RESEARCH ARTICLE

Ichnodiversity in the eastern Canadian Arctic in the context of polar microbioerosion patterns

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Abstract

Studies of marine microbioerosion in polar environments are scarce. They include our recent investigations of bioerosion traces preserved in sessile balanid skeletons from the Arctic Svalbard archipelago and the Antarctic Ross Sea. Here, we present results from a third study site, Frobisher Bay, in the eastern Canadian Arctic, together with a synthesis of our current knowledge of polar bioerosion in both hemispheres. Barnacles from 62 to 94 m water depth in Frobisher Bay were prepared using the cast-embedding technique to enable visualization of microboring traces by scanning electron microscopy. In total, six ichnotaxa of traces produced by organotrophic bioeroders were found. All recorded ichnotaxa were also present in Mosselbukta, Svalbard, and most in the Ross Sea. Frobisher Bay contrasts with Mosselbukta in that it is a siliciclastic-dominated environment and shows a lower ichnodiversity, which may be accounted for by the limited bathymetrical range and a high turbidity and sedimentation rate. We evaluate potential key ichnotaxa for the cold-temperate and polar regions, of which the most suitable are *Flagrichnus baiulus* and *Saccomorpha guttulata*, and propose adapted index ichnocoenoses for the interpretation of palaeobathymetry accordingly. Together, the three studies allow us to make provisional considerations about the biogeographical distribution of polar microbioerosion traces reflecting the ecophysiological limits of their makers.

Introduction

Bioerosion is "the process by which animals, plants and microbes sculpt or penetrate surfaces of hard substrates" (Bromley 1994: 1). The process is an important mechanism of calcium carbonate recycling in marine environments and has been referred to as 'the other ocean acidification problem' because chemical biocorrosion is assumed to increase significantly with ongoing ocean acidification, leading to an imbalance (see the review by Schönberg et al. [2017]). As ocean acidification most significantly effects polar water masses (see Fabry et al. [2009] for details), it is crucial to better understand bioerosion patterns in these regions.

Bioeroding agents are categorized as grazers, attached epiliths, or macro- and microborers (Wisshak 2012). Typical microboring organisms include cyanobacteria, chlorophytes and fungi (Golubic et al. 1975; Wisshak 2012), while macrobioeroders are, for instance, sponges, bivalves and polychaetes (Glynn & Manzello 2015). Bioerosion is performed either chemically (biogenic dissolution) or mechanically (e.g., rasping or biting of substrate), or by a combined technique. Microborers, however, exclusively bioerode by chemical means (Schönberg et al. 2017).

During bioerosion, characteristic traces are produced, which often allow conclusions about the trace maker. Traces by bioeroding microendoliths often conform to the outline of their producers and are commonly less than a millimetre in size (Wisshak 2012). These traces are addressed as ichnotaxa, with more than 300 valid ichnospecies (Wisshak, Knaust et al. 2019). Ichnotaxa may serve as useful indicators of palaeotemperature, as some trace makers are limited to a specific temperature range (see the review by Wisshak 2012). In addition, ichnotaxa may offer insights into palaeobathymetry (Wisshak et al. 2011): index ichnocoenoses were initially defined by

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Glaub (1994) and are based on the co-occurrence of specific key ichnotaxa and general characteristics in the trace assemblage, relying on the phototrophic character of many euendoliths and their dependence on the availability of light (see the review by Wisshak [2012]).

Most studies of bioerosion have been conducted in the biogeographical provinces of the warm to warm-temperate oceans (e.g., Kiene & Hutchings 1992; Chazottes et al. 1995; Kiene et al. 1995; Le Campion-Alsumard et al. 1995; Vogel et al. 2000; Tribollet & Golubic 2005; Alvarado et al. 2017; Fig. 1). These studies have focussed on a variety of topics, such as different bioerosion agents in and on various substrates, their traces, and bioerosion pace and rate, as well as expected changes with climate change.

The very few studies from the cold-temperate province of the Northern Hemisphere are mainly from the North-east Atlantic (e.g., Akpan & Farrow 1985; Schmidt & Freiwald 1993; Glaub et al. 2002; Beuck & Freiwald 2005; Wisshak 2006) and North-east Pacific (e.g., Young & Nelson 1988). Studies from the cold-temperate province of the Southern Hemisphere include Patagonia (e.g., Malumián et al. 2006; Richiano et al. 2017; Aguirre et al. 2019), of which the most recent substrate dates from the Quaternary period, Chile (Försterra et al. 2005) and New Zealand (Nelson et al. 1988).

The very few studies are from the polar carbonate realm (Aitken & Risk 1988; Casadío et al. 2001; Cerrano et al. 2001; Casadío et al. 2007; Hanken et al. 2012). So far, the most comprehensive studies, including lists of microbioerosion traces and their bathymetric trend, have been our previous studies from Arctic Svalbard (Meyer et al. 2020) and the Antarctic Ross Sea (Meyer et al. 2021).

