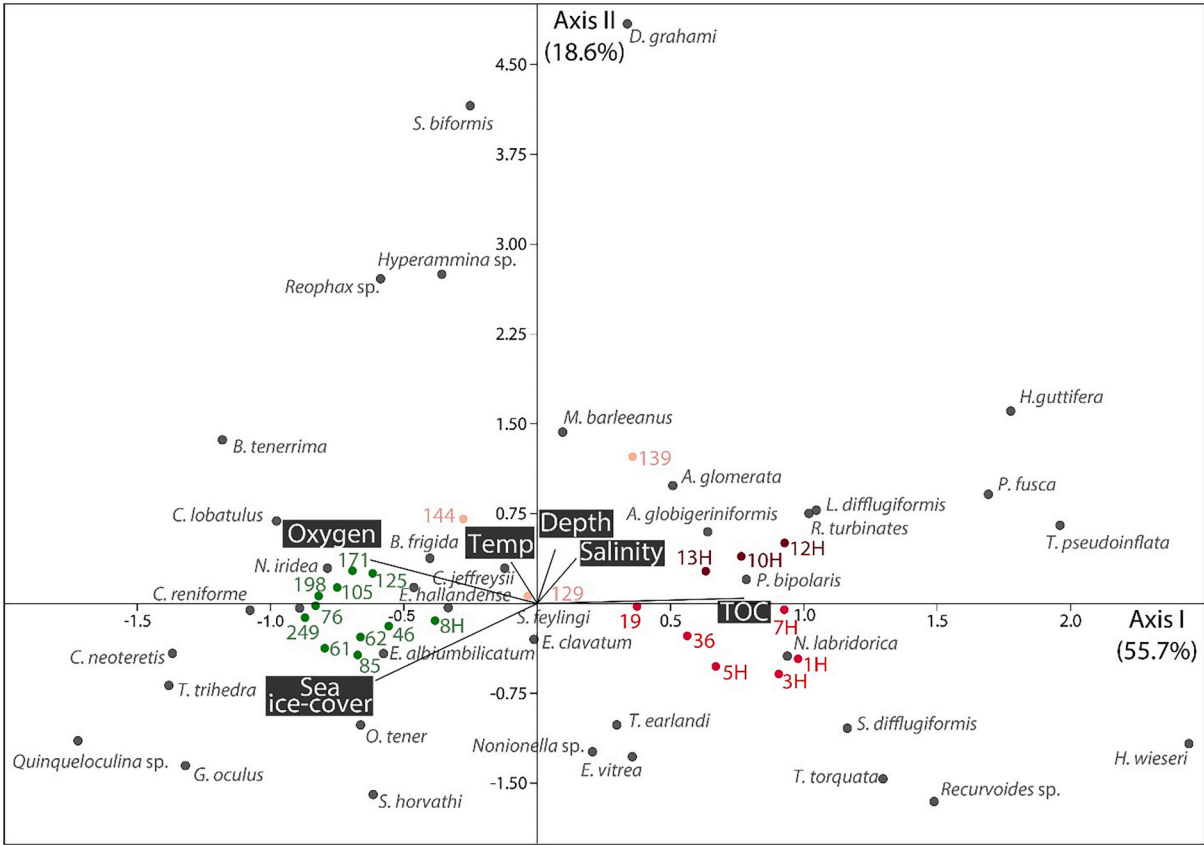


Fig. 14. CCA of foraminiferal species (>2% in at least one sample) and six environmental variables. The length of lines (black) represents the importance of each variable. Samples are colour coded depending on their faunal zones and subzones: FZ1 (green) and FZ2 (red). Subzones 2a (red), 2b (dark red), and 2c (light red) are also shown. Benthic foraminifera species are shown in grey. The variance explained by Axis I and II is shown in brackets. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

