



OPEN Benthic foraminiferal colonisation of phytodetritus during spring bloom within the marginal sea ice zone off Northern Svalbard continental margin

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Phytodetritus is transient organic material derived from phytoplankton blooms that sinks to the seafloor. Benthic foraminifera act as primary consumers of this nutrient-rich material, yet their distribution patterns in phytodetritus and underlying associated surface sediment in Arctic regions remain poorly understood. This study investigates the distribution of living benthic foraminifera in phytodetritus and underlying associated surface sediment during the spring bloom, examining their density, relative abundances, and microhabitat preferences. Distribution patterns were analysed in relation to water depth, bottom water conditions, and organic matter availability. At the highly productive Barents Sea slope station, *Alabaminella weddellensis*, *Adercotryma glomeratum*, and *Cassidulina neoteretis* occupied freshly deposited phytodetrital material, whilst *Melonis zaandami* dominated the sediment. At the moderately productive Yermak Plateau site, both layers hosted *Cassidulina reniforme* and *C. neoteretis*, with *Lagenammmina arenulata* preferring the phytodetrital layer. At the *Phaeocystis* bloom site in Sophia Basin, *Epistominella arctica* and *Quinqueloculina akneriana* were abundant in phytodetritus, whilst *Ioanella tumidula* and *Hormosinelloides guttifer* inhabited the sediment. Our findings emphasise the significant role of environmental factors in shaping remarkably distinct foraminiferal communities within the phytodetrital layer and the associated surface sediment, as reflected in faunal composition, density, and relative abundances.

Keywords Benthic foraminifera, Phytodetritus, Northern Svalbard

The Northern Svalbard Continental Margin represents a transitional zone in the high Arctic, where the northward-flowing Atlantic Water (salinity ≥ 34.9 PSU, temperature > 0 °C), transported by the West Spitsbergen Current, subducts beneath the fresher Polar Water layer (salinity ~ 31 – 34 PSU) and surrounding Arctic water masses^{1,2,3}. Due to rising heat advection of Atlantic Water, the inflow regions (eastern Barents Sea and north of Svalbard) experience earlier and more extensive sea-ice retreat, which in turn leads to increased primary production in the area⁴. Over the past decades, the progressively earlier retreat of sea ice north of Svalbard has led to a prolongation of the phytoplankton growing season, an expansion of under-ice blooms, and *Phaeocystis*-dominated blooms^{5,6}. As a consequence, the major spring phytoplankton bloom tends to start earlier and last longer, impacting the food web structure in the area⁵. Phytoplankton blooms serve as a source of phytodetritus that develops in the photic zone, sinks throughout the water column, undergoes recycling along the way, and is eventually exported to the seafloor^{7,8}. The exported material is mainly composed of organic (decaying phytoplankton and other organic remains such as faecal pellets) and inorganic (terrigenous and cryogenic particles) components^{7,8,9}. In the Arctic, the main ballasting particles that facilitate carbon export to depth are cryogenic gypsum crystals, which are formed in sea ice and preferentially released in the marginal ice zone^{9,10}. This carbon transfer from the surface ocean to the deep ocean, termed “the biological carbon pump”, is an important contributor to CO₂ storage in the deep sea. However, the future of the Arctic biological carbon pump remains under debate. Recent