We report on a third study site in the eastern Canadian Arctic, here, to further develop our understanding of polar microbioerosion and to evaluate the results in a global context. We chose Frobisher Bay, on south-eastern Baffin Island, because its marine geology is relatively well studied (see references in Todd et al. 2016; Herder et al. 2021). Although Frobisher Bay is below the Arctic Circle (Fig. 2), it experiences climatic and oceanographic conditions typical of the Canadian Arctic, and represents the polar carbonate realm, which is characterized by heterozoan carbonates (after James & Lukasik 2010). In contrast to our Svalbard study sites, Frobisher Bay is not a carbonate factory setting, mostly on account of its high terrigenous sediment input, although carbonate bioclasts are abundant within the dominantly siliciclastic sediment (Zammit 2017). Comparing Frobisher Bay with Svalbard and Antarctica can improve our insights into the variability of microbioerosion trace assemblages in polar environments. In this study, we visualize, analyse and list microbioerosion traces in barnacles from different water depths by implementing the commonly applied cast-embedding
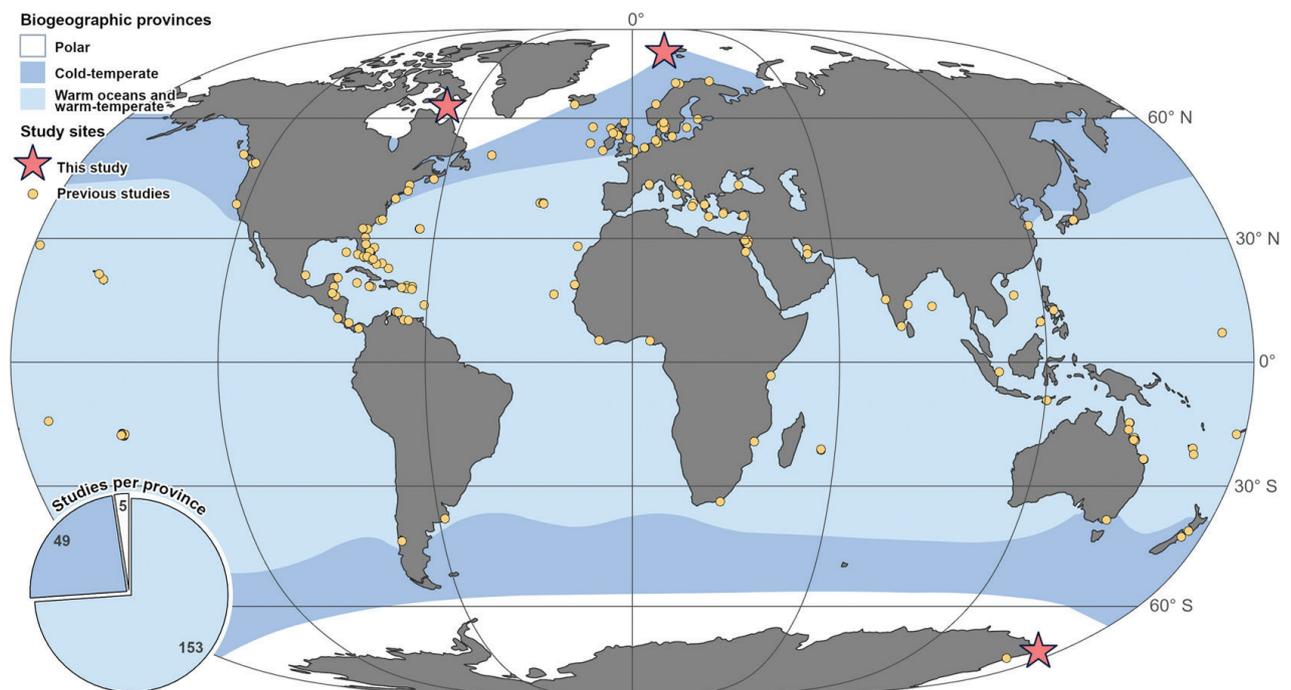
Fig. 1 The marine biogeographic provinces (based on Briggs & Bowen [2012]) and illustration of previous study sites regarding the recent microbioerosion and euendoliths (yellow dots). Featured studies are based on the bibliography by Radtke et al. (1997), Wisshak (2006) and a Thomson (now Clarivate) ISI Web of Knowledge (2020) search from 2006 to 2020 with the keywords 'microbioerosion' and 'microendoliths' (figure modified from Meyer 2020).
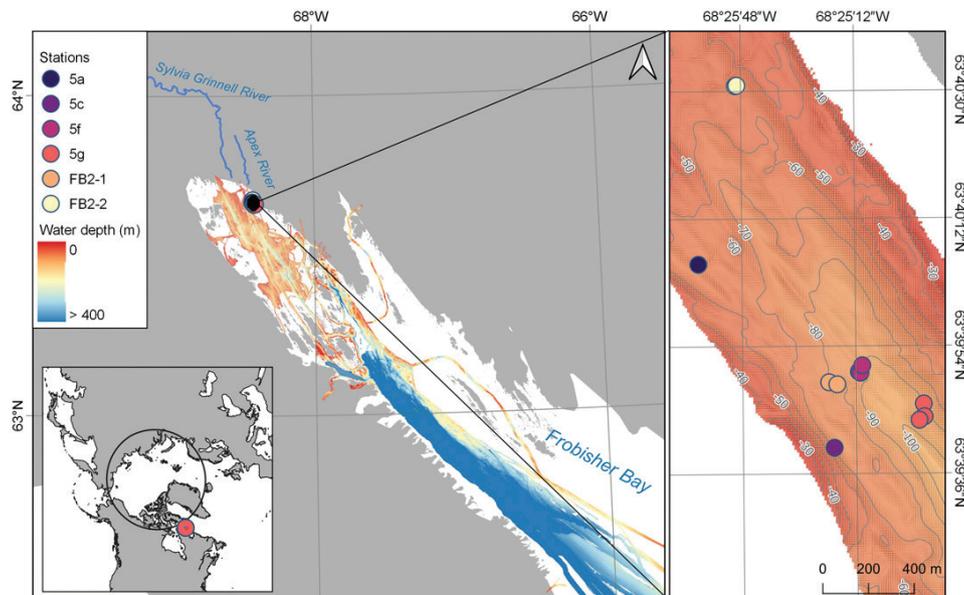
Fig. 2 Map of the southern Baffin Island and details of the sample origin in Frobisher Bay. Bathymetric data for Frobisher Bay were retrieved from the Canadian Hydrographic Service (2018) and for the inset map from Misiuk et al. (2019). The Frobisher Bay shoreline and the two rivers shown were extracted from CanVec Series (2017).

technique, and we evaluate their occurrence in light of new calcium carbonate saturation data from Frobisher Bay. Additionally, we evaluate whether there are alternative key ichnotaxa for the polar regions.

Materials and methods

Study site

Barnacles were sampled in the inner Frobisher Bay, Baffin Island, eastern Canadian Arctic, close to the northern tip of the bay and the eastern shore from 62 to 94 m water depth (Fig. 2, Table 1).

Frobisher Bay is a partially enclosed embayment, ca. 250 km long, at the widest point towards the entry of the Hudson Strait ca. 65 km wide, and ca. 20 km wide in the inner area. The outer bay is up to 800 m deep, while the inner bay is shallower, with one-third deeper than 100 m (Misiuk et al. 2019). The bay experienced high deposition of glacially derived sediments following deglaciation (Deering et al. 2018). Abundant cobbles and boulders from moraines and other glacial deposits, and from ice-rafted debris, support hard-substrate-dependent epifauna (Misiuk et al. 2019), including the barnacles studied here.

Frobisher Bay is at ca. 63.60 °N and 68.40 °W and is, therefore, without true polar days but long day lengths from June to July (Fig. 3). Sea ice is stable by December, with the maximum sea-ice thickness in late May/early June (Fig. 3; Fetterer et al. 2017) and no multi-year sea

ice (Grainger et al. 1985). Sea-ice scouring was observed in water depths shallower than 50 m (Deering et al. 2018) and extensive iceberg scouring down to 80 m (Todd et al. 2016).

