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RESEARCH

Billefjorden's benthic biodiversity: the impact of glacier retreat on faunal communities in a high Arctic fjord

Arjen A. W. van der Kamp[1,2] · **Víctor González Triginer**[1,3] · **Arunima Sen**[1]

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Abstract

Glaciers cover approximately 60% of the Svalbard archipelago, but despite extensive research on Svalbard's glaciers and their retreat, little is known about the effect of glaciers with different termination points on fjordic benthic communities in the Arctic. Billefjorden, Svalbard, includes bays influenced by runoff from inland glaciers and Nordenskiöldbreen, a glacier that, due to retreat, has split into a marine- and a shore-terminating side since 2017. We investigated the benthic faunal community composition in relation to environmental factors (bottom water temperature and salinity, TOC, percent pelite and sediment pigments) within Billefjorden to examine the effects of inland glaciers, a shore-terminating glacier, and a marine-terminating glacier on benthic communities. Despite their close proximity, the different locations displayed distinct community parameters and environmental conditions. Specifically, the strongly glacier-influenced locations were less diverse and had lower faunal abundance compared to the location with minimal glacier influence, likely due to higher sedimentation rates and lower food availability. The marine-terminating glacier side had a particularly sparse community, likely due to high turbidity and food deprivation. Our results suggest that glaciers and their retreat impact local-scale environmental factors which drive differentiation of benthic communities over small spatial scales within a single fjord system.

Keywords Benthos · Climate change · Fjordic system · Marine-terminating glacier · Sedimentation · Svalbard

Introduction

The Arctic is experiencing rapid warming, and polar amplification causes greater climate change in the Arctic compared to other regions (Callaghan et al. 2011; Comiso and Hall 2014; Kavan et al. 2023). This is driven in part by changes in the albedo resulting from the decreased extent of snow cover, sea ice, permafrost and glaciers (Callaghan et al. 2011; Serreze and Barry 2011; Comiso and Hall 2014; Kavan et al. 2023). Both current observational and paleo-data show that the Arctic is warming up to 3–4 times faster than the average of the northern hemisphere (Serreze et al. 2009; Miller et al. 2010; Piskozub 2017). Climate change has been well documented in the Svalbard archipelago, with the meteorological station at Svalbard airport in Longyearbyen recording an air temperature warming rate of 1.7 °C/decade since 1991, which is more than twice the Arctic average, seven times the global average (Nordli et al. 2020), and one of the highest rates of modern warming recorded on earth (Isaksen et al. 2016). Rising temperatures have a negative impact on winter precipitation, snow accumulation and firn characteristics. One of the biggest impacts of rising temperatures is on glaciers, causing their retreat (Rachlewicz et al. 2007; Van Pelt et al. 2016, 2021; Peeters et al. 2019; Kavan et al. 2023). An important driver of this retreat in marine-terminating glaciers is the intrusion of warm seawater, which melts the glacier's front from below (Kochtitzky et al. 2022). Moreover, the morphology of the seabed plays an important role on marine-terminating glaciers, as underwater ridges can either facilitate or restrict the access of warm water (Cottier et al. 2005; Nilsen et al. 2008). Overall, a phenomenon that is occurring all over Svalbard is that marine-terminating glaciers are retreating to such a large extent that they are transitioning to terminating on land.

✉ Arjen A. W. van der Kamp
aaw.vanderkamp@gmail.com

[1] Department of Arctic Biology, University Centre in Svalbard, N-9171 Longyearbyen, Norway

[2] Department of Marine Animal Ecology, Wageningen University & Research, Wageningen, The Netherlands

[3] Faculty of Biosciences, Fisheries and Economics, The Arctic University of Norway, Tromsø, Norway

A marine-terminating glacier has a near-vertical calving front ending in the fjord where the glacier loses most of its mass due to frontal ablation (Kochtitzky et al. 2022). Freshwater from melting or calving, can create seasonal stratification in the water column. Subglacial circulation causes the upwelling of mineral-rich water, leading to a high flux of nutrients to surface waters (Meire et al. 2017). This results in high levels of primary production and subsequently, high biomass of higher trophic levels like fish, seabirds and marine mammals (Urbanski et al. 2017; Meire et al. 2023). However, subglacial discharge plumes also deposit sediment in the water, which can increase turbidity that inhibits light penetration and thereby photosynthesis. Moreover, through the break-off of glacier ice, sediment and rocks are deposited into the water, churning up the seafloor (Hartvich et al. 2017; Cantoni et al. 2020; Li et al. 2023, 2024). Therefore, marine-terminating glacier fronts are dynamic systems with variable physical processes and biota.

One major change that takes place as marine-terminating glaciers retreat to land is that new seafloor is exposed for infaunal macrobenthos. Within the marine ecosystem, the benthic community plays a critical role in carbon cycling by remineralizing organic material to carbon dioxide, which is subsequently transported up into the water column by mixing and then used by surface primary producers (Renaud et al. 2007). In addition, benthic organisms serve as a food source for higher trophic levels like bentophagous fish, whales (Schonberg et al. 2014; Tokranov et al. 2022) or sea ice-based organisms such as walruses (Darnis et al. 2012; Dunton et al. 2017). Therefore, changes to benthic communities can affect carbon transfer and food webs, and the emergence of new seafloor can impact carbon cycles and trophic transfer in fjordic systems.

In addition to new seafloor, the transition from marine- to shore-terminating glaciers will change drainage into the fjord, potentially leading to increased turbidity, similar to that of river bays with turbid drainage from inland glaciers (Fellman et al. 2010). Meltwater channels below glaciers can transport sediment into fjords, regardless of where the glacier terminates, therefore the impact of retreating glaciers can be individualistic and differ on a case-by-case basis. Despite massive glacier retreat being recorded across the Arctic and Svalbard, little work has been conducted on the effect of such retreat on benthic fjordic communities. The Svalbard fjord, Billefjorden, functions as a natural laboratory where this can be investigated because the marine-terminating glacier, Nordenskiöldbreen, has retreated such that one entire side is mostly shore-terminating since 2017 (Kavan et al. 2023), while the other side is still mainly marine-terminating. Furthermore, the inner part of the fjord has a river system fed by inland valley glaciers (Láska et al. 2012), within close proximity to Nordenskiöldbreen (González Triginer et al. 2024a, b).

We investigated the benthic communities in relation to environmental variables in the river bay with input from inland glaciers, both sides of the glacier (marine- and shore-terminating) and at a reference location that deglaciated 11000 years ago in Billefjorden (Baeten et al. 2010), to examine the potential effect of glacier retreat on benthic faunal communities. We predicted that the reference location would have the highest diversity because its distance from glaciers minimizes the impact of high sedimentation rates, which impede species settlement at other locations (Kokarev et al. 2017). Moreover, higher benthic diversity was anticipated around the shore-terminating glacier front compared to the marine-terminating front because sediment plumes have been seen at the marine-terminating glacier front, which suggests higher turbidity there that should inhibit light availability and surface primary production, reducing food availability for the benthos (Kanna et al. 2018; Szeligowska et al. 2021). Additionally, we expected the communities at the shore-terminating glacier location and the inland glacier location to be similar to each other because they both represent land-terminating glacier locations and should have similar terrestrial inputs and physical characteristics (Meire et al. 2017).