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studies suggest that its efficiency may decline and slow down^{11, 12}, whilst other authors highlight considerable uncertainty⁹. Upon reaching the seafloor, phytodetritus takes on variable appearances, ranging from flocculent or phytodetritus aggregates to gelatinous or mucilaginous textures, and can appear green, brown, or grey⁸. The phytodetritus reaching the seafloor, provides food and habitat for benthic organisms⁸. Numerous studies showed that fauna can be rapid consumers of fresh phytodetritus, such as bacteria¹³, and benthic foraminifera^{14, 15}, particularly in the northern latitudes, following the deposition of slightly altered phytoplankton remains^{11, 16}. Transient phytodetrital aggregates can function as temporary microhabitats for foraminiferal communities¹⁷, primarily investigated in the North Atlantic¹⁸, and Weddell Sea¹⁹. However, similar observations remain missing in the Arctic Ocean, particularly in springtime, due to logistical challenges associated with accessing these remote environments. In the present study, we report the first investigations on living (Rose Bengal-stained) benthic foraminifera within phytodetritus deposits, including surface sediments collected during a late spring phytoplankton bloom event in the Arctic Ocean. This study aims to compare foraminiferal fauna in the accumulated phytodetrital layer, or phytodetritus, and underlying associated surface sediment from three sites: the Svalbard Shelf, Yermak Plateau, and Sophia Basin; to calculate the faunal density and relative abundances; and to identify potential microhabitat preferences of benthic foraminifera. This research will contribute to our understanding of the impact of labile organic matter fluxes on Arctic benthic communities and the broader implications for Arctic marine ecosystems.

Results

The foraminiferal density was variable across the accumulated phytodetrital layer and underlying associated surface sediment samples. The density in the phytodetrital layer was on average 18.5 times higher compared to sediment. It is worth mentioning that samples were collected in markedly different volumes. Faunal densities and relative abundances of dominant species in the phytodetrital layer and surface sediment samples are shown in Fig. 1. At the station PS92/32, *Alabaminella weddellensis* was the most abundant species in the phytodetritus (17.8%). It was accompanied by other prevalent species such as *Adercotryma glomeratum* (17.6%) and *Cassidulina neoteretis* (11%). In contrast, *Melonis zaandami* (22%) was found predominantly in the underlying sediment. At the site PS92/46, *Cassidulina reniforme* and *C. neoteretis* were significant in both phytodetritus (13.1% and 10.4%, respectively) and sediment (16.9% and 16.2%, in accordance). *Lagenammina arenulata* was another dominant taxon in the phytodetrital layer (10.4%). At the site PS92/47, the phytodetritus yielded the dominant species *Epistominella arctica* (30.8%) and *Quinqueloculina akneriana* (14.3%). On the contrary, the underlying substrate contained *Ioanella tumidula* (13.1%) and *Hormosinelloides guttifer* (29.2%). A summary of ecology of dominant foraminiferal species based on the references presented in Table 1. Raw and extrapolated counts, densities, and relative abundances of the foraminiferal species across stations and substrates are presented in Supplementary Tables S1–S5. Plates of foraminiferal species exhibiting well-developed greenish cytoplasm and living (Rose Bengal-stained) species that colonised the phytodetrital layer are shown in Supplementary Figs. S1 and S2, respectively. Non-metric multidimensional scaling (NMDS) based on the Morisita similarity index was

