

'Ten Years After'—a long-term settlement and bioerosion experiment in an Arctic rhodolith bed (Mosselbukta, Svalbard)

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Abstract

Rhodolith beds and bioherms formed by ecosystem engineering crustose coralline algae support the northernmost centres of carbonate production, referred to as polar cold-water carbonate factories. Yet, little is known about biodiversity and recruitment of these hard-bottom communities or the bioeroders degrading them, and there is a demand for carbonate budgets to include respective rates of polar carbonate build-up and bioerosion. To address these issues, a 10-year settlement and bioerosion experiment was carried out at the Arctic Svalbard archipelago in and downslope of a rhodolith bed.

The calcifiers recorded on experimental settlement tiles (56 taxa) were dominated by bryozoans, serpulids and foraminiferans. The majority of the bioerosion traces (30 ichnotaxa) were microborings, followed by attachment etchings and grazing traces. Biodiversity metrics show that calcifier diversity and bioerosion ichnodiversity are both elevated in the rhodolith bed, if compared to adjacent aphotic waters, but these differences are statistically insignificant. Accordingly, there were only low to moderate dissimilarities in the calcifier community structure and bioerosion trace assemblages between the two depth stations (46 and 127 m), substrate orientations (up- and down-facing) and substrate types (PVC and limestone), in that order of relevance. In contrast, surface coverage as well as the carbonate accretion and bioerosion rates were all significantly elevated in the rhodolith bed, reflecting higher abundance or size of calcifiers and bioerosion traces. All three measures were highest for up-facing substrates at 46 m, with a mean coverage of 78.2% (on PVC substrates), a mean accretion rate of 24.6 g m⁻² year⁻¹ (PVC), and a mean bioerosion rate of -35.1 g m⁻² year⁻¹ (limestone). Differences in these metrics depend on the same order of factors than the community structure. Considering all limestone substrates of the two platforms, carbonate accretion and bioerosion were nearly in balance at a net rate of -2.5 g m⁻² year⁻¹.

A latitudinal comparison with previous settlement studies in the North Atlantic suggests that despite the harsh polar environment there is neither a depletion in the diversity of hard-bottom calcifier communities nor in the ichnodiversity of grazing

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traces, attachment etchings and microborings formed by organotrophs. In contrast, microborings produced by phototrophs are strongly depleted because of limitations in the availability of light (condensed photic zonation, polar night, shading by sea ice). Also, macroborings were almost absent, surprisingly. With respect to carbonate production, the Svalbard carbonate factory marks the low end of a latitudinal gradient while bioerosion rates are similar or even higher than at comparable depth or photic regime at lower latitudes, although this might not apply to shallow euphotic waters (not covered in our experiment), given the observed depletion in bioeroding microphytes and macroborers. While echinoid grazing is particularly relevant for the bioerosion in the rhodolith bed, respective rates are far lower than those reported from tropical shallow-water coral reefs. The slow pace of carbonate production but relatively high rates of bioerosion (both promoted by low carbonate supersaturation states in Arctic waters), in concert with high retention of skeletal carbonates on the seafloor and no calcite cements forming in open pore space created by microborers, suggest a low fossilisation potential for polar carbonates, such as those formed in the Mosselbukta rhodolith beds.

KEYWORDS

settlement experiment, hard-bottom communities, carbonates, marine calcifiers, biodiversity, microbioerosion, ichnodiversity