The inner bay experiences extreme tides up to 12.6 m (McCann & Dale 1986; Deering et al. 2018), which is the maximum tidal amplitude in the Canadian Arctic (Collins et al. 2011). The high tidal amplitudes with great amounts of suspended sediment may occlude the sea floor, reducing the light that reaches the bottom. Sediment movement from the land to the sea depends on the season due to snow melting (Andrews 1987). The highest sedimentation rate (Andrews 1987; Atkinson & Wacasey 1987) and the primary productivity peak (Grainger 1979) occur from June to July, together with the phytoplankton bloom right after the sea ice break-up (Hsiao 1992). In this study site, the Sylvia Grinnell River and Apex River are of importance regarding the turbidity and sediment input (Fig. 2).

Marine environment

The marine environment in Frobisher Bay, particularly the state of ocean acidification, was investigated. Samples for TIC and TA analysis were collected using a CTD rosette package (SeaBird 911+) in 2016, 2017 and 2018 on board the CCGS *Amundsen*. Instruments on the CTD probe measured temperature, conductivity, dissolved oxygen, dissolved nitrates, chlorophyll *a* (via fluorescence), CDOM, turbidity via beam transmission and % irradiance, measured as CPAR. The sample collection, storage and

Table 1 Details of barnacle sample collection. Latitude, longitude and water depth were recorded at the start of deployment.

Water depth (m)	Sample ID	Date	Survey vessel[a]	Latitude	Longitude	Gear	No. of samples
62	FB2-2_G3	16 July 2016	*Amundsen*	63.67522	–68.43048	Box corer	3
63	FB2-2_G1	16 July 2016	*Amundsen*	63.67523	–68.43035	Box corer	4
74	5c_G4	10 November 2016	*Nulialjuk*	63.66102	–68.42195	Van Veen grab	4
80	FB2-1_G1	16 July 2016	*Amundsen*	63.66358	–68.42238	Box corer	4
81	FB2-1_G3	16 July 2016	*Amundsen*	63.66350	–68.42167	Box corer	4
86	5g_G3	10 November 2016	*Nulialjuk*	63.66272	–68.41404	Van Veen grab	4
90	5f_G6	10 November 2016	*Nulialjuk*	63.66395	–68.41961	Van Veen grab	4
90	5f_G8	10 November 2016	*Nulialjuk*	63.66424	–68.41944	Van Veen grab	4
91	5g_G4	10 November 2016	*Nulialjuk*	63.66222	–68.41398	Van Veen grab	4
93	5g_G2	10 November 2016	*Nulialjuk*	63.66209	–68.41443	Van Veen grab	4
94	5g_G1	10 November 2016	*Nulialjuk*	63.66209	–68.41443	Van Veen grab	4

[a]CCGS *Amundsen* and MV *Nulialjuk.*
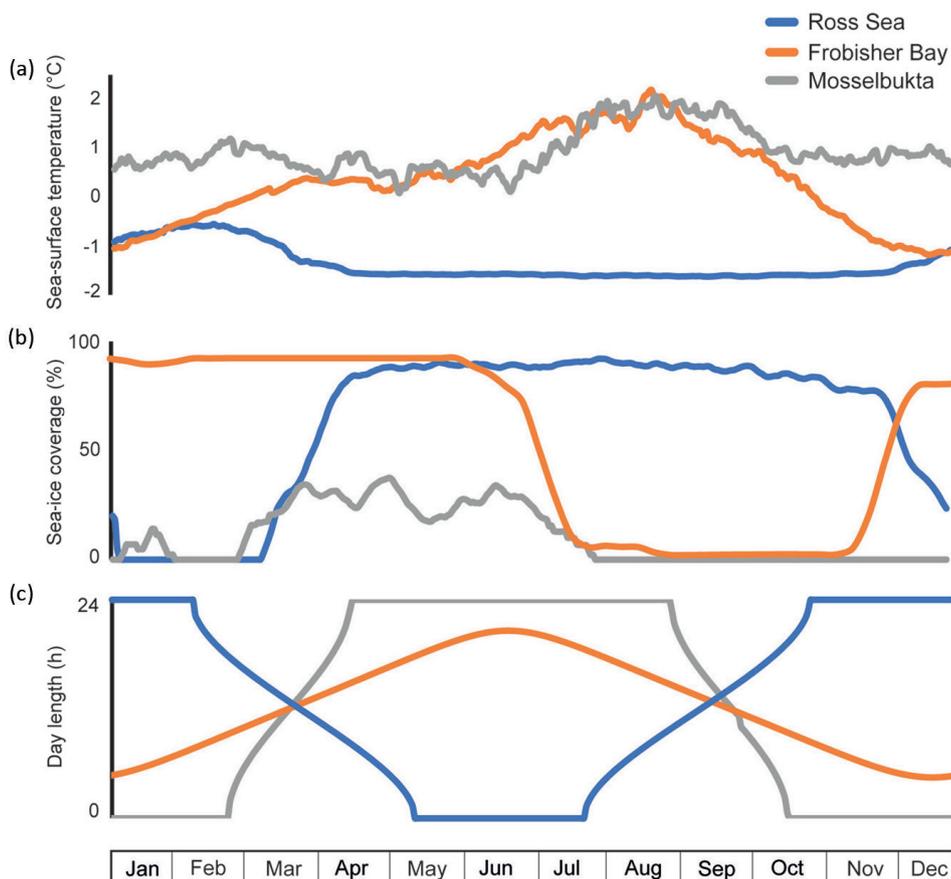
Fig. 3 Schematic overview of the seasonality of (a) sea-surface temperature, (b) sea-ice coverage and (c) day length at the three study sites (figure modified from Meyer 2020). Day length data for 2016 were obtained from the internet (www.timeanddate.com), sea-ice coverage for the Ross Sea, Antarctic and Mosselbukta, Svalbard, was retrieved as daily means from 2004 to 2016 from Fetterer et al. (2017) and for Frobisher Bay as weekly means from 2007 to 2016 from Canadian Ice Service (2009). Sea-surface temperature is the daily mean from 2004 to 2016 from Physical Science Laboratory (2020).

analytical methods for TIC and TA were described by Punshon et al. (2019). The analytical precision was 0.03% for TIC and 0.05% for TA, respectively. The saturation states of seawater with respect to aragonite (Ω_{arg}) were calculated from the TIC and TA measurements using the CO2SYS programme (Lewis & Wallace 1998).

Integrated uncertainties of Ω_{arg} based on propagated uncertainties from replicate TIC and TA measurements are at most 0.013.