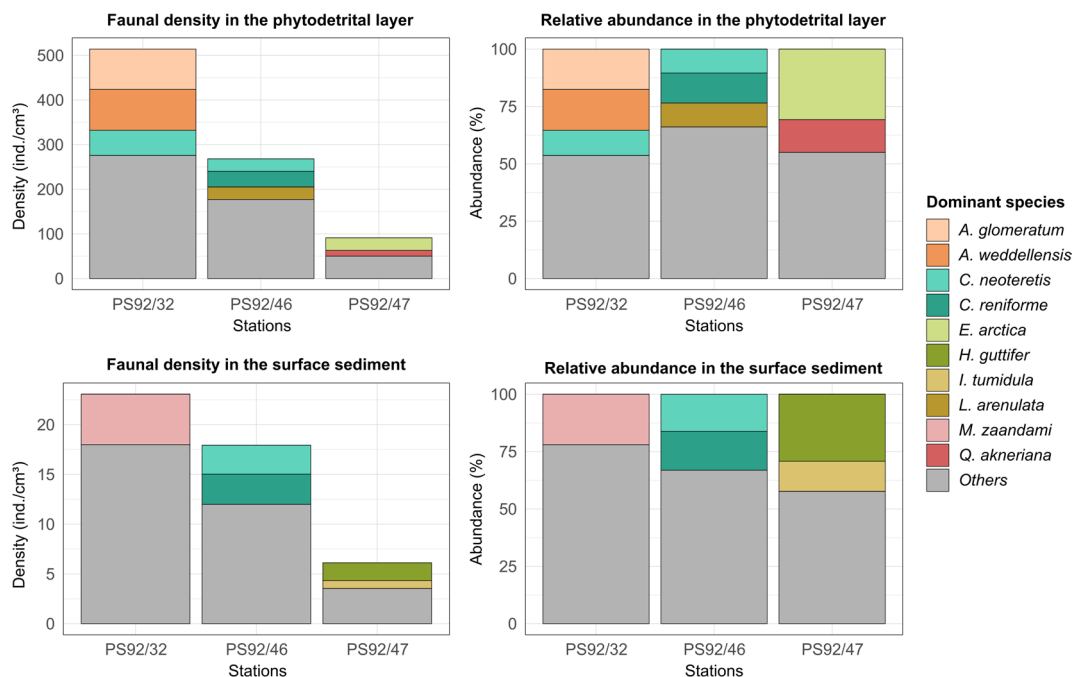


Fig. 1. Cumulative faunal density and relative abundances of dominant species (> 10%) in the accumulated phytodetrital layer and underlying associated surface sediment. Category “Others” includes species whose relative abundance is less than 10% at the corresponding station.

Dominant species	Ecology
<i>Adercotryma glomeratum</i>	Motile behaviour (epifaunal to infaunal modes) ^{24, 36, 46} Opportunism ^{24, 36, 46}
<i>Alabaminella weddellensis</i>	Epifaunal mode ^{17, 18, 24, 30–33} Opportunism ^{18, 24, 30–33} Phytodetritus ¹⁸
<i>Cassidulina neoteretis</i>	Infaunal mode ⁶⁴ Opportunism ⁶⁴ High productivity ⁶⁴ Modified/cooled Atlantic water ⁶⁴ Stable salinities ⁶⁴ Fine-grained sediments ⁶⁴
<i>Cassidulina reniforme</i>	Motile behaviour (epifaunal to infaunal modes) ^{37, 65} Cold-water areas ⁴⁴ Seasonal sea-ice coverage ⁴⁴ Muddy sediments ⁴⁴
<i>Epistominella arctica</i>	Epifaunal mode ^{19, 28} Opportunism ^{19, 28} Phytodetritus ^{19, 28} Oligotrophic environments ²⁸
<i>Hormosinelloides guttifer</i>	Motile behaviour (epifaunal to infaunal modes) ^{46, 55}
<i>Ioanella tumidula</i>	Epifaunal mode ³⁸ Fine grained sediments ³⁸ Water depths between 1500 and 3000 m ³⁸ Seasonally ice-free areas ³⁸
<i>Lagenammina arenulata</i>	No prior reports describe the environmental preferences of this species
<i>Melonis zaandami</i>	Infaunal mode ²⁸ High productivity ^{26, 27}
<i>Quinqueloculina akneriana</i>	No prior reports describe the environmental preferences of this species

Table 1. Summary of the ecology of dominant foraminiferal species based on the references.

used to visualise differences between foraminiferal communities in phytodetritus and those in sediment, in a two-dimensional ordination plot (Stress = 0.09) (Supplementary Fig. S3).