1 | INTRODUCTION

The marked environmental constraints in polar environments render the build-up of carbonate by calcifying encrusters and carbonate recycling by bioeroding organisms comparatively slow processes. In consequence, reefal structures that grew after the retreat of the polar ice shield formed during the Pleistocene Last Glacial Maximum are rare. Prominent exceptions are bioherms and rhodolith beds formed by crustose coralline algae of the genera *Clathromorphum* and *Lithothamnion*, respectively, which have adapted to survive the long spell of the polar night by means of storage of carbohydrates (floridean starch) produced during the season of active photosynthesis in the perithallial cell compartments (Freiwald & Henrich, 1994). The relevance of these algae for the formation of polar marine carbonate deposits was recognised already by pioneer researcher Frans Reinhold Kjellman (1883: p. 96) who noted '*It is gregarious. On the coast of Spitzbergen and Novaya Zemlya it [Lithothamnion glaciale] covers the bottom in deep waters for several miles, and altogether determines the general aspect of the vegetation, wherever it occurs. In the formation of future strata of the earth's crust in these regions it must become of essential importance.*' And indeed, these algae support Arctic cold-water carbonate factories ('C factory' sensu Schlager, 2000, 2005) that in recent years have received increased attention as important sites of non-tropical carbonate production and deposition (e.g. Andrulleit et al., 1996; Henrich et al., 1996, 1997; James & Clarke, 1997; Pedley & Carannante, 2006; Teichert et al., 2012, 2014; Wisshak et al., 2019). Yet, very little is known about settlement and biodiversity of the calcifier hard-bottom communities and

the bioeroders degrading them. Moreover, there is a lack of data on rates of carbonate build-up versus bioerosion in polar carbonate factories.

To address these key aspects of polar carbonate production and degradation, we here report on a long-term settlement and bioerosion experiment carried out in Mosselbukta in the far north of the Arctic Svalbard archipelago. This embayment harbours some of the northernmost bioherms (called clathrostromes; Adey et al., 2013) of *Clathromorphum compactum* (Kjellman) Foslie, 1898 and rhodolith beds formed by the local ecosystem engineer *Lithothamnion glaciale* Kjellman, 1883 (Kjellman, 1875a, 1875b, 1883; Teichert et al., 2012, 2014; Wisshak et al., 2019). Three experimental platforms were placed along a bathymetrical transect in euphotic, dysphotic and aphotic water depths (Figure 1). While the shallowest platform (11 m) must be considered lost, likely because of an unforgiving winter storm or scouring of piling drift ice, the one situated in 46 m depth, directly in the rhodolith belt, was retrieved in perfect order, together with 15 months' worth of environmental data recorded by an autonomous data logger. Likewise, the platform located in 127 m depth, below the reach of phototrophic calcifiers and bioeroding endolithic microphytes, was successfully recovered, allowing a comparative analysis.

With this carbonate cycling experiment we conclude a latitudinal transect across the various biogeographical zones in the North Atlantic, building upon earlier experiments carried out in the equatorial Caribbean (e.g. Scoffin et al., 1980; Stearn et al., 1977) and tropical Bahamas (Hoskin et al., 1986; Vogel et al., 1996, 2000), and including our own experiments in the warm-temperate Azores