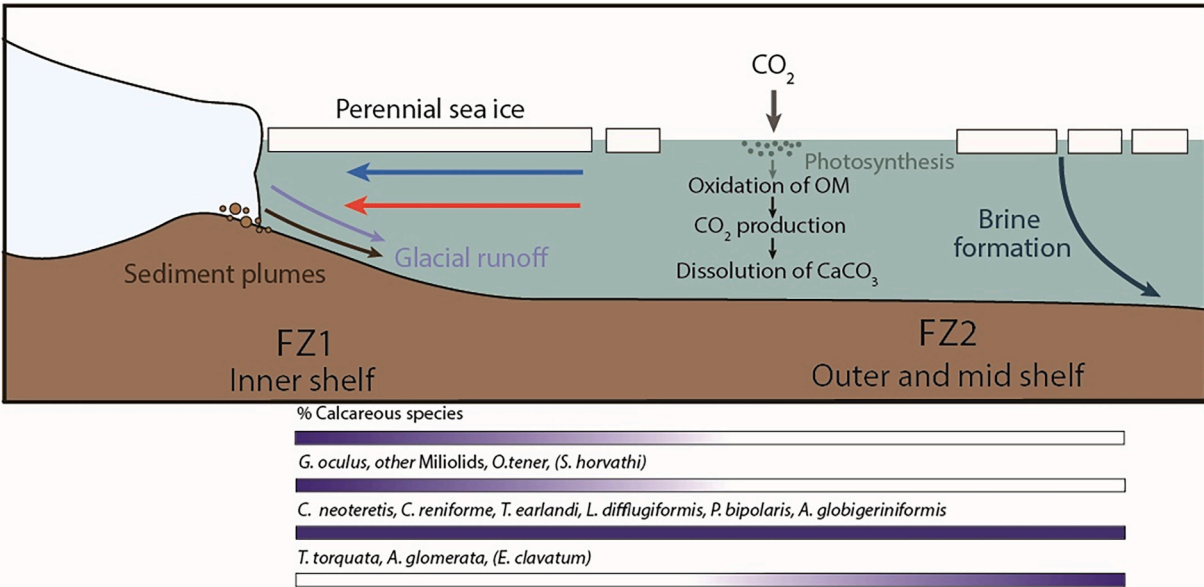


Fig. 15. Schematic of the processes that characterise the inner shelf and mid and outer shelf with seasonal sea-ice/polynya. Indicator species are shown in the lower panel, coloured according to abundance from high abundances (dark blue) to low abundances (white). Species that do not show a definitive pattern are shown in brackets. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 3

Ecology of key foraminifera species. New data from NE Greenland compared to literature information from the Arctic region.