Discussion

In spring, the Barents Sea slope, where the PS92/32 site is located, is influenced by the inflow of Atlantic Water and receives high fluxes of fresh organic matter to the seafloor²⁰. The site was classified as a bloom site, with increased diatom-associated chlorophyll *a*, abundant under-ice fauna, and signs of active grazing by sea-ice and under-ice fauna^{6,21,22}, suggesting recent phytodetritus deposition. Despite heavy ice cover reaching 94% during sampling (ice and snow thickness measured at 1.4 m), the conditions were productive, likely due to the presence of leads in the ice and proximity to open water, which triggered enhanced light penetration through the water column^{6,23}. Under warm (2.1 °C) and saline (35 PSU) bottom water conditions, *Alabaminella weddellensis*, *Adercotryma glomeratum*, and *Cassidulina neoteretis* flourished in the densely populated and freshly deposited phytodetritus, whereas the surface sediment below was predominantly colonised by *Melonis zaandami*. *Alabaminella weddellensis* is a calcareous species known as one of the phytodetritus group members. The group is typically associated with seasonal primary production pulses²⁴, extended sea ice retreats, and regions with no permanent sea ice^{25, 26, 27, 28}. Also, foraminifera associated with the phytodetritus (such as *A. weddellensis*) have a high dispersion potential²⁹. Our findings are consistent with earlier evidence suggesting that *A. weddellensis* is an opportunistic phytodetritus-dwelling species, which is often found alongside another calcareous phytodetritus inhabitant *Epistominella exigua*^{18,24,30,33}. Despite the specialist nature of *E. exigua*, it was found in low abundance across all samples (raw and extrapolated counts, densities, and relative abundances of *E. exigua* is presented in Supplementary Table S5). According to a previous study of Neogene samples³⁴, *A. weddellensis* may be more prevalent than *E. exigua* in specific types of phytodetritus, such as dense diatom mats, implying the phytodetritus composition at the station may favour *A. weddellensis*. Therefore, the abundance of these opportunistic species may fluctuate depending on the phytodetritus type³⁵. The agglutinated species *A. glomeratum* was present across both layers at all stations, showing its preferences to the high productive station. *Adercotryma glomeratum* is an opportunistic, detritivore infaunal species that exhibits epifaunal motile behaviour in response to episodic phytodetritus deposition³⁶. Also, it was noted that the species tends to be associated with both phytodetritus and underlying sediment¹⁸ supporting our data. The calcareous Arctic and subarctic dwelling species *C. neoteretis* was one of the main contributors at the PS92/32 and PS92/46. However, it was absent at the deepest station, PS92/47, likely due to its preference for water depths between 200 and 1400 m²⁶. The infaunal *C. neoteretis* is an opportunistic species previously reported as a phytodetritus indicator during an interglacial period in the fossil record³⁷. It is well adapted to strong seasonal fluctuations in food supply^{28,32,38,39}, and reproduction pulses are frequently associated with spikes in marine productivity⁴⁰. The species benefits from the nutrient-rich conditions provided by phytoplankton blooms^{41,38,39}, and is likely to feed on degraded organic matter and phytodetritus-associated bacteria^{28,32}. Interestingly, it was stated that the species does not typically invade the phytodetritus³². However, our findings contradict this, as we observed the presence of *C. neoteretis* actively ingesting phytodetritus and inhabiting it (Supplementary Fig. S1). Therefore, our results may reflect its adaptive

ecological flexibility that was not acknowledged in the past. Additionally, it was recognised as an indicator of modified Atlantic Water⁴². Nonetheless, some studies described that the exact nature of the relationship between *C. neoteretis* and Atlantic Water remains uncertain²⁶. The sediment conditions appeared highly favourable for Arctic infaunal calcareous species *M. zaandami*. In accordance with the present results, earlier investigations demonstrated that the species tends to be associated with high fluxes of slightly altered organic matter and linked to increased phytodetritus accumulations^{26,27}.