Methods

Study area

Billefjorden is the innermost branch of Isfjorden, a large fjord that essentially bisects the island of Spitsbergen, Svalbard (Fig. 1). The basin of Billefjorden is up to 226 m deep and has a shallow sill at the mouth of the fjord (Baeten et al. 2010). This sill acts as a barrier for the relatively warm Atlantic Water from the West Spitsbergen Current (WSC), causing a lower water temperature within Billefjorden compared to other fjords in Isfjorden (Svendsen et al. 2002; Cottier et al. 2005; Nilsen et al. 2008; Dunlop et al. 2021).

Billefjorden is influenced by the calving Nordenskiöldbreen glacier (78°40′N, 17°E) in the inner northeastern part of the fjord, which has an area of ~206 km^2 and a length of ~22 km (Rachlewicz et al. 2007; Raup et al. 2007; Kavan et al. 2023). Nordenskiöldbreen is estimated to be retreating at a rate of 12–35 m per year (Szczuciński et al. 2009). The calving glacier front is now divided in the middle by Retrettøya (retreat island), which was in 1960 completely covered by the glacier (Kavan et al. 2023). Recent observations indicate major shrinkage of the northern side, causing it to have transitioned to mainly terminating on the shore, since 2017 (Kavan et al. 2023; Copernicus 2024; González Triginer et al. 2024b). Although there are still parts on the northern side where the glacier reaches the water, it is nonetheless by and large shore-terminating, therefore we treated

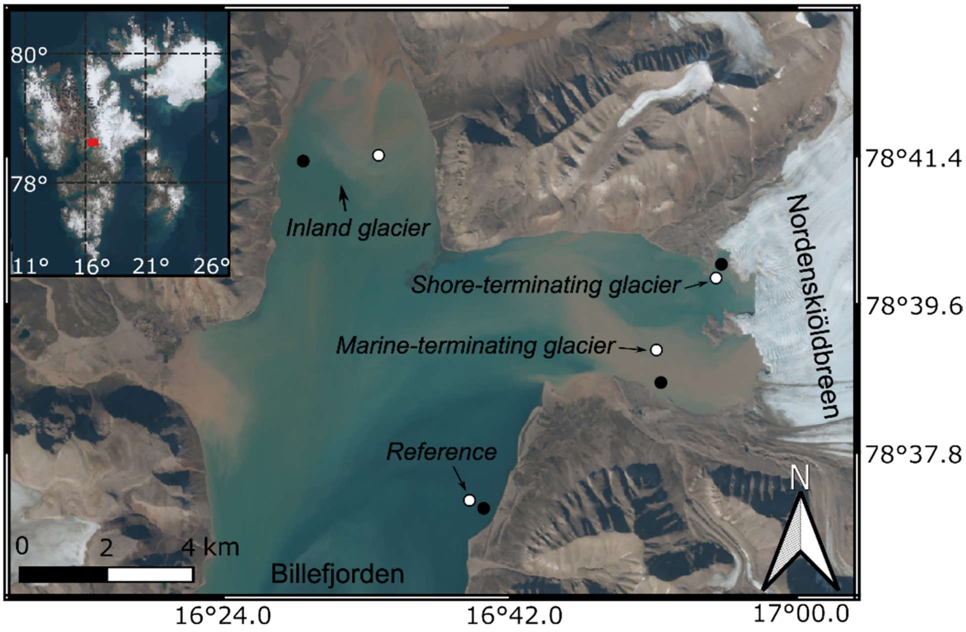

Fig. 1 Satellite image of Svalbard archipelago and Billefjorden. Dots represent the different stations (black = ~ 20 m, white = ~ 60 m depth). Map source: Norwegian Polar Institute. Made with QGIS 3.34.10 and edited with Inkscape 1.3.2

it as such in this study and refer to it as the shore-terminating glacier location (Fig. 1). Similarly, retreat has led to parts of the southern side terminating on shore, however, most of the southern side is still marine-terminating and was so in 2023 during our time of sampling, therefore we refer to this location as the marine-terminating glacier front.

Situated west of Nordenskiöldbreen, the river bay Petuniabukta receives freshwater and sediment from several rivers descending from the valleys of Ebbadalen, Ragnardalen and Hørbyedalen. This influx is attributed to the presence of valley glaciers and mountainous terrain (Láska et al. 2012), creating a river bay with a large tidal flat (González Triginer et al. 2024b). Petuniabukta therefore served as a location where runoff descends from inland glaciers, with the closest glacier ~ 3 km land inwards. We refer to this river bay location as the inland glacier location. Additionally, we targeted Scottvika, a bay in Billefjorden that deglaciated 1100 years ago (Baeten et al. 2010). Scottvika is located out of the river and glacier bays (González Triginer et al. 2024a), with minimal influence from both the river and glacier bays due to its location on the eastern side of Billefjorden and the counterclockwise water circulation pattern within the fjord. It therefore served as a reference location. Our inland glacier, shore-terminating glacier and reference locations are the same as those studied by González Triginer et al. (2024b) and therefore we use the same short names as these authors which are RIV for the inland glacier location, GLA for the shore-terminating glacier and CON for the reference location. We use the short name MGL to refer to the marine-terminating glacier location. Overall, the longer, descriptive names are used for ease of comprehension. The gradient of a largely marine-terminating glacier side, a recently largely shore-terminating glacier side, a river bay with inland glacier-derived input, and a location with minimal glacial influence all within close proximity allows for a systematic assessment of glacial retreat and the possible effect it has on benthic communities in Billefjorden (Fig. 1).

Sampling and species identification

Sampling took place from the boat *Hanna Resvoll* (UNIS) in July and August 2023 for the inland glacier, shore-terminating, and reference locations and in October 2023 for the marine-terminating location (Table 1). At each location, two stations were established, a shallow, relatively nearshore station (approximately 20 m water depth) and a deeper station (between 50 and 60 m water depth; Table 1). A CTD cast was first taken to measure temperature, salinity and turbidity for the entire water column at each station, with the exception of the marine-terminating location due to sampling being conducted at a much colder time of the year. Subsequently, two replicate Van Veen grabs (0.1 m^2) were taken. Each grab was sieved and rinsed on board using a 1.0 mm mesh sieve. The macrofauna in the residue was immediately preserved in 4% neutralized formaldehyde solution to preserve tissues of the organisms for later laboratory identification.