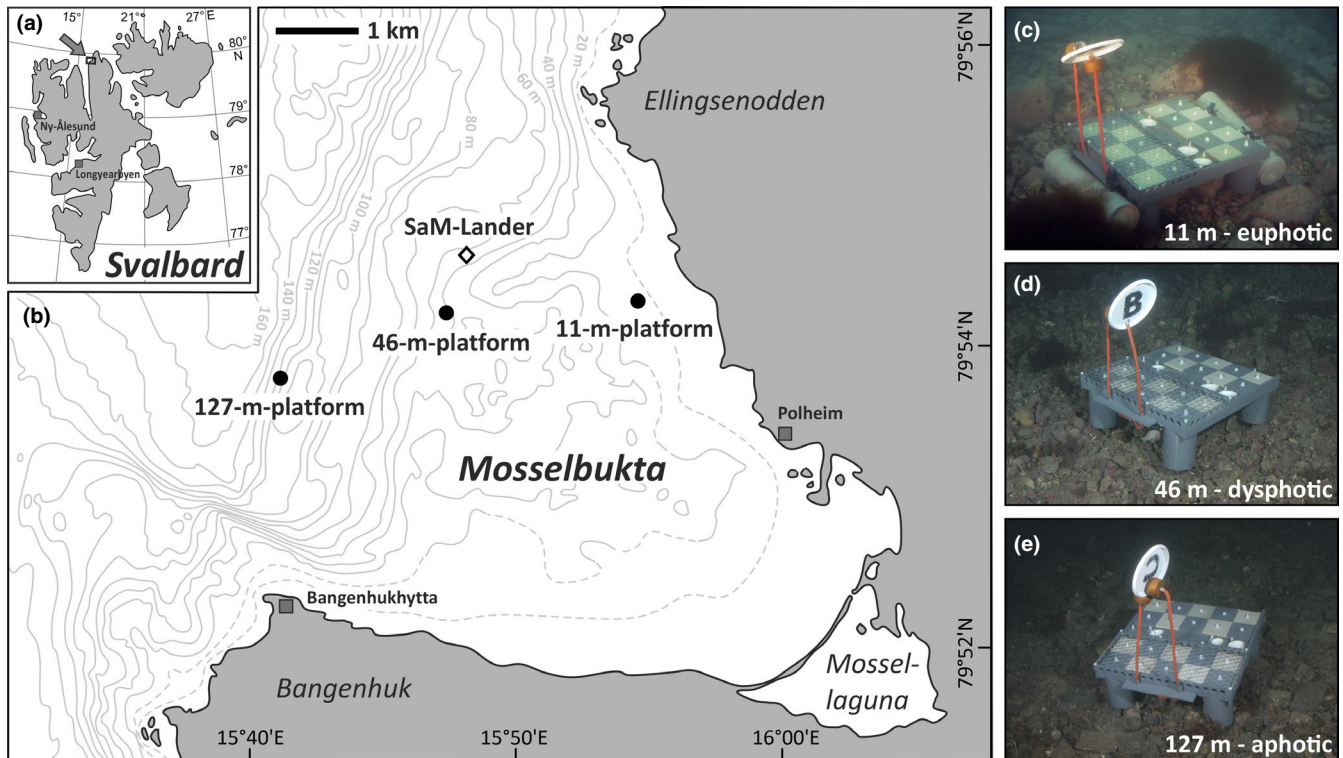


FIGURE 1 Study site and experimental design. The Arctic Svalbard archipelago (a) with Mosselbukta in northernmost Spitsbergen (b) harbouring the three settlement platforms deployed in 2006 at euphotic 11 m water depth (c), dysphotic 46 m water depth in the *Lithothamnion glaciale* rhodolith bed (d) and in aphotic 127 m water depth (e); all platforms photographed directly upon deployment

(Wisshak et al., 2010, 2011, 2015) and cold-temperate coastal waters of SW Sweden (Wisshak, 2006; Wisshak et al., 2005; Wisshak & Rüggeberg, 2006). The Mosselbukta experiment represents the polar end-member in this series of settlement experiments of similar design, allowing us to draw comparisons of the diversity and rates of carbonate accretion and bioerosion to lower latitudes and to discuss implications for the preservation potential of polar skeletal carbonates.

Given an expected low pace of polar carbonate accretion and bioerosion, we left the platforms exposed longer than above experiments (usually only a year or two): 10 years—a comparatively long exposure for a settlement experiment, albeit not as enduring as the blues-rock band ‘Ten Years After’ (founded in 1967) that inspired the title of this paper ...