Station PS92/46, located on the eastern Yermak Plateau, was characterised as a pre-bloom station with dense sea-ice cover reaching 99% (ice and snow thickness measured at 1.2 m), and a low chlorophyll *a* standing stock⁶. Furthermore, low abundances of under-ice and sea-ice fauna, lack of grazing, and an estimated carbon demand nearly twice phytoplankton production indicated an insufficient carbon supply for local under-ice communities^{21,22}. This evidence may support the hypothesis that the phytodetritus was likely either degraded and originated from earlier blooms rather than recent ones, or it represented the first material settling during the pre-bloom phase. This aligns with total organic carbon (TOC) results from the same cruise, showing lower TOC in Yermak Plateau sediments, likely due to prolonged sea ice cover and reduced fresh organic matter input compared to the Barents Sea slope²⁰. *Cassidulina reniforme* and *C. neoteretis* occurred abundantly in both layers, although *Lagenammina arenulata* favoured the phytodetritus. These species thrived under cold (−0.3 °C) and saline (34.9 PSU) bottom water conditions. The Arctic infaunal calcareous *C. reniforme* is typically associated with cool, saline waters^{43,44}, which confirms our examinations. A positive correlation between living *C. reniforme* abundance and both organic carbon content and phytoplankton density was reported in the earlier study⁴⁵. In contrast, its abundance demonstrated resilience to pre-bloom, food-limited condition in our samples. Another dominant taxon of the *Cassidulina* genus is *C. neoteretis*, an indicator of high productivity. Its microhabitat preferences are discussed above. Its presence at this site may indicate its environmental adaptability to varying food availability and temperature conditions. Another species that achieved maximum abundance in the phytodetrital layer was agglutinated *L. arenulata*. The ecology of this species is not well understood. In general, *Lagenammina* genus is an infaunal, detritivorous taxon that prefers cold-temperate environments⁴⁶. It was highlighted as a dominant component of the benthic community at the Suiko Seamount, a subarctic site characterised by stable and higher fluxes of organic matter from July to December⁴⁷. Moreover, *L. arenulata* was identified as one of the main components of the assemblages in Baffin Bay and Nares Strait, where it appeared at stations marked by cold temperatures and corrosive conditions⁴⁸. Finally, it was noted that members of *Lagenammina* genus are not directly associated with phytodetritus¹⁷.

The station PS92/47 in the Sophia Basin was notable for its classification as a bloom station⁶. The station demonstrated heavy ice cover reaching 100% (ice and snow thickness measured at 1.4 m), moderate abundances of sea ice and under-ice fauna, and particularly high abundances of grazers²¹. During the PS92 cruise, the export of *Phaeocystis* to the seafloor was significantly enhanced through the ballasting of *Phaeocystis* aggregates with gypsum minerals released from melting sea ice at the site^{10,49}. A video recording of the MUC deployment and aggregate accumulation on the seafloor indicated a rapid downward flux of gypsum-ballasted *Phaeocystis* during sampling¹⁰. However, some studies reported that *Phaeocystis* phytodetritus is found less frequently in the deep sea compared to diatoms, likely due to recycling and grazing in the water column^{7,8}. Supporting this, cruise observations⁶ recorded that faecal pellets from krill and copepods contributed a substantial fraction to vertical carbon export in certain areas, especially where blooms of *Phaeocystis* dominated. Therefore, we can suggest that the phytodetritus was freshly delivered and partly originated from faecal pellets. *Epistominella arctica* and *Quinqueloculina akneriana* thrived in the phytodetritus, whilst *Hormosinelloides guttifer* and *Ioanella tumidula* extensively inhabited the sediment. These species flourished under the cold (−0.8 °C), saline (34.9 PSU) conditions as well as at the previous station PS92/46. The Arctic-dwelling calcareous species *E. arctica* exhibits an opportunistic life strategy, reproducing during periods of high seasonal productivity in oligotrophic environments and becoming less abundant during extremely low food availability²⁸. The accumulated phytodetritus yielded juveniles of *E. arctica*, indicating active reproduction and favourable conditions for its lifecycle. Our results are consistent with previous observations, which show that the distribution of *E. arctica* in the Arctic is linked to phytodetritus and, as a result, it tends to release large numbers of offspring in the Sophia Basin²⁸. Our results also support findings from Weddell Sea samples, which showed that small phytodetritus balls were abundantly populated by *E. arctica*¹⁹. The site may be characterised by minimal to absent current activity, as indicated by the abundant occurrence of *E. arctica*. This species possesses minute lightweight tests that can be readily transported within the accumulated labile carbon on the seabed²⁸. However, the study lacks the necessary data on bottom currents to quantitatively evaluate this parameter. An abyssal Arctic species^{38,50} that appeared in the phytodetritus was porcelaneous *Q. akneriana*. The ecology of this species remains insufficiently studied. The genus *Quinqueloculina* is generally classified as an epifaunal, herbivorous taxon⁴⁶. Records from the abyssal stations of the Porcupine Abyssal Plain, NE Atlantic, showed that *Q. sp.* responded to flux events by migrating to the upper sediment layers and the sediment-water interface, where they grew and reproduced before returning to a dormant state in deeper layers as phytodetrital food becomes depleted^{51,52}. Another genus representative, *Q. seminula*, was observed with its protoplasm filled with pennate diatoms and dinoflagellates following a sedimentation event under the East Greenland Current^{53,54}. In the feeding experiments, *Q. seminula* and *Q. sp.* demonstrated similar behaviour by collecting detrital plugs around their apertures and ingesting food, with their youngest chambers containing coccoid algae, diatoms, and stercomata^{53,54}. These findings highlight the adaptability of *Quinqueloculina* representatives, potentially including *Q. akneriana*, to fluctuating food availability. The agglutinated species *H. guttifer* is described as a surface sediment-dwelling taxon that responds to the input of labile organic matter⁵⁵. It was reported as a characteristic species on the Yermak Plateau⁵⁶. This species may be associated with higher C_{org} fluxes than *A. glomeratum*²⁸. In our samples, *H. guttifer* was accompanied by the epifaunal calcareous deep-water species *I. tumidula*, whose distribution is primarily influenced by water depth, biological competition, and food availability³⁸. Additionally, our examinations