Identification of the various taxonomic groups was done under a Leica MZ16 A microscope to the lowest possible taxonomic level (depending on the state of preservation and the available literature). Annelids were often identified to family and genus level, while molluscs were mainly identified to species level. After identification, the number of individuals were counted per identified taxon and the total

Table 1 Stations sampled from July until October 2023

Date (2023)	Station full name	Station short name	Latitude (°N)	Longitude (°E)	Distance between shallow and deep stations (m)	Distance to shore (m)
28-Jul	Shore-terminating glacier shallow	GLA_20 m	78° 40.063′	16° 55.279′	280	324
28-Jul	Shore-terminating glacier deep	GLA_60 m	78° 39.952′	16° 54.777′	280	502
07-Aug	Inland glacier shallow	RIV_20 m	78° 41.305′	16° 28.365′	1410	2400
04-Aug	Inland glacier deep	RIV_60 m	78° 41.360′	16° 33.504′	1410	2260
18-Oct	Marine-terminating glacier shallow	MGL_20 m	78° 38.586′	16° 51.259′	1020	2350
18-Oct	Marine-terminating glacier deep	MGL_60 m	78° 39.124′	16° 50.695′	1020	2450
04-Aug	Reference shallow	CON_20 m	78° 37.076′	16° 40.568′	458	8160
02-Aug	Reference deep	CON_60 m	78° 37.177′	16° 39.430′	458	8200

Distance to shore refers to the distance from a station to the shore. For the reference, shore- and marine-terminating glacier stations, we used the Nordenskiöldbreen shore and for the inland glacier stations, we used the northern shore of the bay where the river leads into the fjord

wet weight of each identified taxon was measured on a balance to 0.0001 g (Online Resource 1). Scientific names of the taxa were checked with the World Register of Marine Species (WoRMS) (April 2024).

Sediment parameters: TOC and percent pelite

Small sediment samples were taken from each replicate grab to measure total organic carbon (TOC) and grain size, specifically percent pelite (percentage of sediment < 63 µm). Care was taken to avoid collecting macrozoobenthos. Sediment samples were immediately frozen at − 20 °C on board. In the lab, the sediment samples were freeze-dried at − 50 °C for 36 h in a FreeZone 2.5L Bench-top Freeze Dry Systems (Labconco, Kansas City, USA). To measure TOC, the dried sediment was first weighed to obtain dry weight (DW) and subsequently burned at 520 °C for 6 h (Heiri et al. 2001; Putyrskaya et al. 2020) in a Nabertherm B-170 muffle furnace (Nabertherm, Lilienthal, Germany). We used the loss of ignition (LOI) method to measure the ash-free dry weight (AFDW), which was used to calculate the TOC (in percent weight). To calculate percent pelite, dried sediment was wet sieved with a 63 µm mesh sieve. The residual material was dried at 60 °C for 24 h and weighed. Percent pelite was calculated by dividing the residual material weight with the total weight and subtracting that value from 1.

Sediment parameters: chlorophyll a and phaeopigments

Similar to sediment samples taken for TOC and percent pelite, a sediment sample was taken from each replicate grab to measure sediment chlorophyll *a* and phaeopigment concentrations. Samples were frozen at − 20 °C immediately on board and kept in the dark. In the lab, the samples were thawed at room temperature in darkness before extraction with 100% methanol for 24 h in a − 20 °C freezer. Subsequently, the samples were centrifuged for 15 min at 6000 rpm and aliquots of the supernatant were measured in a Turner Designs Trilogy fluorometer (Turner Designs, San Jose, USA) before and after acidification with 2 drops of 10% HCl (Holm-Hansen et al. 1965; Jordà-Molina et al. 2023). Chlorophyll *a* and phaeopigment values were calculated with the following equations, respectively.

$$Chla\left(mg/m^3\right) = F_d * T_{au} * \left(R_{before} - R_{after}\right) * V_{methanol}/V_{filtered}$$

$$Phaeo\left(mg/m^3\right) = F_d * T_{au} * R_{after} * V_{methanol}/V_{filtered}$$

F_d and T_{au} are calibration coefficients, R_{before} and R_{after} are the fluorescence values before and after acidification, respectively, and $V_{methanol}$ is the volume of added methanol, while $V_{filtered}$ is the volume of the filtered sample.

Statistical analysis

Community characteristics (abundance, taxa richness, Shannon index (H’ ($\log_e$)), Pielou’s evenness index (J’) and Simpson’s index (D’)) were calculated based on abundance data with the R package “vegan” (Oksanen et al. 2013). Kruskal–Wallis tests were performed (because of unequal variances between the samples) to determine if these community parameters differed between locations. Thereafter, a pairwise Wilcoxon test using the R package “stats” (R Core Team 2024) was performed to identify which pairs of locations were significantly different from each other in terms of community characteristics. Moreover, an average linkage (UPGMA) method cluster analysis of community abundance data based on the Czekanowski-Sørensen index (Sørensen 1948) was performed using PAST v.4.03 (Hammer et al. 2001) with a cutoff value of 0.6 to visualize grouping patterns and to assess how similar or dissimilar entire communities of the different stations were. Analysis of similarities (ANOSIM) based on the Czekanowski-Sørensen index with 9999 permutations on the four locations was conducted with the R package "vegan" to determine whether the observed clustering was significant (Clarke 1993; Clarke and Warwick 2001). Moreover, we performed a one-way permutational multivariate analysis of variance (PERMANOVA) based on the Sczekanowski-Sørensen index with 9999 permutations using PAST v.4.0.3 to test whether benthic communities significantly differ between different glacier types. The function 'multipatt' from the R package "indicspecies" (De Cáceres and Legendre 2009) was used to conduct an indicator species analysis to identify individual taxa that were indicative for the different locations. The indicator test statistic reflects the likelihood of group fidelity, a measure of species concentration in vegetation units (De Cáceres and Legendre 2009). Ideal indicator species are distinguished by high exclusivity and fidelity (Acharya et al. 2019). A heatmap was made with the R package "pheatmap" (Kolde 2019) to visualize the relative abundance of the five most abundant taxa at each replicate, and to investigate which taxa contributed to community clustering patterns. To assess how the different stations grouped together based on both taxa abundances and environmental variables, a Redundancy Analysis (RDA) with 999 permutations was carried out using the R package "vegan". The environmental variables included in the RDA were bottom water temperature (°C), bottom water salinity (psu), percent pelite (percentage of sediment <63 µm), TOC (%), chlorophyll *a* (mg/m^3), phaeopigments (mg/m^3) and distance to shore (m). For the shore-terminating glacier stations, we measured the distance to shore of the northern side of Nordenskiöldbreen and for the inland glacier stations, the northern shore of the bay where the river leads into the fjord. For the marine-terminating stations, we measured the distance to the marine-terminating glacier front and for the reference stations, the nearest site of glacier influence, which is the marine-terminating glacier front, measured as distance over water. The distances to shore was measured using the 'measure' tool in the Copernicus browser (Copernicus 2024) on a Sentimel-2 L2 A satellite picture (date: 06-July-2023). Since we did not obtain bottom water temperature and salinity values at the marine-terminating glacier stations, we used values from Szeligowska et al. (2021) since their IB2 station was directly between our two marine-terminating glacier stations. In addition, a Pearson's correlation analysis with Bonferroni correction for multiple comparisons using PAST v.4.03 was performed to investigate whether environmental characteristics correlated with univariate community characteristics.