The salinity, temperature and Ω_{arg} sections along Frobisher Bay are shown in Fig. 4. The BIC, which is the integrated Arctic outflow through the Canadian Arctic Archipelago, flows into Frobisher Bay along the northern side of the bay. The BIC is modified within the bay by various processes, including fluvial inputs, ice formation/melt and tidal mixing, and flows out to the south. The water in Frobisher Bay is cold (T < 0 °C; Fig. 4e) and fresh (S < 33.36; Fig. 4d), indicative of the Arctic outflow, except at the very surface layer in several locations where the water was warmer. The Ω_{arg} value ranged from 1.97 at the surface layer, where the active biological uptake of carbon increased the Ω_{arg} value to 1.00 at depth (400 m) in the outer bay (Fig. 4a). Limited by the shallow sill, the water exchange between the inner and the outer bay resulted in the lower oxygen saturation, that is, increased respiration, in the sub-surface layer in the inner bay (Fig. 4a). The increased carbon content by respiration, together with the lower salinity, contributes to the decreased Ω_{arg} in the inner bay compared with those at the relevant isobaths in the outer bay. The beam

transmission was low at the surface layer on top of the halocline (<12 m), caused by a combination of primary production and riverine sediments (Fig. 4f). The average 1% surface irradiance depth measured in Frobisher Bay in the summer months of 2016–18 was 19.6 m, slightly shallower in the inner bay (17.2 m) and slightly deeper in the outer bay (20.9 m). Therefore, the euphotic zone (1% surface illumination marks the lower boundary) obtained from PAR data from Frobisher Bay reaches ca. 15–20 m, while the base of the dysphotic zone (0.01% surface illumination) cannot be determined from the data set (Edinger et al. 2016; Edinger et al. 2017; Edinger et al. 2018). It can be assumed that all stations were at least in the dysphotic zone (Table 1).

Sample material

In order to ensure good comparability with our previous studies (Meyer et al. 2020, 2021) and as they have proven to be highly suitable (e.g., Glaub et al. 2002; Feussner et al. 2004), we concentrated on barnacles as a substrate for bioerosion, namely the species *Balanus balanus* (Linnaeus, 1758), which were alive during recovery.
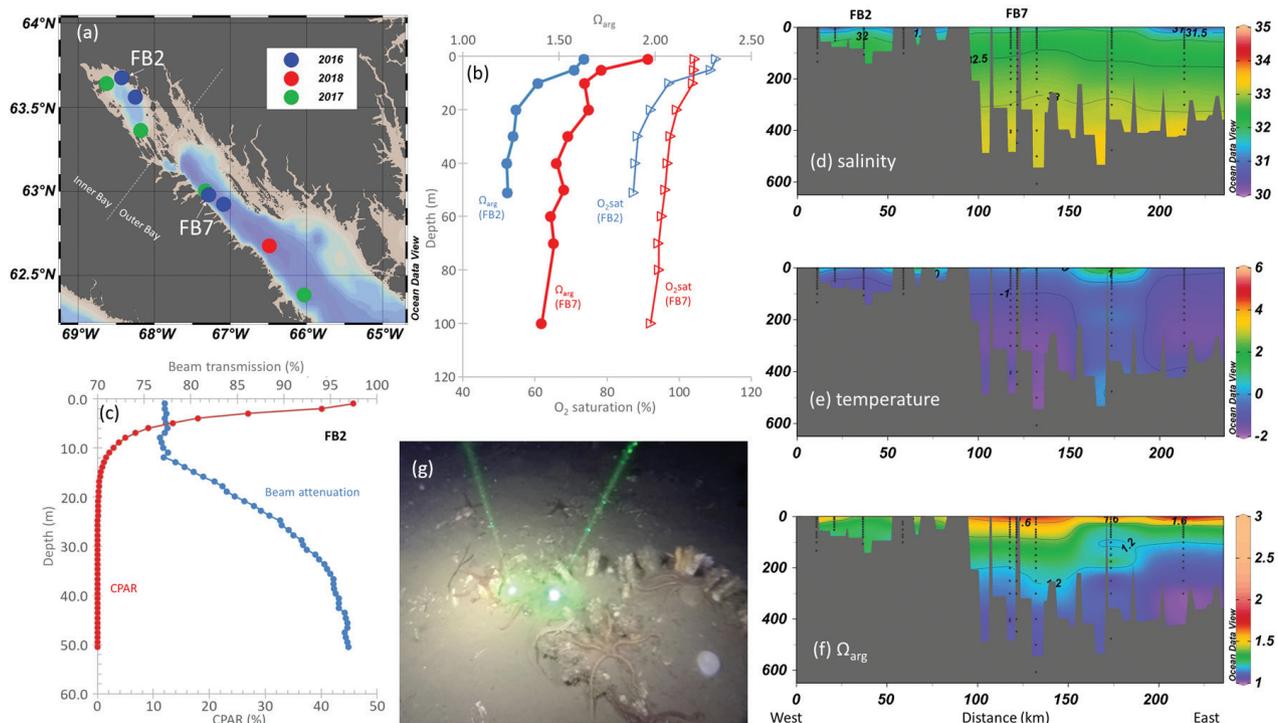
Fig. 4 (a) Frobisher Bay and the locations of stations. (b) The Ω_{arg}, oxygen saturation (O_2 sat) profiles at stations FB2 (inner bay) and FB7 (outer bay, <100 m). (c) Beam transmission and a PAR profile from FB2 (data kindly provided by Amundsen Science Data Collection). Frobisher Bay sections for (d) salinity, (e) temperature and (f) Ω_{arg}, plotted using Ocean Data View (Schlitzer 2021). (g) A snapshot of bottom frame grabs from site 5g, extracted from a video (see Misiuk et al. [2019] for more details about the video acquisition). The laser pointers are 5 cm apart.

Live barnacles were collected opportunistically as part of marine habitat mapping studies in Frobisher Bay during two expeditions in 2016 (see Deering et al. [2018] and Herder et al. [2021] for more details; Table 1). During the CCGS *Amundsen* expedition in July 2016, 0.25 m² aperture box cores were collected at several locations in inner Frobisher Bay. Van Veen grab samples were collected from additional locations of inner Frobisher Bay from the Nunavut Fisheries Research Vessel MV *Nuliajuk* in September 2016, using a Van Veen grab sampler, with a scoop area of 15 cm × 20 cm.

For both the box cores and the grab samples, living carbonate-shelled organisms, including barnacles, and carbonate bioclasts were separated by sieving the sediments through a 1-mm mesh using running seawater. Small samples were fixed in 4% formaldehyde for 48 hrs, and then preserved in 70% ethanol, while large samples, including most of the live barnacles attached to cobbles and boulders, were frozen.