showed that living *I. tumidula* individuals tended to exhibit an epibenthic lifestyle, attaching to hard substrates and occasionally forming agglutinated cysts, which reflects its immobile behaviour and dependence on the substrate.

In conclusion, this study represents the first documented association of benthic foraminiferal species inhabiting the accumulated phytodetrital layers and underlying associated surface sediments within the marginal sea ice zone off northern Svalbard continental margin. This study highlights their ecological versatility during spring bloom. The origin of phytodetritus in the Arctic is shaped by various environmental processes in surface waters and the water column, including proximity to open waters, the activity of under-ice and sea-ice fauna, grazing pressure, ice cover intensity, and overall surface water conditions. These factors influence the composition of phytodetritus and, consequently, the faunal composition of benthic foraminifera, which is primarily driven by food availability, along with secondary factors such as water depth, salinity, and temperature in both the phytodetritus and surface sediment layers. Furthermore, some infaunal foraminiferal species, such as *Adercotryma glomeratum*, *Cassidulina neoteretis*, *C. reniforme*, potentially *Lagenammina arenolata* have been observed to inhabit phytodetritus deposits, highlighting their migratory abilities. This high-resolution study complements both seasonal/annual observations and time-averaged sedimentary archives, which document broader historical and contemporary ecological shifts.

Methods

Study area

From May 19 to June 28, 2015, the German icebreaker R/V Polarstern embarked on expedition PS92 (ARK-XXIX/1), known as “TRANSSIZ” (Transitions in the Arctic Seasonal Sea Ice Zone). This six-week mission aimed to investigate ecological and biogeochemical processes during early spring across the European Arctic margins and the Yermak Plateau. The study focused on three distinct sites in the Arctic Ocean: the Barents Sea slope, the Yermak Plateau, and the Sophia Basin (Fig. 2), all located north of Svalbard. Positioned above 81°N latitude, these regions were heavily covered by ice and snow during sampling, with sea ice coverage ranging from 94% to 100%. Bottom water temperature and salinity varied from −0.8 to 2.1 °C and from 34.9 to 35 PSU⁵⁷. The ice and snow thickness varied from 1.2 to 1.4 m across the study area²¹. The potential environmental characteristics are listed in Table 2.