Results

A total of 88 taxa from 9 phyla were identified in the 16 samples collected from the eight stations at the four locations. The most abundant phylum was Mollusca, accounting for 42.05% of the total taxa, followed by Annelida (37.50%), Arthropoda (6.82%) and Echinodermata (5.68%). Moreover, Mollusca contributed the most to biomass of all the phyla (83.50%), followed by Annelida (7.53%), Chordata (1.59%) and Echinodermata (1.32%).

The annelid family Cirratulidae, with 1760 individuals, was the most abundant taxon across all stations combined, followed by the bivalve *Ennucula tenuis*, with 534 individuals. These two taxa, plus *Axinopsida orbiculata* and *Lumbrineris mixochaeta* were present at all of the eight stations (Fig. 2; Table 2). The ten most abundant taxa (in order: cirratulids, *E. tenuis, Yoldiella solidula, A. orbiculata, L. mixochaeta,* and the bivalves *Macoma calcarea*, *Yoldiella propinqua*, Thyasiridae, *Thyasira gouldi* and *Yoldiella frigida)* accounted for 80.50% of all the organisms counted.

Overall, abundance was significantly lower at the inland glacier location (Kruskal–Wallis, $H = 10.32$ (3), $p = 0.02$; Table 3) compared to the other locations. The reference location had significantly higher taxa richness (Kruskal–Wallis, $H = 11.04$ (3), $p = 0.01$) compared to the other locations and the marine-terminating glacier location was the least diverse of all locations (Table 3).

The two Nordenskiöldbreen front locations (marine- and shore-terminating), clustered separately from each other at approximately 50% similarity, but clustered together with the reference location in comparison to the inland glacier location at 30% similarity (Fig. 2). The inland glacier stations were most different from the other stations and formed two separate clusters from each other, and from all the other stations (Fig. 2). The clustering was significantly different according to the ANOSIM based on the Czekanowski-Sørensen index ($R = 0.57$, $p < 0.001$). Moreover, the different locations showed significant differences in benthic communities across different glacier types (PERMANOVA, $F = 4.42$, df $= 3$, $p = <0.001$, $R^2 = 0.53$).

Ampharetidae and *Tridonta elliptica* were indicator taxa for the inland glacier location and the reference location had four indicator taxa according to the indicator species analysis (Table 2). *Mendicula ferruginosa* was indicative of the marine-terminating glacier location, while the shore-terminating glacier location did not show significant indicator taxa (Table 2).

The reference location showed the highest TOC levels as well as the highest phaeopigment and chlorophyll *a* value (Table 4). In contrast, the marine-terminating glacier location had the lowest values for these parameters. Percent pelite of the sediment was lower at the reference location compared to the other locations (Table 4).

For the shore-terminating glacier and inland glacier stations, evident stratification was visible through the CTD data, with fresher, colder surface layer of water overlying warmer, saltier water (Fig. 3). These stations also exhibited high turbidity in comparison with the reference location (Fig. 3). We did not have CTD measurements ourselves,

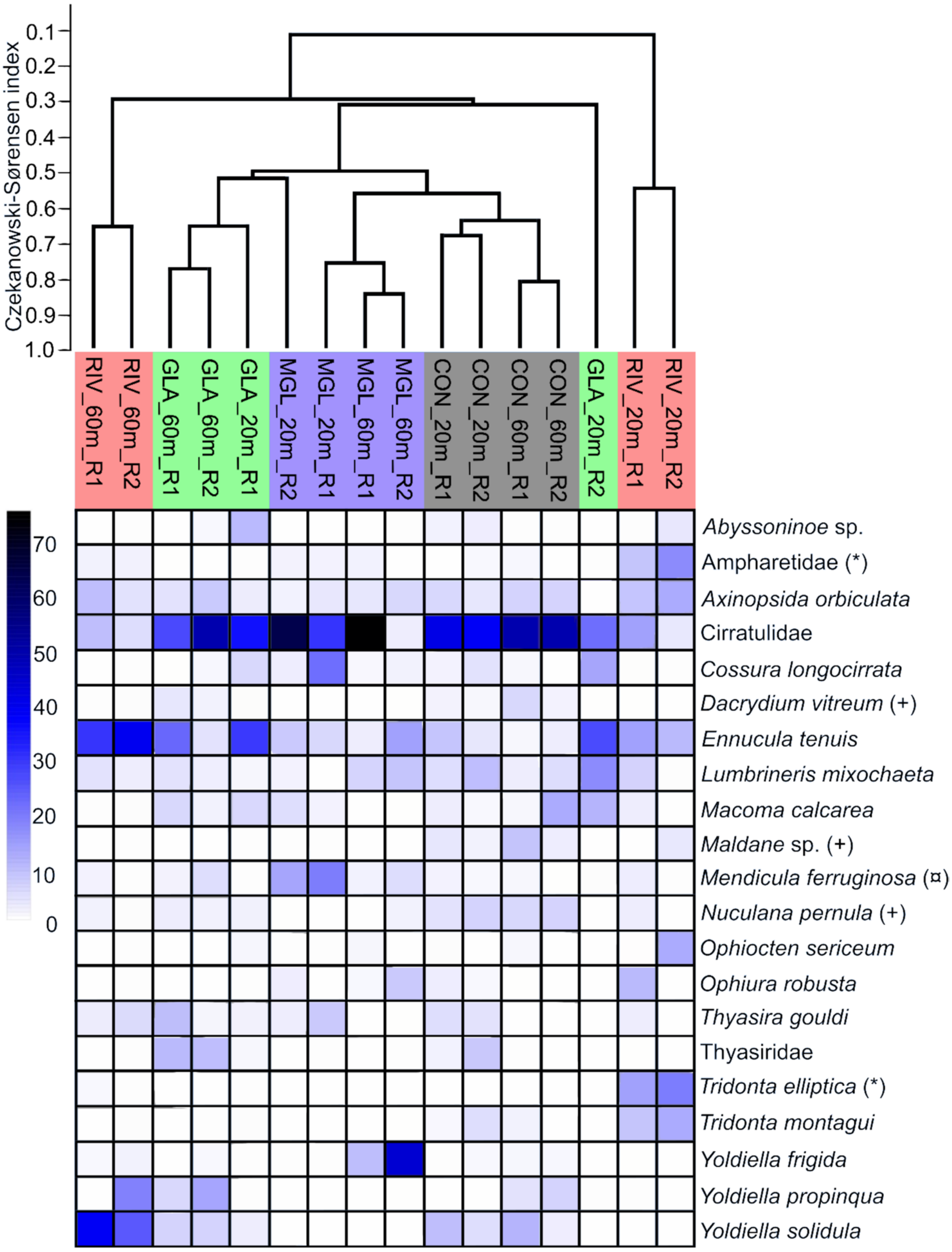

Fig. 2 Dendrogram of a pair grouped UPGMA linkage method cluster analysis based on the Czekanowski-Sørensen index derived from abundance data at the four locations and a heatmap of the relative abundances in percentages of the five most abundant taxa from each grab. Short names are used as per Gonzalez Triginer et al. (2024a). RIV = Inland Glacier (river) Location, MGL = Marine-Terminating Side of Nordenskiöldbreen, GLA = Shore-Terminating Side of Nordenskiöldbreen and CON = Reference Location. Indicator species for the different locations are marked: (*) for the inland glacier location, (¤) for the marine-terminating location and (+) for the reference location with minimal glacial influence. Note that there are no indicator taxa for the shore-terminating glacier location. Edited with Inkscape 1.3.2

however, turbidity at the marine-terminating location was recorded to be order of magnitudes higher than what we measured at the shore-terminating glacier and inland glacier stations (Szeligowska et al. 2021).