1.1 | The study site

Mosselbukta (= ‘shellfish bay’) is an embayment, about 7 km wide and reaching as far inland, located at Mosselhalvøya in the eastern shoreline of Wijdefjorden in northern Spitsbergen (Figure 1a,b). Detailed hydroacoustic mapping has revealed the complex submarine topography of the bay (Wisshak et al., 2019: figure 1). Glaciogenic pebbles to boulders litter the seafloor and provide suitable hardground for calcareous encrusters, foremost crustose coralline algae, barnacles,

bryozoans and serpulid worms (Teichert et al., 2014; Wisshak et al., 2019). In euphotic shallow waters, clathrostromes are formed by the long-living crustose alga *Clathromorphum compactum* (Hetzinger et al., 2019), whereas in deeper waters down to dysphotic 70 m water depth, *Lithothamnion glaciale* is the dominant encrusting rhodophyte species. Its carbonate production appears most pronounced at around 45 m water depth, where rhodoliths of up to 25 cm in diameter cover 60–80% of the seafloor and form a rhodolith belt that is encountered also at many other sites in the archipelago (Teichert et al., 2012, 2014). In the rhodolith beds, the overall benthos biodiversity was found highest, most likely promoted by the ecosystem engineer *Lithothamnion glaciale* (Teichert, 2014; Wisshak et al., 2017). Mobile carbonate producers largely constitute of echinoderms, molluscs and crustaceans (Wisshak et al., 2019). Baseline work on bioerosion in this Arctic environment included an inventory of bioerosion traces documented in barnacle shells sampled along a bathymetrical transect of Mosselbukta (Meyer et al., 2020) and the establishment of a new bioerosion ichnospecies indicative of polar environments (Wisshak et al., 2018).

Mosselbukta is located at close to 80° northern latitude, thus the polar night lasts from late October through late February, during which sea ice starts to form that may persist until the early summer (Wisshak et al., 2019: figure 3). Based on a >200-year geochemical record of *Clathromorphum compactum* sampled at Mosselbukta, however, local sea ice has been shown to be subject of an alarming

decline over the past few decades because of ongoing global ocean warming (Hetzinger et al., 2019), going along with a marked increase in glacier-derived runoff (Hetzinger et al., 2021).

An autonomous data logger on our 46-m platform has provided a complete seasonal cycle of water temperature and salinity at the Mosselbukta rhodolith beds and was analysed in detail in Wisshak et al. (2019) in conjunction with CTD data, water sample analyses and environmental data from a short-term lander deployment in the rhodolith belt. With reference to that study, the hydrographic and oceanographic setting is briefly summarised: Bottom water temperatures peaked towards the end of the polar day in August, with a monthly mean of 4.9°C, while with declining daylight and throughout the polar night the temperature decreased to negative monthly means of as low as -1.0°C in April. Short-term temperature fluctuations were usually below 2°C. Salinities were found rather stable and reflect open ocean conditions with little meltwater influx at the rhodolith beds at 46 m water depth. The water masses at Mosselbukta were characterised as Atlantic Water that during winter mixes with Arctic Water to form Modified Atlantic Water, before further cooling drops temperatures below 0°C, resulting in a Polar Surface Water signature. Tidal influence is low with a range below 1 m. Carbonate saturation states and pH values decreased with depth, but remained well within the range of supersaturation, thus suggesting little effect of physicochemical carbonate dissolution on the marine calcifiers, unless respiration leads to temporal local undersaturation. A marked annual drop in $p\text{CO}_2$ and an increase in oxygen levels during the phase of seasonal sea ice cover and spring plankton bloom was found mirrored by a depletion in dissolved inorganic nutrients, except for elevated ammonium levels. This pattern was interpreted to reflect a recycling system that keeps fuelling primary production after the spring bloom and was understood as an effect of limited air-sea gas exchange during seasonal ice cover in combination with a boost in community photosynthesis during the phytoplankton bloom and the onset of rhodophyte photosynthesis in the rhodolith beds during the polar day upon retreat of the sea-ice. Irradiance levels of photosynthetically active radiation (PAR), logged by the lander in summer 2016 at the rhodolith beds in 46 m depth, were surprisingly low, with only few excursions above the detection limit, reaching a maximum of only $4.5 \mu\text{mol s}^{-1} \text{m}^{-2}$. PAR profiling carried out in summer 2006 had indicated a lower boundary of the euphotic zone (1% surface illumination) at 20–25 m water depth and a base of the dysphotic zone (0.01% surface illumination) at about 64 m water depth (Teichert et al., 2014: figure 6).