Sample collection and processing

During the 2015 TRANSSIZ PS92 (ARK-XXIX/1) cruise aboard the R/V Polarstern, undisturbed seafloor sediments were retrieved from depths of 218.8 to 2174.7 m using a video-equipped multicorer (TV MUC) and a box corer (BC) (Table 3). The inner diameter of the MUC tubes was 10 cm. The MUC frame was equipped with a live broadcasting video system that transfers pictures to the ship via glass fibre cable. A Sanyo HD400P camera captured images of under-ice fauna, marine snow in the water column, and phytodetritus patches on the seafloor (Fig. 3). The BC was deployed to acquire sediment samples from a large area, typically 50 × 50 cm. On

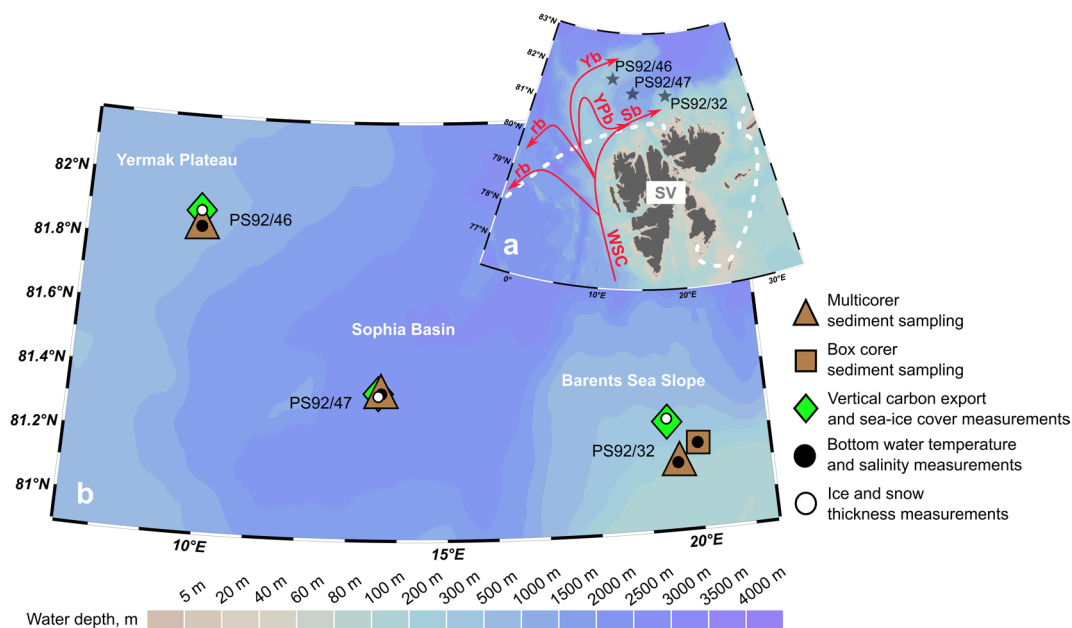


Fig. 2. Map of the study area in the north of Svalbard (a, b), sampled during the Polarstern expedition PS92. Vertical carbon export⁶, sea ice cover data⁶, and bottom water measurements⁵⁷ were extracted from the cruise studies and datasets. The sea ice extent on 15.06.2015 (white line) was based on EUMETSAT's Global Sea Ice Concentration Reprocessing dataset⁶². Red arrows indicate the branches of the Atlantic Water current (WSC: West Spitsbergen Current; Sb: Svalbard branch; Yb: Yermak branch; YPb: Yermak Pass branch; rb: recirculating branch), modified after the reference⁶³.