The significant variables among the explanatory environmental variables in the RDA were TOC (RDA, $F_7 = 5.23$, $p = 0.02$), percent pelite (RDA, $F_7 = 9.55$, $p < 0.01$), bottom water temperature (RDA, $F_7 = 8.92$, $p = 0.01$) and distance to the shore (RDA, $F_7 = 7.59$, $p = 0.01$). The first two axes explained 86.23% of the total variation in the RDA (Fig. 4), where axis 1 was positively correlated with distance to stressor and bottom water temperature, while negatively correlated with TOC and percent pelite. Axis 2 was positively correlated with bottom water temperature and negatively with salinity.

There were several significant correlations between community characteristics and environmental variables according to the Pearson's correlation analysis with Bonferroni correction for multiple comparisons (Fig. 5). Correlations were found between taxa richness and percent pelite ($r = -0.90$), chlorophyll a ($r = 0.85$) and phaeopigments ($r = 0.86$). Distance to shore was positively correlated with TOC ($r = 0.82$) and negatively correlated with percent pelite ($r = -0.83$; Fig. 5).

Table 2 The 3 most abundant species per location and the indicator species for the different locations with test statistics and *p*-value according to the indicator species analysis

Location	3 most abundant taxa	Indicator taxa	Test statistics	*p*-value
Inland glacier	*Ennucula tenuis*	Ampharetidae	0.79	0.01
	Yoldiella solidula	*Tridonta elliptica*	0.70	0.03
	Cirratulidae			
Shore-terminating glacier	Cirratulidae			
	Ennucula tenuis			
	Thyasiridae			
Marine-terminating glacier	Cirratulidae	*Mendicula ferruginosa*	0.62	0.04
	Yoldiella frigida			
	Mendicula ferruginosa			
Reference	Cirratulidae	*Nuculana pernula*	0.95	< 0.01
	Yoldiella solidula	*Ciliatocaridum ciliatum*	0.93	< 0.01
	Lumbrineris mixochaeta	*Dacrydium vitreum*	0.76	< 0.01
		Maldane sp.	0.70	0.03

Note that no indicator species were found for the shore-terminating glacier location

Table 3 Community characteristics at the four locations

	Shore-terminating glacier	Inland glacier	Marine-terminating glacier	Reference	Kruskal–Wallis	
					Chi-sqrt (H)	*p*-value
Abundance	291.25 ± 48.52	135.5 ± 53.00	259.75 ± 32.97	385.00 ± 28.3	10.30	0.02
Biomass (g)	25.26 ± 12.71	7.53 ± 2.03	2.98 ± 1.31	22.53 ± 12.09	5.56	0.14
Taxa richness	21.25 ± 2.69	16.00 ± 1.49	14.50 ± 0.65	35.75 ± 4.19	11.00	0.01
Shannon index (H′)	2.15 ± 0.06	2.11 ± 0.21	1.22 ± 0.11	2.37 ± 0.13	9.29	0.03
Pielou’s evenness index (J′)	0.71 ± 0.04	0.77 ± 0.08	0.46 ± 0.05	0.66 ± 0.02	8.89	0.03
Simpson’s index (D′)	0.83 ± 0.02	0.84 ± 0.05	0.50 ± 0.04	0.80 ± 0.02	8.93	0.03

Numbers are averages and standard errors based on the four replicates taken at each location (pooling ~ 20 and ~ 60 m stations). The last two columns refer to the results of the Kruskal–Wallis testing that specific community characteristic displayed significant differences across all locations

Discussion

We investigated benthic communities in Billefjorden at locations near different types of glacier fronts which represent different stages of glacier retreat, to assess the possible impact of climate change and retreating glaciers on benthic fjord fauna. Species from the phyla Annelida and Mollusca dominated our samples, which is similar to what has been seen in other benthic infaunal studies in the western fjords of Spitsbergen (Włodarska-Kowalczuk and Pearson 2004; Renaud et al. 2007; Ugelstad 2019; Díaz et al. 2023). Only four taxa (Cirratulidae, *Ennucula tenuis, Axinopsida orbiculata* and *Lumbirneris mixochaeta*) were present at all eight stations. Cirratulids inhabit areas with soft sediment and can tolerate high sedimentation rates, wide salinity ranges and different sediment types (Włodarska-Kowalczuk et al. 1998; Włodarska-Kowalczuk and Pearson 2004; Kędra et al. 2011; Carroll and Ambrose 2012). Therefore, their ubiquity and dominance in our samples is likely due to them being capable of tolerating the different environments represented at our study locations. *E. tenuis* and *A. orbiculata* are both surface deposit-feeders (Bour et al. 2018; Degen and Faulwetter 2019) and have been found in other Arctic bays (Kędra et al. 2012; Mokievsky et al. 2020). *L. mixochaeta* has been found around the whole Svalbard archipelago in high abundances (Carroll and Ambrose 2012; Jordà-Molina et al. 2023). In short, these taxa are common in west Spitsbergen fjords (Kędra et al. 2011; Carroll and Ambrose 2012) and have wide ranges of tolerances for different environmental factors, which is likely why these taxa were found at all of our eight stations that are highly variable in terms of local conditions.

Although species and taxa being similar to what is seen overall in Svalbard fjords, we nonetheless expected differentiation between communities at the study locations since the locations represent different environmental conditions. Indeed, despite their close proximity, benthic communities significantly differed across the different locations according to the one-way PERMANOVA.

Table 4 Environmental variable values measured from each grab in the four study locations

Grab	TOC (%)	Pelite (%)	Chlorophyll a (mg/m^3)	Phaeo (mg/m^3)	Salinity (psu)	Temperature (°C)
GLA_20 m_R1	6.16	91.03	206.85	345.59	33.82	4.42
GLA_20 m_R2	6.14	88.36	237.99	438.18	33.82	4.42
GLA_60 m_R1	5.65	87.64	92.42	280.16	34.73	− 0.82
GLA_60 m_R2	5.97	80.81	91.41	341.43	34.73	− 0.82
RIV_20 m_R1	9.69	92.26	3.91	41.16	34.00	4.87
RIV_20 m_R2	10.11	94.45	4.02	33.86	34.00	4.87
RIV_60 m_R1	10.42	90.77	115.67	250.01	34.94	− 1.49
RIV_60 m_R2	10.24	89.89	61.08	161.90	34.94	− 1.49
MGL_20 m_R1	5.47	99.28	9.52	28.13	34.30	4.09
MGL_20 m_R2	5.89	97.71	10.27	69.87	34.30	4.09
MGL_60 m_R1	5.40	98.24	10.06	57.18	34.30	4.09
MGL_60 m_R2	4.66	96.70	14.79	80.88	34.30	4.09
CON_20 m_R1	12.38	61.94	335.87	611.93	34.10	5.23
CON_20 m_R2	11.55	51.14	366.07	677.44	34.10	5.23
CON_60 m_R1	13.71	65.63	85.74	353.86	34.87	− 1.51
CON_60 m_R2	13.38	64.00	175.65	593.87	34.87	− 1.51