2 | MATERIALS AND METHODS

2.1 | Experimental design and deployment

The design of the experimental platforms closely follows that of an earlier experiment carried out in the Azores (Wisshak et al., 2010, 2011, 2015). The basic units (Figure 1c,d,e) were PVC frames with tube-legs filled with concrete for ballast. On these platforms,

various kinds of substrates and a data logger were mounted with nylon bolts and nuts, so that the experiments were inert to corrosion. Three sets of five precision-weighed substrate tiles, $10 \times 10 \times 1$ cm in size each, of PVC (for carbonate accretion) and a fine-grained micritic limestone (Upper Jurassic Solnhofen Lithographic Limestone; for carbonate accretion and bioerosion; sealed on all but the upper side with epoxy resin) were mounted up-facing and down-facing. For the analysis of bioerosion traces, a set of three pristine *Callista* bivalve shells, the outer side embedded in a block of epoxy resin to avoid breakage, was mounted up- as well as down-facing. Four additional *Callista* shells were mounted down-facing in the bottom of the open tube-legs as an approach to study cryptic substrates that are in contact with the sediment. *Callista* shells were chosen for their dense aragonitic microstructure with little organic matrix and have proven particularly suitable for high-quality vacuum epoxy casts and SEM visualisation of microbioerosion traces in our previous experiments.

Deployment took place during RV *Maria S. Merian* cruise MSM 2-3 (cruise report: Lherminier et al., 2009) on 8 June 2006, when the three settlement platforms were placed on the seafloor with the aid of the manned submersible JAGO in 127 m (station MSM2-3/680; 79°53.859'N, 15°42.860'E), 46 m (MSM2-3/681; 79°54.352'N, 15°47.854'E) and 11 m water depth (MSM2-3/682; 79°54.413'N, 15°54.902'E) (Figure 1).

Recovery was achieved with submersible JAGO from aboard RV *Maria S. Merian* during cruise MSM 55 (cruise report: Wisshak et al., 2017). On 17 June 2016, the 127-m platform was relocated (station MSM55/430) and on 19 June 2016, the 46-m platform was successfully retrieved (MSM55/455). A dive at the shallowest site (MSM55/442) in search for the 11-m platform failed to relocate the experiment, as did an excursion to the adjacent shore (MSM55/437).

Upon recovery, each substrate was photographed to preserve colour information of the live organisms (diagnostic for instance in the case of spirorbins) and then air-dried for transport.

2.2 | Cataloguing calcareous epiliths

Calcifying encrusters were recorded on both the PVC and limestone tiles after treatment with ca. 5% hydrogen peroxide, rinsing with demineralised water and drying at 70°C. These substrates were then studied with a stereo microscope and representative specimens were documented with a digital microscope (Keyence VHX-2000) using extended focal imaging. The calcareous epiliths were taxonomically identified to species level and otherwise reported in open nomenclature, all considered as 'species' for the sake of biodiversity analyses. As some of these bins may contain several biological species (e.g. those serpulids that cannot be identified to species-level based on their skeletal morphology and colour alone) the resulting species richness is to be considered a conservative estimate. Morphometrical measurements were performed with ImageJ.