Station	Bottom water temperature (°C)	Salinity (PSU)	Bloom stage	Sea ice cover (%)	Ice and snow thickness (m)
PS92/32	2.1	35	Bloom (Diatoms)	94	1.4
PS92/46	− 0.3	34.9	Pre-bloom (Prasinophytes & Diatoms)	99	1.2
PS92/47	− 0.8	34.9	Bloom (<i>Phaeocystis</i>)	100	1.4

Table 2. List of the potential environmental characteristics.

Station	Gear	Date	Latitude	Longitude	Water depth (m)	Volume (cm ³)	Sample type
PS92/32	BC	06.06.15	81.15633	20.01267	311.5	2	Phytodetrital layer
	TV MUC	08.06.15	81.09967	19.61583	218.8	235.6	Surface sediment
PS92/46	TV MUC	18.06.15	81.84367	9.758	886.1	1	Phytodetrital layer
						235.6	Surface sediment
PS92/47	TV MUC	20.06.15	81.34467	13.66567	2174.7	2	Phytodetrital layer
						235.6	Surface sediment

Table 3. Sampling stations for the accumulated phytodetrital layer and the underlying surface sediments.



Fig. 3. Organic material export to the seafloor. Large aggregates or accumulations of aggregates are indicated by dotted green circles (image was taken and provided by Jutta Erika Wollenburg).

the surface of MUC tubes and BC, marine snow could be observed either as recently deposited ball-like green aggregates ballasted by cryogenic gypsum at the site PS92/47¹⁰ or as more featureless “green soup” at the site PS92/32. Immediately after retrieval, three specific-volume samples of phytodetritus were extracted from the sediment surfaces of both the MUC and BC using a one-way pipette. Sediments were sampled from 0 to 15 cm in 1 cm steps, but only surface sediments (0–1 cm) are considered in the current study. Following retrieval of sediment cores from three MUC tubes, samples corresponding to the same depth interval from each tube were combined into a single Kautex bottle and homogenised. The phytodetritus and underlying associated surface sediment samples were preserved in Rose Bengal-ethanol mixture (2 g L^{−1}), washed through a 63 µm mesh, and dried. Each fraction was then split into subsamples using a microsplitter.

Taxonomical identification

Benthic foraminifera from fraction > 63 µm were isolated from both matrixes and were identified based on external morphological features. We aimed to collect a minimum of 300 Rose Bengal-stained individuals from whole sample splits of each sample, whenever possible. Picked individuals were mounted on micropalaeontology slides. Identification was performed using a Nikon SMZ-18 stereo microscope and using available literature. Nomenclature followed the World Register of Marine Species⁵⁸, with taxon names validated by protist taxonomy experts within the team.

Statistical analysis and data visualisation

The foraminiferal counts from the split samples were calculated by multiplying the picked total number of individuals of each taxon by the splitting factor. Subsequently, foraminiferal counts from the phytodetritus and underlying associated surface sediment samples were standardised to individuals per cm³ (ind./cm³) to compare the foraminiferal absolute abundances between samples. Dominant species were defined as those comprising more than 10% of the assemblage. Those species, occurring at proportions below 10%, were included in quantitative analyses but are not discussed in the present study. The figures were plotted in RStudio version 2024.12.1 + 563. The RStudio package ggplot2 3.5.1⁵⁹ was used. The maps were produced in Ocean Data View software version 5.7.1⁶⁰. The photo and illustration were prepared with Inkscape 1.2.2. Non-metric multidimensional scaling (NMDS) based on the Morisita similarity index was performed and plotted using PAST software⁶¹.

Data availability

Publicly available bottom water temperature and salinity were obtained from PANGAEA database (<https://www.pangaea.de>) at <https://doi.pangaea.de/10.1594/PANGAEA.861865>. All other data from this study are available in the main text, references, supplementary information, or on request from the corresponding author.

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Declarations

Conflict of interests

The authors declare no competing interests.

Additional information

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