Cast-embedding technique

In order to visualize the microbioerosion traces inside the calcareous barnacle armour, we treated them with the commonly applied cast-embedding technique (Wisshak 2006; Wisshak 2012). For the analysis, we used two to three barnacles per water depth and one or two plates of each individual; thus, up to four samples per station (details in Table 1). Firstly, we removed organic material by immersing the barnacles in sodium hypochlorite (customary cleaning agent) for 24–48 hrs. The barnacles were then rinsed with deionized water, before drying at 30 °C for 12 hrs. By utilizing the vacuum chamber of the CitoVac (Struers), the cleaned tunnels inside the barnacle shells were filled with R&G 'water clear' epoxy resin. The hardened resin pieces were cut on all sides with a stone saw (water-cooled, diamond-bladed), and then placed in ca. 5% hydrochloric acid, until the exposed carbonate was dissolved. In total, we glued 43 samples on stubs about the size of a fingernail. Prior to scanning electron analysis (Tescan VEGA3 xmu, with the secondary electron detector at 20 kV), the stubs were sputter-coated with gold (Cressington sputter coater 108).

Whenever applicable, bioerosion traces were identified at ichnospecies level and otherwise given informal names. As an accurate quantification is not practicable for several reasons (traces differ in size; they may superimpose each other; some are networks, while other ones are individual borings), we carried out a semi-quantitative analysis and categorized each trace into one of four abundance classes: very rare, only one or very few specimens; rare, few specimens; common, many specimens but not dominant; very common or dominant.

Results

The overall diversity and abundance of microborings in the studied acorn barnacles from the Canadian Arctic are low, with six different microbioerosion traces being rare to very rare, and only *Nododendrina europaea* found to be common at 91 and 62 m water depth. Four of the ichnotaxa were probably bioeroded by fungi, one by foraminifera and one by bacteria. All were produced by organotrophic trace makers (Table 2), so the ichnotaxonomic inventory was limited to traces of light-independent organotrophs.

Scolecia serrata was exclusively found at 62 m water depth, and *Flagrichnus* cf. *profundus* appeared at a water depth of 86 m and below, while the other traces occurred almost in the entire bathymetric transect (Table 2).

We occasionally observed small deviations to the originally described morphology of some ichnotaxa. *Flagrichnus baiulus* (Fig. 5a) and *Nododendrina europaea* (Fig. 5h), for instance, showed a great variety of forms and sizes (e.g., pancake-form in *Flagrichnus baiulus*; Fig. 5b).

The Large tongue-form has not yet been taxonomically described and is therefore briefly described in terms of morphology. The trace consists of an initial point of entry into the substrate (measured opportunistically on four traces: 2–5.5 μm wide, 4.3–10.6 μm long), with a gradual transition to a central spherical cavity (maximum diameter: 6.2–12.5 μm), which sometimes looks flattened and slightly bent, like a tongue. We observed a resemblance to the ichnogenus *Saccomorpha*; however, this form is strikingly larger, solitary and is therefore not interconnected by small (hyphal) galleries.

Discussion

Characteristic polar environmental parameters, such as cold temperatures, compressed photic zonation and seasonal sea-ice formation affect the trace assemblages (Wisshak 2006; Meyer et al. 2020, 2021). The ichnodiversity (and abundance of bioerosion; Table 2) obtained in the Canadian Arctic is very low compared with the 26 microborings found by Wisshak (2006) in a cold-temperate setting and the 37 microborings found by Wisshak et al. (2011) in a warm-temperate setting. We relate this to three factors: (1) the seasonal light conditions in Frobisher Bay are extreme (Fig. 3); (2) its extreme tides
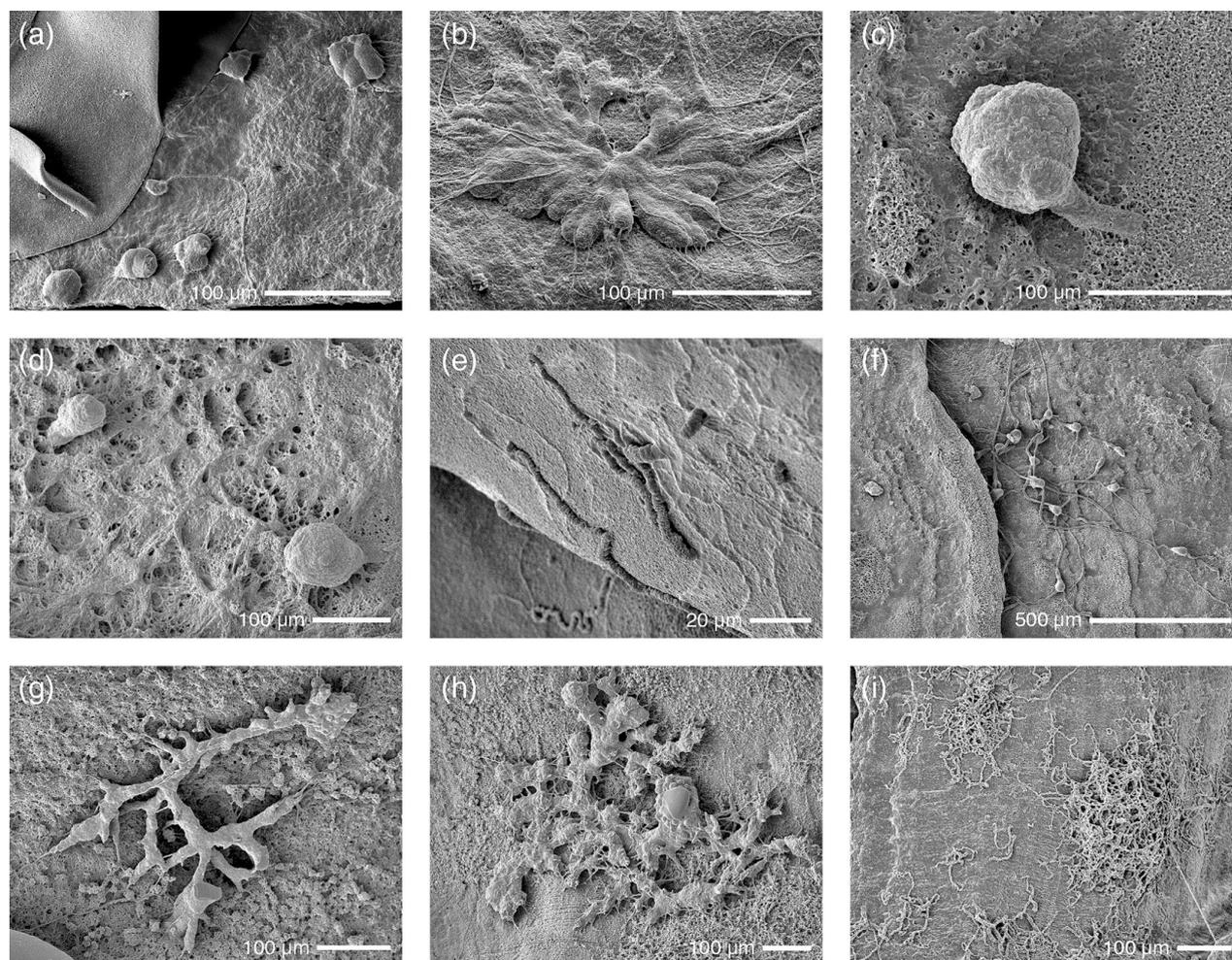
Fig. 5 Observed microborings from Frobisher Bay. (a) *Flagrichnus baiulus* from 93 m. (b) Unusual *Flagrichnus baiulus* from 63 m. (c) Large tongue-form from 74 m and (d) from 90 m. (e) *Flagrichnus* cf. *profundus* from 91 m. (f) *Saccomorpha guttulata* from 74 m. (g) *Nododendrina europaea* from 91 m and (h) two larger forms also from 91 m. (i) *Scolecia serrata* from 62 m.