2.3 | Cataloguing bioerosion traces

Two complementing methods were employed for documenting bioerosion traces of various types. First, the air-dried *Callista* shells were treated with ca. 5% hydrogen peroxide to remove organic biofilm and epiliths, then cleaned in an ultrasonic bath, rinsed with demineralised water, and dried at 40°C. The shells were then studied with a digital microscope (Keyence VHX-2000) allowing extended focal imaging of the observed bioerosion traces. Using oblique lighting, this method was particularly suited for documenting shallow attachment etchings and grazing traces. Second, the shells were impregnated in epoxy resin in a Struers CitoVac vacuum chamber, using the protocol for the vacuum cast-embedding technique outlined in detail in Wisshak (2012), followed by dissolution of the host substrate with ca. 5% hydrochloric acid, rinsing in demineralised water, and drying at 70°C. The resulting epoxy casts of the inner side of the *Callista* shells with the positive replicas of the bioerosion traces were then sputter-coated with gold and visualised with a Tescan VEGA3 XMU scanning electron microscope (SEM), applying the secondary electron detector at 20 KeV. The traces were ichnotaxonomically identified to ichnospecies level and otherwise reported in open nomenclature or addressed by informal names, all treated as 'ichnospecies' for the sake of ichnodiversity analyses. An inspection of the limestone tiles did not yield any additional ichnotaxa. Morphometrical measurements were performed on SEM images in the VEGA TC software and on Keyence images using ImageJ.

2.4 | Assessment of epilith biodiversity and bioerosion ichnodiversity

For a uniform approach and given that accurate counts of microbioerosion traces in epoxy casts are not feasible for various reasons, the evaluation of both the biodiversity of calcareous encrusters and the ichnodiversity of bioerosion traces relies on semi-quantitative abundances, following the protocol developed in Wisshak et al. (2011). That is, calcifiers and bioerosion traces were semi-quantified, if present, using the four abundance classes 'very common' (++) , 'common' (+) , 'rare' (-) and 'very rare' (--) that were transformed for further analysis in ordinal numbers ranging from 1 ('very rare') to 1000 ('very common'). Bio- and ichnodiversity indices were computed using the software package PAST 4.03 (Hammer et al., 2001), including the (ichno)species richness S (= number of taxa), the Simpson index of dominance D ($0 = \text{low dominance}$; $1 = \text{high dominance}$), the Shannon index H' ($0 = \text{one taxon}$; $\ln S = \text{all taxa present}$), and the Pielou's equitability J (Shannon index normalised for species richness).

Testing for significant differences in the (ichno)faunal community composition between water depths, substrate orientations and substrate types, non-parametrical one-way analyses of similarity (ANOSIM) were run with PRIMER 6 (Clarke et al., 2014) via a Bray-Curtis similarity matrix based on untransformed abundance classes (ordinal data) and a limit of 999 permutations. Additionally, non-metric multidimensional scaling plots (NMDS) and cluster analyses

with similarity profiles (SIMPROF) were computed in PRIMER 6 based on the Bray-Curtis matrix to visualise similarity clusters. The medians of the ichno- and biodiversity indices were tested for significant differences between the two depth stations using non-parametric Mann-Whitney U -tests computed in PAST 4.03 after rejecting normal distribution via Shapiro-Wilk tests.

2.5 | Assessment of carbonate accretion and bioerosion rates

Rates of carbonate accretion and bioerosion were determined by measuring the weight the PVC and limestone tiles had gained or lost during exposure: Before deployment, the substrates were dried for 5 days at 70°C before precision scaling (accuracy ± 1 mg with a Mettler Toledo AB204-S for the PVC tiles; accuracy ± 10 mg with a Mettler Toledo PB3002-S Delta Range for limestone tiles). Upon recovery, all encrusters on the lateral sides of the tiles were removed and the substrates were soaked in ca. 5% hydrogen peroxide to remove organic biofilm and non-calcareous epiliths. Calcareous encrusters that became detached during that process (due to weak attachment when overgrowing organic biofilm), were caught with a 125- μm sieve during rinsing. All substrates were then dried for 5 days at 70°C before precision scaling (accuracy ± 1 mg with a Sartorius CPA324S). The limestone tiles were weighed again after careful removal of all encrusters with a scalpel.