Short names are used as per Gonzalez Triginer et al. (2024a). *RIV* inland glacier (river) location, *MGL* marine-terminating glacier side of Nordenskiöldbreen, *GLA* shore-terminating glacier side of Nordenskiöldbreen and *CON* reference location. TOC refers to the total organic carbon as percent weight, percent pelite to the percentage of sediment < 63 µm, chlorophyll *a* and phaeo to the chlorophyll *a* and phaeopigment concentrations, respectively, salinity to the bottom water salinity and temperature to the bottom water temperature. Note that the salinity and temperature values written here of the marine-terminating glacier location are taken from the IB2 station in Szeligowska et al. (2021)

We hypothesized higher diversity at the reference location with minimal glacier influence compared to the other locations as sedimentation and turbidity around glaciers can restrict taxa (Kokarev et al. 2017). Turbidity values were indeed higher at the shore-terminating and the inland glacier river locations compared to the reference location (Fig. 3), indicating higher sedimentation rates around these locations. Even higher turbidity values have been recorded at the marine-terminating glacier location (Szeligowska et al. 2021). Accordingly, as hypothesized, taxa richness at the reference location was significantly higher than at the other locations. High levels of sedimentation can bury infauna and the clog feeding apparatus of filter feeders. The high sedimentation rates of all three glacier stations could therefore favour high abundances of relatively few opportunistic taxa that rapidly colonize disturbed areas (Pearson 1978), thereby resulting in lower richness and diversity of these locations in comparison to the reference location.

Another way in which high sedimentation rates can restrict species recruitment is through light inhibition which subsequently leads to low rates of surface primary production and reduced food export to the seafloor (Hartvich et al. 2017; Cantoni et al. 2020; Li et al. 2023, 2024). Indeed, our results indicate lower food supply at the three glacier-influenced and high turbidity locations compared to the reference location with lower turbidity values: We measured highest chlorophyll *a*, phaeopigments and TOC at the reference location (Table 4). The reference location is therefore relatively more food-rich, allowing for many different species and taxa to thrive as opposed to more specialized or opportunistic ones. This suggests that the high turbidity and sediment influx from glaciers, regardless of whether they are marine-terminating or on land appears to limit the number of taxa that can colonize and settle on the fjord seafloor, at least compared to locations further away from and less influenced by glaciers. It is of note that González Triginer et al. (2024a) found higher pelagic density at the reference location compared to the shore-terminating glacier and inland glacier locations, indicating that glacier-based sedimentation impacts pelagic communities in similar ways to benthic communities.

In line with Fetzer et al. (2002), percent pelite was lower (larger grain size) at the reference location than at the other locations (Table 4). Our stations in Billefjorden were sampled at approximately similar depths, which suggests that glacier-based sedimentation affects percent pelite, probably through the deposition of fine, glacial muds (Zaborska et al. 2006). We found percent pelite to be a significant environmental variable in explaining differences in benthic communities among the locations based on the RDA (Fig. 4). Moreover, percent pelite was strongly correlated with taxa richness (Fig. 5). Percent

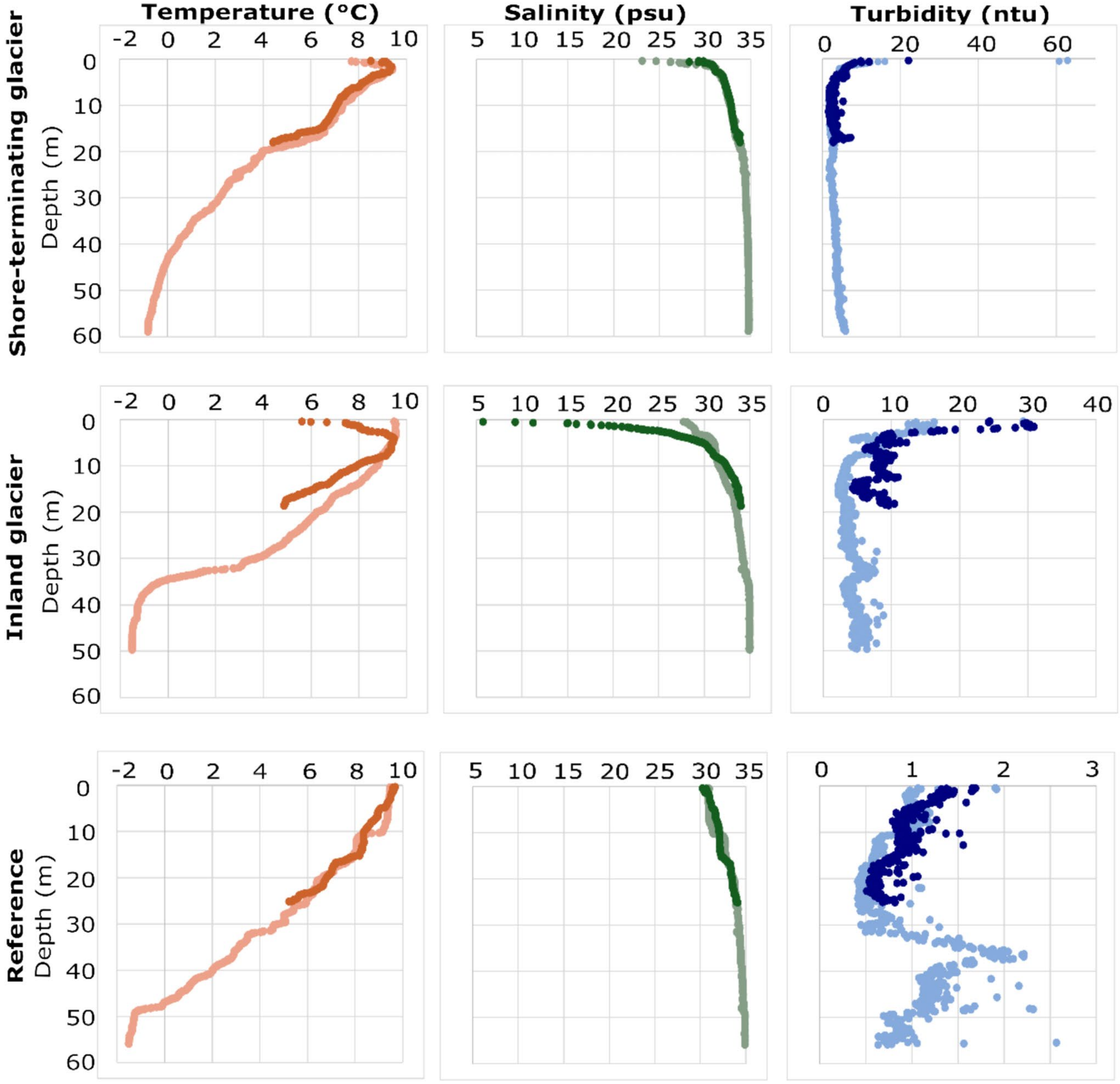

Fig. 3 CTD water column profiles of temperature, salinity and turbidity. Dark orange = temperature 20 m station, light orange = temperature 60 m station, dark green = salinity 20 m station, light green = salinity 60 m station, dark blue = turbidity 20 m station and light blue = turbidity 60 m station. Note the different scales between the turbidity graphs. Edited with Inkscape 1.3.2