and turbidity, which agitate the water and cause lower bioerosion (Scoffin et al. 1980); and (3) the narrow bathymetric sampling range. With more samples from other water depths, we probably could have found more bioerosion traces and thus other ichnospecies.

In order to acquire a broader understanding of polar microbioerosion patterns, we have compared our case study with two related polar microbioerosion studies from Svalbard (Meyer et al. 2020), in the Arctic and the Ross Sea (Meyer et al. 2021; Fig. 6), in the Antarctic. We exclude that variations in ichnospecies composition between the three studies are the result of different approaches, as the same substrate and the same methods were applied, except for the bathymetric range. Minor differences in carbonate saturation states among regions were unlikely to have affected our evaluation in

that all samples come from regions where carbonate saturation values were above 1.00 (Azetsu-Scott et al. 2010; Hauck et al. 2012; Zammit 2017; Wisshak, Neumann et al. 2019).

Comparing previous microbioerosion studies: Canadian Arctic versus Eurasian Arctic

The Canadian and Eurasian Arctic were covered by ice sheets during the Last Glacial Maximum: Frobisher Bay by the Laurentian Ice Sheet (Andrews 1987; Deering et al. 2018) and Svalbard by the Barents Ice Sheet (Landvik et al. 1998). After the retreat of these ice sheets, (re-)colonization of at least the shallower waters both by calcareous benthic organisms (including the balanids we have studied) as well as bioeroding communities took

Table 2 List of ichnotaxa recorded in barnacles from the Canadian Arctic and their assumed trace makers (based on the original interpretation of the ichnotaxon authority) and results of the semi-quantitative analysis.

Ichnotaxon	Trace-maker	Fig.	Abundance[a] Water depth (m)										
			62	63	74	80	81	86	90.1	90.2	91	93	94
Flagrichnus baiulus Wisshak & Porter, 2006	Fungi	3a–b	--	--		--	--		--	--		-	
Large tongue-form	Fungi	3c–d			--	-	--		-		--		--
Flagrichnus cf. *profundus* Wisshak & Porter, 2006	Fungi	3e						--		--	--		--
Saccomorpha guttulata Wisshak et al., 2018	Fungi	3f	--	--	--	--		--	--			--	--
Nododendrina europaea (Fischer, 1875)	Foraminifera	3g–h	+	--	--		--	--	--	--	+	-	--
Scolecia serrata Radtke, 1991	Bacteria	3i	--										

[a]Common (+), rare (-) and very rare (--).

place. Despite these similar starting conditions, the samples from the Canadian Arctic show a much lower ichnodiversity compared with those from Svalbard (six vs. 20 in barnacles from the genus *Balanus*). All the recorded ichnotaxa have also been observed in Svalbard (the Large tongue-form was not reported by Meyer et al. [2020] but by Wisshak et al. [2021]). This difference is possibly an artefact of the availability of more samples from Svalbard, covering a wider range of water depths, that is, the euphotic to aphotic zones. However, if only samples from the dysphotic to aphotic zones are considered, Svalbard waters were still richer in species with 14 ichnotaxa compared with six ichnotaxa in Frobisher Bay. Reasons for that difference could be threefold: (1) high turbidity and sedimentation rate in Frobisher Bay; (2) a general depletion in bioerosion communities in the colder and fully Arctic Frobisher Bay compared with the warmer and marginally Arctic Svalbard sites; and (3) Frobisher Bay, in contrast to our study sites in Svalbard, is not a pronounced carbonate factory (sensu Schlager 2000), though sediments contain abundant carbonate bioclasts, dominated by bivalves and barnacle plates (Zammit 2017). Gastropods and bryozoan bioclasts in Frobisher Bay sediments were rare. While most of the dominant bivalve species were infaunal, the abundant barnacle plate bioclasts in Frobisher Bay sediments indicate the importance of hard substrate fauna in contributing to the carbonate bioclasts pool. The samples collected in Frobisher Bay were too deep for abundant calcareous algae, although these are common in shallow waters (photic zone) throughout the Canadian Arctic where hard substates occur (Adey & Hayek 2011).

Furthermore, the terrestrial freshwater flux and relatively low saturation states of water in the BIC push the carbonate saturation horizons in Frobisher Bay to much shallower depths than in the open and well-ventilated, northern Labrador Sea (Azetsu-Scott et al. 2014). Nonetheless, the summer-time aragonite saturation horizon in our Frobisher Bay sites was deeper than the sites of our sample collection.

In addition to being siliciclastic dominated, Frobisher Bay sediments are organic rich, with the average organic content of about 5%, which is higher than the average carbonate content. Organic-rich sediments and generally high productivity may help to explain the dominance of organotrophic microbioeroding organisms, even in the plates of live-collected barnacles. Pervasive macrobioerosion was reported on other carbonate bioclasts in Frobisher Bay (Zammit 2017).

Comparing previous microbioerosion studies: polar north versus polar south

Our studies have recorded a total of 21 microbioerosion ichnotaxa in the Arctic (six ichnotaxa in Frobisher Bay, 20 in Svalbard) and 18 in the Antarctic (Meyer et al. 2021). At first, this marginal difference could be explained by the milder polar conditions in Svalbard, as demonstrated by longer lasting sea-ice cover in Antarctica and Frobisher Bay (Fig. 3). However, this explanation is too simple, and it seems to be more reasonable to highlight the similarities.