Carbonate accretion rates (mean \pm SD) were calculated based on the weight gain of the five PVC plates per substrate orientation, divided by the exposure time and normalised for the upper surface area of the plates (= 10×10 cm minus 2.3 cm^2 for the central mounting bolt). The resulting rates are expressed as grams carbonate per square metre of planar substrate surface and year ($\text{g m}^{-2} \text{ year}^{-1}$). Bioerosion rates (mean \pm SD) were determined via the weight loss of the limestone plates after removal of the carbonate accretion ($\text{g m}^{-2} \text{ year}^{-1}$; reported as negative values).

Box plots including outliers were computed in PAST 4.03 using the rounding quartile method. All rates (and accretion densities; see below) were tested for significant differences between water depths, substrate orientations and substrate types, by two- and three-way permutational analysis of variance (PERMANOVA) after rejecting normal distribution with Shapiro-Wilk tests (with PAST 4.03) and $\log(x+1)$ transformation. Bioerosion rates were treated as positive values for that purpose and net rates (including positive and negative values) were rendered positive by adding the most negative value plus one. All PERMANOVA tests were based on a fixed factor design, a Bray-Curtis similarity resemblance, and a maximum of 999 permutations, using the software PERMANOVA+ for PRIMER 6 (Anderson et al., 2008).

2.6 | Assessment of carbonate accretion densities

Carbonate accretion densities, expressed as per cent surface coverage, were determined via phase analysis using the image analysis

software Fiji 1.53 by detecting the colour difference of the dark grey PVC versus the grey to white carbonate accretion on evenly lit digital photographs stitched in Adobe Photoshop CS6 from 4 × 4 high-resolution images captured with a Nikon D700 DSLR and a macro lens. The phase analysis was done by reducing the colour depth to 8 bit, applying the 'threshold' tool and quantifying the detected area of carbonate accretion with the 'analyse particles' tool, including the 'watershed' process where needed. The detached encrusters were analysed, accordingly, from separate photos on a black background, so that their area could be added to the results obtained from the PVC tiles. The limestone tiles showed too little difference in colouration, so that the accretion areas were instead based on analysis of the photos of the detached and the removed carbonate accretion.

3 | RESULTS AND DISCUSSION

3.1 | Calcareous encrusters

A total of 56 taxa of calcifiers were recorded and semi-quantified on the experimental substrates, 47 at the 46-m station and 45 at the 127-m station (Table 1, Figure 2). These include bryozoans (36 taxa), followed by serpulids (11) and foraminiferans (6), complemented by one balanid, bivalve and rhodophyte alga species each.

3.1.1 | Bryozoans

This group of colonial organisms with 36 taxa recorded was the richest in species among of all investigated calcareous encrusters. This dominance is in good accordance to previous settlement experiments in Arctic, Antarctic and temperate seas (e.g. Barnes, 1996; Barnes & Kuklinski, 2005; Kuklinski et al., 2013; Meyer et al., 2017; Stanwell-Smith & Barnes, 1997; Turner & Todd, 1993; Wisshak et al., 2015) as bryozoans are known to be opportunistic and among the first to colonise new available substrate (Barnes, 1996). In Mosselbukta, bryozoans settled on both types of substrate (PVC and limestone) and both substrate orientations (facing up and down). Cheilostome bryozoans (29 taxa) had a much higher proportion in comparison to cyclostomes (seven taxa) which is also a common pattern observed worldwide. Four colony morphotypes were recorded, including sheet-like colonies, runners (single zooid chain-like colonies), erect flexible and erect rigid forms. Sheet-like colony forms were by far the most diverse and abundant. The highest species richness (32 taxa) and abundance was encountered at the 46-m station. Although differences in species richness between both substrate types and substrate orientations were low, there was slightly higher colony abundance at down-facing substrates in comparison to up-facing substrates. Also, there was distinctly higher space occupation by bryozoan colonies at down-facing substrates. *Porella* cf. *concinna*, *Stomacrustula producta*, *Cylindroporella tubulosa*, *Hippoponella hipopus* were the most abundant and overall