pelite can impact benthic community composition as it affects the amount of carbon that can be bound to the sediment (Secrieru and Oaie 2009) and certain species require specific sediment types for constructing protective tubes or burrows (Dudgeon 2020). Generally, finer sediment is associated with higher carbon content due to the greater surface area and capacity to retain organic matter (Secrieru and Oaie 2009; Quoc et al. 2021). However, we found the inverse: Sediment was coarsest at the reference location, where also the highest TOC values were measured. Coarser sediments could offer more oxygenated conditions, which could benefit a broader range of species, while finer sediments might indicate more oxygen-depleted environments (Quoc et al. 2021). Therefore, the coarser sediment of the reference location compared to the glacier locations is potentially more aerated than the sediment at the glacier locations and this, in combination with higher food content and lower disturbance from sedimentation might explain the higher abundance and taxa richness at the reference location.

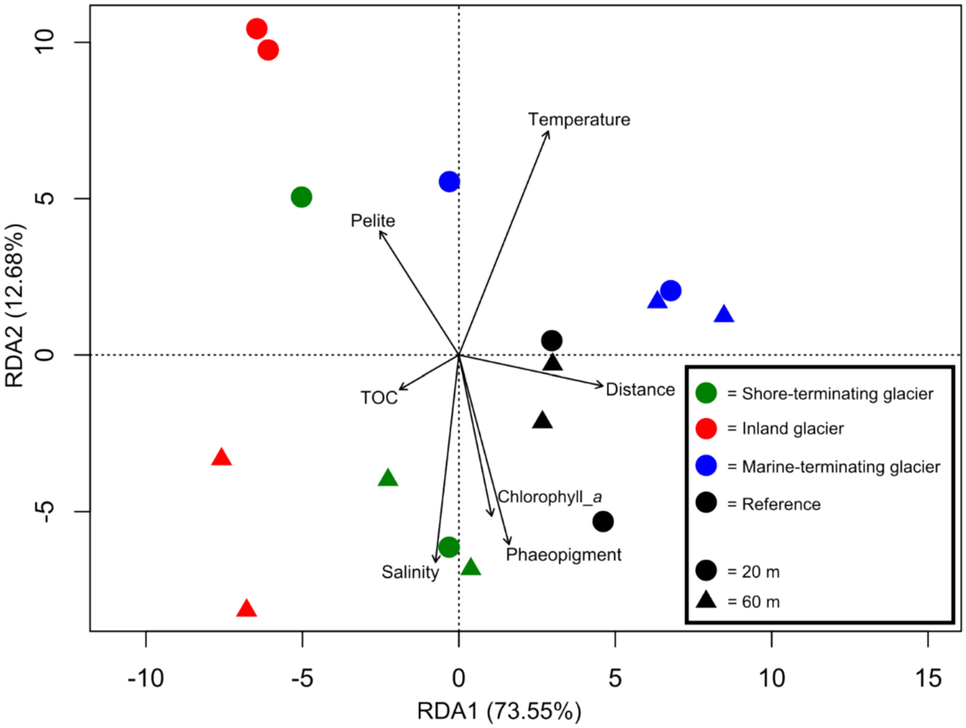

Fig. 4 Redundancy analysis (RDA) of abundance and environmental data. The two axes together explain 86.2% of the variance among the 16 different grabs. Edited with Inkscape 1.3.2

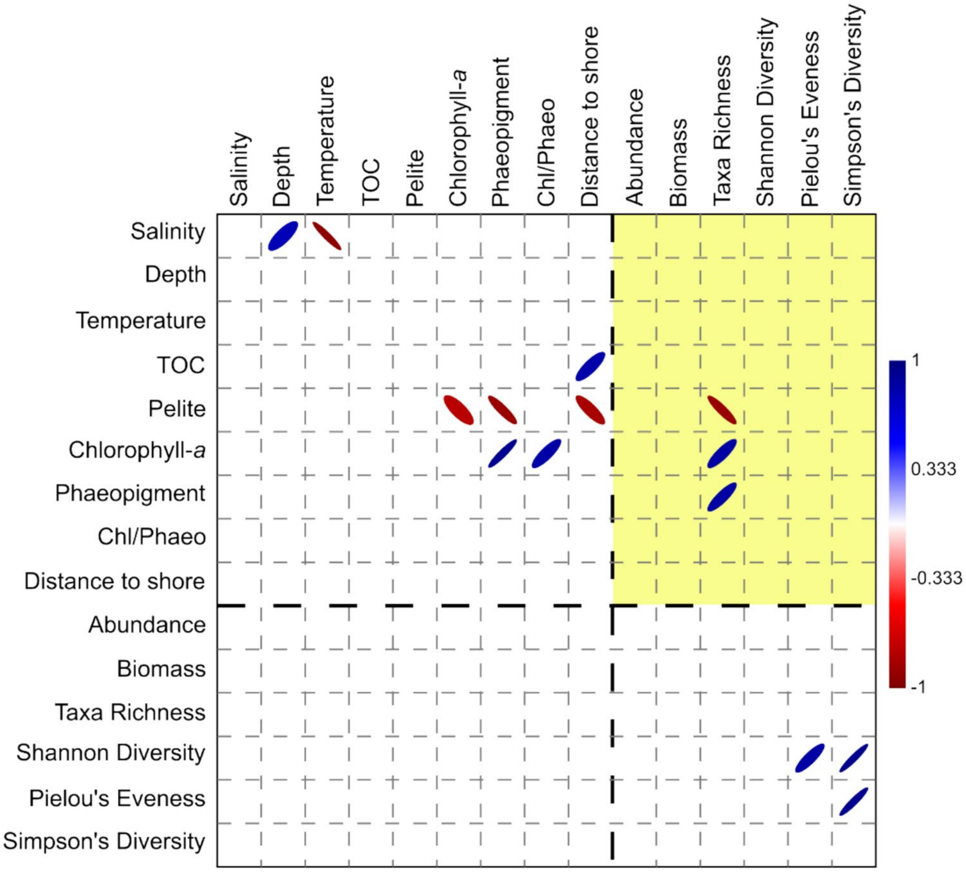

Fig. 5 Pearson's correlation analysis plot with Bonferroni correction for multiple comparisons. Positive (blue) or negative (red) *r*-value directions illustrate the collinearity between faunal community characteristics and environmental variables. Only significant relationships are displayed ($p < 0.05$). The yellow polygon is displayed to emphasize the collinearity between community characteristics with environmental variables. Edited with Inkscape 1.3.2

Despite the reference location exhibiting higher abundance and taxa richness compared to the other locations, this was not the case for diversity; contrary to our predictions, diversity indices at the reference location were not significantly higher than at the other locations, with the exception of the marine-terminating glacier location (Table 3). This may be attributed to the influence of dominance patterns within the benthic community at the reference location. The Shannon diversity index considers both the number of taxa as well as evenness, and the strong dominance of cirratulids at the reference location (41.06% of the total number of individuals) may have contributed to the lower Shannon diversity scores despite hosting far more taxa than the other locations. As previously noted, cirratulids can inhabit both disturbed and stable environments, which is in line with our findings as we found cirratulids in great abundances at the reference location where disturbances from glaciers are likely very low, and also at the marine-terminating location where glacial disturbances could be high. Overall, the reference location hosts a greater number of taxa compared to the other locations, but the dominance of cirratulids results in similar diversity indices to the other locations.