Figure 6 illustrates that fungal traces dominate the assemblages. Traces of phototrophic organisms often
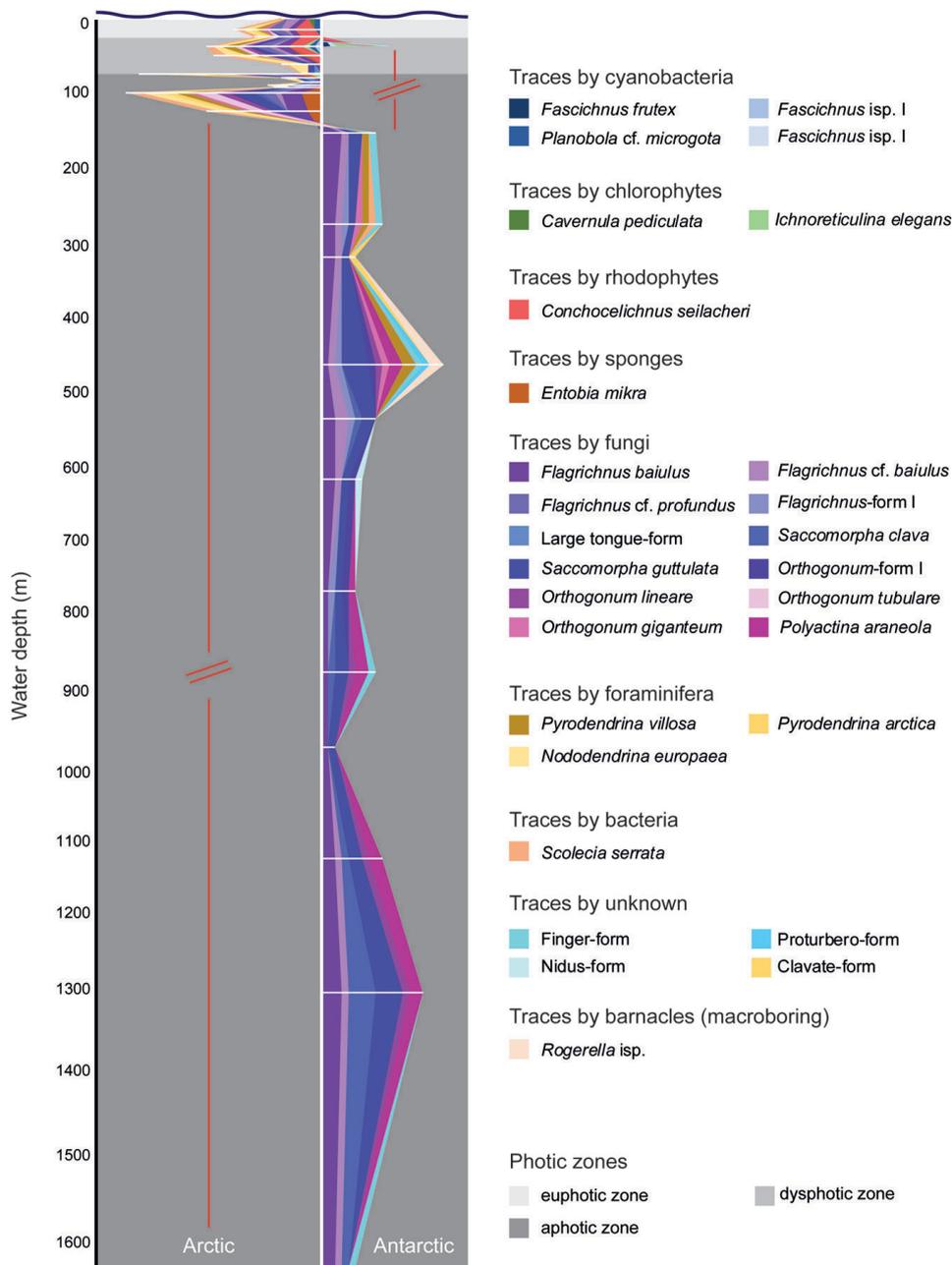
Fig. 6 Stacked area chart showing ichnodiversity (indicated by the different colours for depths) and abundance (indicated by the width of the areas) data from this study, Meyer et al. (2020) and Meyer et al. (2021) in the Arctic and Antarctic. The white horizontal lines denote the actual water depth of sample; the areas in between are interpolated. The red vertical lines indicate that no samples were available from these water depths and not that no ichnodiversity was observed (figure modified from Meyer 2020).

account for the largest proportion in non-polar environments (Wisshak 2012); however, owing to the extremely low-light conditions at ice-covered high latitudes, their quantity is reduced in our series of studies (see discussion by Meyer et al. 2020, 2021). While this could be proven for Svalbard, we can only assume this to hold true for the Ross Sea and Frobisher Bay, given the small number of samples

from the euphotic zone. Hence, the comparison focusses on the aphotic bioerosion recorded at 60 m and downwards: we can compare 46 samples from the Antarctic, with 79 from the Arctic (36 from Svalbard, 43 from Frobisher Bay). This approach shows a similar maximum number of ichnotaxa (Fig. 6), with 15 traces in Svalbard and 16 in the Ross Sea. Three traces are restricted to Svalbard (*Entobia mikra*,

Orthogonum tubulare and *Pyrodendrina arctica*), and seven to the Ross Sea (*Flagrichnus*-form I, *Polyactina araneola*, Finger-form, Nidus-form, Proturbero-form, Clavate-form, *Rogerella* isp.). Three traces occur exclusively in either one of the Arctic regions (*Flagrichnus* cf. *profundus*, *Nododendrina europaea*, Large tongue-form), regardless of their occurrence at lower latitudes. The highest number of new (and therefore potentially 'endemic'?) ichnospecies was recorded in the Ross Sea.

In summary, the number and abundance of ichnotaxa are almost identical in barnacle samples from both hemispheres, despite the differing number of samples. Three traces occurred at both poles (*Flagrichnus baiulus*, *Saccomorpha guttulata* and *Scolecia serrata*), and this observation of the same ichnospecies suggests to some degree of past or present interconnectivity between the bioeroding faunas of the two polar regions.

Ichnotaxa indicative of cold-water and of polar environments

Certain ichnotaxa can serve as indicators for (palaeo-) temperatures, and thus can help in the identification of (palaeo-)biogeographical zones (see Wisshak [2012] for a review), although it needs to be taken into account that there is some analogy between deep-water conditions at low latitudes and temperature and light conditions at high latitudes.