Species	Environmental preference in Northeast Greenland (this study)	Environmental preference in the Arctic and elsewhere
<i>Cassidulina neoteretis</i> Seidenkrantz, 1995	Dominant species at almost all sites across the shelf, suggesting it is an indicator species in NEG. There is no clear link between this species and the strength of the influx (temperature) of Atlantic Waters across the NEG continental shelf.	Used to infer the presence of stable stratification of chilled Atlantic Water beneath cold Polar Waters (Cage et al., 2021; Jennings and Helgadottir, 1994; Seidenkrantz, 1995; Jennings et al., 2020b; Wollenburg et al., 2004).
<i>Cassidulina reniforme</i> Nørvang, 1945	Dominant species at almost all sites across the shelf, suggesting it is an indicator in NEG. However, there is no clear link between this species and the strength of the influx of Polar Water across the shelf.	Used to infer the presence of low saline, Polar Water (Hald and Korsun, 1997; Jennings et al., 2020b; Polyak et al., 2002), but has also sometimes been used as an indicator of chilled Atlantic Water (Ślubowska-Woldengen et al., 2007).
<i>Oridorsalis tener</i> (Brady, 1884)	Present at some inner shelf sites, and notably absent from all but one outer and mid shelf sites. This suggests it can tolerate proximal glaciomarine conditions with oligotrophic conditions and extensive sea-ice cover.	Found to tolerate environments with a lower food supply, characteristic of more extensive sea-ice cover (Husum et al., 2015; Mackensen et al., 1985).
<i>Stetsonia horvathi</i> Green, 1959	Present across the shelf, but most dominant at sites located on the inner shelf, suggesting it is a glaciomarine indicator, that can also tolerate extensive sea-ice cover and a limited supply of food. However, its presence at some mid and outer shelf sites indicates other factors may be controlling its abundance in NEG. These do not appear to be related to polynya activity in this instance.	This species has been linked to perennial sea-ice cover, with colder surface waters, and used as a glaciomarine indicator. It has low trophic requirements and can survive with limited food supply (Jennings et al., 2004, 2020b; Polyak et al., 2002; Wollenburg and Kuhnt, 2000; Wollenburg and Mackensen, 1998).
<i>Nonionella iridea</i> Heron-Allen & Earland, 1932	Found in higher abundances on the inner shelf at proximal glacier sites with more extensive sea-ice cover, suggesting an affinity to this environment. Can survive in environments with a low input of organic matter.	In the NE Atlantic this species has been defined as an opportunistic species, linked to input of phytodetritus (Gooday and Hughes, 2002), and shown in laboratory experiments to feed on degrading organic matter (Duffield et al., 2015). However, it has also been suggested that it can survive in periods of low food supply, but dominates when phytodetritus input increases (Duchemin et al., 2005). In the Petermann Fjord, this species was widespread, present in higher numbers beneath the ice tongue. However, no living specimens were found in this environment, suggesting its small size makes it susceptible to advection (Jennings et al., 2020b).
<i>Elphidium clavatum</i> Cushman, 1930	Relatively abundant across the shelf, but more so in mid and outer shelf sites. It is noticeably absent, or present in low numbers, in sites proximal to marine terminating glaciers, with more extensive sea-ice cover.	Has been used to infer unstable, glaciomarine environments which are characterised by reduced salinities, cool temperatures and high turbidity (Hald and Korsun, 1997). Suggested that it does not live beneath perennial sea-ice (Jennings et al., 2020b; Vilks, 1980).
<i>Glomulina oculis</i> Jennings, Seidenkrantz and Knudsen, 2020	Found in higher abundances on the inner shelf suggesting this is a proximal glaciomarine indicator preferring extensive sea-ice cover.	Inferences suggest this species is associated with proximity to glaciers, with perennial-to-mobile sea-ice cover (Jennings et al., 2020a,b).
Other Miliolid species (<i>Triloculina trihedra</i> , <i>Quinqueloculina</i> sp., <i>Miliolinella chukchiensis</i> , <i>Miliolinella subrotunda</i>)	Miliolid species are clearly more abundant at inner shelf sites in NEG suggesting that they have an affinity to more extensive sea-ice conditions and are key glaciomarine indicators.	Miliolid species are most commonly associated with normal-marine conditions (Murray and Smart, 1994).
<i>Textularia earlandi</i> Parker, 1952	This species is abundant across the NEG continental shelf.	Found to be driven by substrates rather than water mass characteristics (Lloyd, 2006).
<i>Portatrochammina bipolaris</i> Brönnimann and Whittaker, 1980	This species is most abundant in the outer and mid parts of the NEG continental shelf.	Linked to polar, less saline water masses (Jennings and Helgadottir, 1994; Lloyd, 2006; Vilks, 1989).
<i>Adercotryma glomerata</i> (Brady, 1878)	This species is more abundant at sites in the mid and outer shelf.	Linked to Atlantic sourced waters in Arctic regions (Hald and Korsun, 1997; Lloyd, 2006).
Agglutinated/calcareous ratio	The ratio of agglutinated and calcareous species differs significantly between the inner shelf and the outer and mid shelf sites. More extensive sea-ice cover (inner shelf) results in an environment better suited to preserving calcareous species. However, the use of this proxy in paleo-reconstructions must also take into account the wider environmental context.	Linked to high primary productivity and brine formation, associated with seasonal sea-ice, that cause the dissolution of calcareous tests (Fig. 15) (de Vernal et al., 1992, 2020; Rasmussen and Thomsen, 2014; Schroder-Adams et al., 1990; Scott et al., 1989; Seidenkrantz et al., 2007).

polynya activity in NEG.