Other than differences between the reference location and the locations at glacier fronts, we found, as expected, differences between the two Nordenskiöldbreen locations. Diversity indices were consistently lower at the marine-terminating glacier location compared to the shore-terminating glacier location (Table 3). Moreover, the biomass and sediment pigment values at the marine-terminating glacier location were also lower than at the shore-terminating glacier location, demonstrating that there is likely less food available for the benthos at the marine-terminating glacier location. It is of note that marine-terminating glacier fronts are considered as Arctic productivity hotspots (Meire et al. 2017, 2023; Urbanski et al. 2017). However, these hotspots tend to be some distance away from the glacier front itself. Close to the glacier front, environmental conditions can be unstable, and within the sediment plume, light availability is limited. With increasing distance from the glacier, nutrient levels may decrease while light availability increases and if a balance is reached, where nutrient levels are still relatively high and light levels are not inhibitory, productivity hotspots might emerge. Our marine-terminating glacier sampling stations were close to the glacier front, in the middle of a large sediment plume (Szeligowska et al. 2021), where turbidity values are exceedingly high, which likely leads to low surface primary production and low food availability on the seafloor. This is supported by the low sediment pigment and TOC values at the marine-terminating glacier location (Table 4). Consequently, the benthos at the marine-terminating glacier side is considerably sparser and less diverse than at the shore-terminating glacier side, located nearby. It is not clear how the sediment plume at the marine-terminating glacier location originates, however, the two fronts of Nordenskiöldbreen appear to generate distinct benthic environments and subsequently, distinct communities.

Some taxa present at the marine-terminating glacier location could represent the food-poor environment. *Mendicula ferruginosa* is a species from the small, mobile bivalve family Thyasiridae (Dufour 2005). *M. ferruginosa* is typically considered a deeper water species with a currently known depth range of 40 to 4582 m (Keuning et al. 2011). Our findings of *M. ferruginosa* at approximately 20 m therefore represents a record for the species' shallowest depth. Despite the shallow depth, the marine-terminating glacier location may resemble the relatively food-poor environment of the deep sea that this species is adapted for, which could explain the species' high exclusivity and fidelity at this location. As the indicator species of the marine-terminating glacier location, it appears to be able to thrive in water shallower than its common depth range, perhaps due to this location exhibiting some aspects, such as food scarcity, that are similar to deeper water environments.

Other than the two sides of Nordenskiöldbreen, we also wished to compare the two land-terminating glacier front locations, i.e., the inland glacier location and the shore-terminating side. We expected similar benthic community structure at these two locations as both locations have terrestrial inputs and similar physical characteristics (Meire et al. 2017; Adakudlu et al. 2019). In both cases, sediment is deposited on the fjord floor from glaciers that terminate on land, the difference being how far inland those glaciers are. Diversity indices were indeed comparable between the inland and shore-terminating glacier locations (Table 3), however these locations clustered separately from each other in the cluster analysis (Fig. 2). In fact, the inland glacier samples clustered separately from all the other samples. Ugelstad (2019) observed a similar phenomenon; benthic communities of the shore-terminating side of the Nordenskiöldbreen location clustered separately from the inland glacier driven river-runoff benthic communities in Petuniabukta. González Triginer et al. (2024b) mapped kelp in the shallow water (< 15 m depth) at the shore-terminating glacier front of Nordenskiöldbreen, while kelp was barely present in the Petuniabukta inland glacier river bay. Kelp is known to be an ecosystem engineer (Shunatova et al. 2018). Although not directly present at our sampling sites, drift material, nutrients and organic material from kelp beds may be transported to the deeper shore-terminating glacier stations, which could lead to differences in benthic communities between the shore-terminating glacier and inland glacier locations specifically within Billefjorden. It is uncertain whether similar differences exist between shore-terminating glacier fronts and inland glacier river bays in other areas. If kelp beds in adjacent areas drive the differences observed between the shore-terminating glacier and inland glacier locations in Billefjorden, then for similar patterns to appear elsewhere, glacier retreat would have to expose hard substrate and provide enough light availability for kelp to colonize and grow.

In addition to the differences between the shore-terminating and inland glacier locations, an unexpected finding was that the two inland glacier stations were distinct from each other (Fig. 2). At all other locations, the shallower and deeper water stations were more similar to each other than to stations at the same depth at other locations, but the inland glacier stations were the exceptions to this. At the inland glacier location, the two stations were further apart from each other (1410 m) than at the other locations (Table 1). As the river runoff gradually deposits sediment, the transition from shallow to deeper water occurs slowly at this location, causing the distance between the shallow and deeper station to be greater at the inland glacier location compared to the other locations. A gradual change in depth over a greater distance means that environmental conditions can change slowly across the location (Riesch et al. 2018). In contrast, at the other locations where the distance between stations was shorter, environmental conditions between the shallow and deeper stations were more similar. Therefore, the gradual depth transition at the inland glacier location possibly fosters bigger differences between benthic communities at the two stations, compared to the other locations.

Conclusion

Benthic communities in locations of different stages of glacier retreat in the high Arctic Billefjorden are highly distinct. Specifically, high sedimentation and turbidity from glaciers may result in limited food supply for the benthos, leading to less diverse and lower abundance communities compared to locations with minimal glacier influence. The two sides of the same glacier host strikingly distinct benthic communities with lower diversity and abundance at the marine-terminating side, likely due to destructively high sedimentation rates that also severely limits food supply to the benthos. This low food environment may have further led to the expansion of certain deeper water species to shallow water depths. Despite runoff from inland glaciers and a shore-terminating glacier being functionally similar, distinct benthic communities were found between the shore-terminating glacier front and the inland glacier location. However, this difference is likely not specifically due to glacier-related processes, but rather due to the presence of ecosystem engineers like kelp nearby, whose presence and colonization is contingent upon adequate hard substrate being present. Fjordic benthic community composition therefore varies across the study locations which represent different stages of glacier retreat. Our findings highlight the importance of understanding localized environmental gradients in Arctic fjords, as glacier retreat due to climate change is likely to drive shifts in fjordic benthic community structures in a changing Arctic.

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Declarations

Competing interests The authors declare no competing interests.

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