Flagrichnus baiulus, *Entobia mikra*, *Nododendrina europaea*, *Saccomorpha guttulata* and *Orthogonum*-form 1 were previously suggested as cold-water indicators (Wisshak et al. 2005; Wisshak & Porter 2006; Bromley et al. 2007; Wisshak et al. 2018; Meyer et al. 2020) and were found

in Svalbard waters (Meyer et al. 2020). Today, they are exclusive to cold-temperate and polar regions, and are all presumably formed by organotrophic organisms. *Entobia mikra* and *N. europaea*, however, did not occur at all three of our study sites (Fig. 6). *Nododendrina europaea* is common in both Arctic studies, but was not observed in the Antarctic and may, therefore, be limited to the Northern Hemisphere. *Flagrichnus baiulus* and *S. guttulata*, in contrast, were both present and dominant at all three regions and appear to be most suitable as key ichnotaxa for cold-water settings (Fig. 7). Two additional ichnospecies that were previously suggested as indicative of cold-water settings include *Saccomorpha stereodiktyon* (see Golubic et al. 2014) and *Flagrichnus profundus* (Wisshak 2006). These were absent at all three locations, so they have been so far restricted to cold-temperate provinces.

Fascichnus isp. I and II, *Flagrichnus*-form I, Finger-form and Nidus-form, have only been recorded in our studies, so they may have some potential as additional indicator ichnospecies, once they become ichnotaxonomically established as such. However, the value of all the indicator ichnospecies depends on negative evidence from warm-water environments at lower latitudes: their absence must be confirmed in future studies.

In turn, the absence of ichnotaxa common in warm-water settings can indicate cold-temperate and polar waters, although, again, this relies only on negative evidence. Some of the most common ichnotaxa are *Eurygonum nodosum* (thus far latitudinally limited up to Kosterfjord [Wisshak 2006]), *Irhopalia* (e.g., *I. catenata*, thus far latitudinally limited up to Tromsø [Glaub et al. 2002]), S*accomorpha* (e.g., *S. stereodiktyon*, thus far latitudinally limited up to Kosterfjord [Wisshak 2006]) and
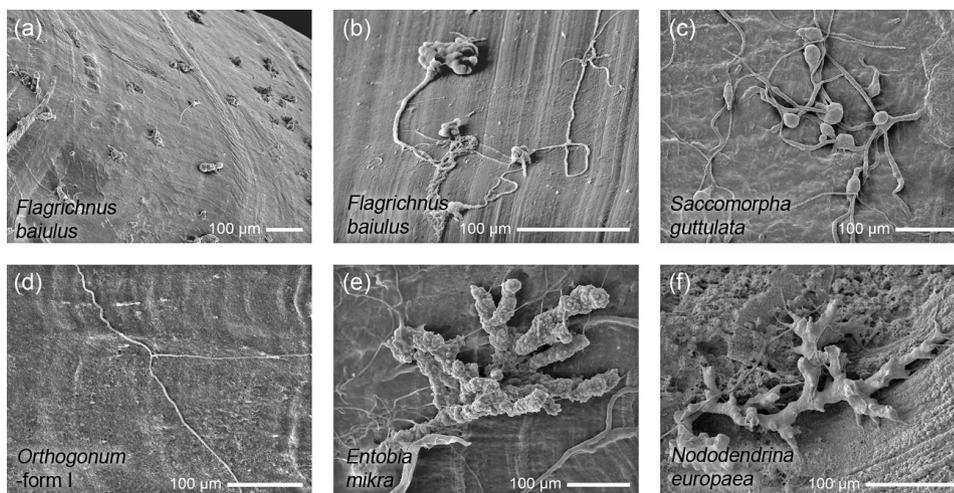
Fig. 7 Indicator ichnotaxa for cool- to cold (palaeo)environmental conditions. Specimens were sampled in (a) the Ross Sea at 1130 m water depth, (b) Bjørnøybanken, Svalbard, 88 m water depth, (c) Ross Sea, 1130 m water depth, (d) Bjørnøybanken, Svalbard, 47 m water depth, (e) Mosselbukta, Svalbard, from 75 m water depth, and (f) Frobisher Bay, from 93 m water depth.

Orthogonum fusiferum (Kosterfjord [Wisshak 2006]). None of these have been observed in the polar regions so far.

Applicability of palaeobathymetrical index ichnocoenoses

Light has repeatedly been identified as the main factor in the composition of microbioerosion trace assemblages (e.g., Glaub 1994; Vogel et al. 1995; Glaub et al. 2002; Meyer et al. 2020). On the basis of the light dependence of many phototrophic euendoliths and their specific low-light tolerance limit, a set of index ichnocoenoses were established to address relative bathymetry (e.g., Glaub 1994; Vogel et al. 1995; Glaub et al. 2002). While the originally established set of index ichnocoenoses are in good agreement with microbioerosion trace assemblages in tropical to warm-temperate environments, they are of limited applicability for cool- to cold-water settings, and hence, alternative key ichnotaxa have been proposed (see Wisshak [2012] for a review).

Given our lack of data from the shallow to deep euphotic zone, we here focus on the dysphotic and aphotic zone in proposing suitable key ichnotaxa for these zones in polar palaeoenvironments.

The dysphotic zone was originally characterized by *Ichnoreticulina elegans* and *Saccomorpha clava*, but *S. clava* was absent or very rare in our study sites and is hence considered unsuitable for the polar realms. Instead, *Conchocelichnus seilacheri* is suggested to complement the cosmopolitan *I. elegans*. Both ichnotaxa are bioeroded by phototrophs well adapted to low-light conditions. It must be stressed, however, that the index ichnocoenoses alone does not allow an unambiguous interpretation, and it is essential to assure the absence of other traces by phototrophic euendoliths (except for the rare cyanobacterium *Plectonema terebrans* and its trace *Scolecia filosa*) in the dysphotic zone.

For the aphotic zone, the original key ichnotaxa assemblage for the polar environments is not applicable either, as both *S. clava* and *Orthogonum lineare* were too rare or absent in our studies. Instead, we consider that the very common *Saccomorpha guttulata* is a strong index ichnotaxon, together with the similarly common *Flagrichnus baiulus*. As both can be present at all water depths, the aphotic nature needs to be confirmed by the absence of any traces produced by phototrophic organisms.

Conclusions

In the context of polar microbioerosion studies, barnacles from Frobisher Bay, eastern Canadian Arctic, were investigated regarding their ichnodiversity. The assemblage consists of six different types of traces, most of which were rare to very rare. Compared with two corresponding studies from the Arctic (Svalbard, 20 traces) and Antarctic (Ross Sea, 18 traces), the ichnodiversity of Frobisher Bay is lowest, most likely as a result of high turbidity and the limited bathymetrical range of the samples. Comparison of the three studies indicates that the ichnodiversity in the aphotic zone is similar in these polar environments although it differs in composition.

Our research study allowed us to propose suitable cold-water indicator ichnotaxa and modified key ichnocoenoses for interpreting the palaeobathymetry of carbonates formed in polar regions. A promising avenue for further research is to evaluate potential ways of bioeroding fauna evolution in the polar realm, including more polar sample sites, samples from potential migration pathways, and suitable substrates from intertidal and shallow–subtidal water depths.

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