Whilst *P. bipolaris* is present at all sites across the NEG continental shelf, its abundance is higher in FZ2, suggesting its potential affinity to areas of higher primary productivity, characteristic of seasonal sea-ice formation and polynya activity. Elsewhere, this species has been linked to colder, less-saline polar waters (Jennings and Helgadottir, 1994; Lloyd, 2006; Vilks, 1989).

5.3. 25 years of change on the Northeast Greenland continental shelf

Results from samples collected in 1993 from the NEW Polynya and Belgica Trough offer insights into changes in benthic foraminiferal assemblages that have occurred in the last 25 years, specifically with respect to the agglutinated and calcareous ratios (Ahrens et al., 1997). In contrast to the samples collected from close the NEW polynya in 2016/17, which are dominated by agglutinated species, the samples collected in 1993 are generally dominated by calcareous species. We suggest that this change is caused by the expansion of the NEW polynya, which has

become a more stable feature in recent years. This is driven by more than two decades of Arctic warming (Turton et al., 2019) and results in intensified brine formation which causes the dissolution of calcareous tests (cf. Fossile et al., 2020; Nardelli et al., 2022). However, it must be noted that the data from 1993 is based on living (rose-bengal stained) foraminifera collected between May and July, compared to data based living and dead foraminifera combined, collected in August–October for the 2016/17 samples. Thus, seasonal changes may also play a role in driving these differences in benthic foraminiferal communities. In fact, foraminiferal fauna analysis, undertaken at different times between May and July, in 1993, show the total abundances of dominant species (e.g. *C. neoteretis*, *E. clavatum*) varying substantially throughout this period (Ahrens et al., 1997). Since the 1993 sample analysis was undertaken on only living foraminifera (stained with Rose Bengal), these results indicate that benthic foraminifera respond quickly to summer food inputs (Ahrens et al., 1997). As very few of the sites with stained foraminifera from 2016/17 overlap with these locations we cannot make direct conclusions about assemblage changes with any certainty.

6. Conclusions

The analysis of benthic foraminifera from 23 surface samples collected on the NEG continental shelf provides the following conclusions:

1. Cluster analysis of benthic foraminiferal assemblages divide the NEG continental shelf into two main faunal zones: 1) the inner shelf (FZ1) and 2) the mid and outer shelf (FZ2).
2. CCA links environmental variables to benthic foraminiferal assemblages: foraminifera at inner shelf sites are positively correlated with September sea-ice cover and bottom water oxygen content. Mid and outer shelf sites are primarily positively correlated with TOC (a measure of productivity) and negatively correlated with September sea-ice cover. This suggests that high primary productivity and seasonal sea-ice are key driving factors of the faunal assemblage in this region.
3. A key difference between the two zones is the concentration and percentage of agglutinated versus calcareous species. Agglutinated species dominate the outer and mid shelf, and calcareous species dominate the sites located on the inner shelf. We conclude that this is likely to be driven by the higher primary productivity and sea-ice formation in the outer and mid shelf region, which creates a harsh environment, with dissolution of calcareous tests. The lower concentrations of agglutinated species in the glacier-proximal zone may be due to the competition from the calcareous foraminifera.
4. Several conclusions can be drawn about specific species in these two zones. *C. assidulina neoteretis* and *C. reniforme* dominate most sites in both zones, indicating that they are indicator species in NEG. *Glo-mulina oculus oculus*, *S. horvathi*, *O. tener*, and miliolid species in general dominate the inner shelf region, suggesting a preference for environments characterised by more extensive sea-ice cover and lower primary productivity. An extensive list of specific species inferences can be found in Table 3.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data for this research is available in the supplementary information as well as on PANGAEA.

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Appendix A. Supplementary data

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