constitute the largest proportion of colony forming bryozoans at the 46-m station on all substrates. All four species are cheilostomes forming sheet-like colonies. *Einhornia arctica*, which forms runner-like colonies, although abundant, had not occupied much space on the investigated substrates. Among cyclostome bryozoans *Patinella hispida*, *Disporella* cf. *crassiuscula* and *Stomatopora* sp. were the most abundant, yet species of the genus *Oncousoecia* spp. were the ones which occupied the largest amount of space on the investigated substrates at the 46-m station. At the deeper 127-m station the diversity of bryozoans was only marginally lower (28 taxa), but several species recorded here were not present at the shallower station, including *Porella acutirostris*, *Escharella dijmphnae* and *Ramphonotus gorbunovi*. Vice versa, *Hippoponella hipopus*, *Hemicyclopora emucronata* and *Celleporella hyalina* are examples of species which occurred only at the 46-m station. Among the cheilostome bryozoans from the 127-m station *Ragionula rosacea* and *E. arctica* were the most abundant colonies. *Patinella verrucaria* and *P. hispida* were the most abundant cyclostome bryozoans which have a circular colony shape with deterministic size. Most bryozoan species had no preference to either type of substrate or orientation. Exceptions include the erect form of *Cystisella saccata* or sheet-like colonies of *Ramphonotus gorbunovi* that occurred only on up-facing surfaces, while encrusting sheet like forms of *Rhamphostomella* cf. *hincksi* or *E. dijmphnae* occurred only on the down-facing substrates.

3.1.2 | Serpulids

Calcareous tubeworms were the second-most diverse group of encrusters, with spirorbin serpulids clearly outnumbering non-spirorbin serpulids, both in diversity and abundance. The dextrally coiled spirorbins (five species) are represented at both depth stations by the common planispiral *Circeis armoricana* and the erect *Circeis spirillum*, whose host selectivity for bryozoans (Rzhavsky et al., 2014) was confirmed. The second genus of dextrally coiled spirorbins found in high numbers at both depth stations and substrate orientations was *Paradexiospira*, including the bright red *P. vitrea*, the purple-brownish *P. violacea*, and, more rarely and restricted to down-facing substrates at the 46-m platform, the large *P. cancellata* with its distinctive peripheral alveoli. Among the recorded sinistrally coiled spirorbins (three species) were the two *Bushiella* species *B. similis*, found commonly at both depth stations and substrate orientations, and the very rare *B. quadrangularis*, found only at down-facing substrates at the 46-m station. Counts of the latter two species might include further *Bushiella* species that are too difficult to distinguish based on the tube morphology alone. Specimens of the type genus *Spirorbis* were found abundantly at both depth stations, showing a morphology reminiscent of *S. spirorbis* and *S. inornatus* but found in unusual deep waters, as they are usually restricted to the intertidal and very shallow subtidal zones (Rzhavsky et al., 2014). The non-spirorbin serpulids were represented by only three species, foremost the common to rare *Chitinopoma serrula* found at both depth stations and substrate orientations, occasionally

TABLE 1 Abundances and biodiversity indices of calcareous encrusters identified on the experimental substrates (PVC and limestone) of the two settlement platforms, as semi-quantified per orientation using the abundance classes ++ = very common, + = common, - = rare, and -- = very rare

Calcifier group and species (biotaxon)	46-m platform				127-m platform			
	Up PVC	Up L	Down PVC	Down L	Up PVC	Up L	Down PVC	Down L
Bryozoans								
<i>Disporella</i> cf. <i>crassiuscula</i> (Smitt, 1867)	-	--	--	--	-	-	-	-
<i>Oncousoecia</i> cf. <i>canadensis</i> Osburn, 1933	+	-	-	-	+	+	+	+
<i>Oncousoecia diastroporides</i> (Norman, 1869)	+	+	+	+	+	+	-	-
<i>Patinella hispida</i> (Fleming, 1828)	+	-	--	--	--	--	-	--
<i>Patinella verrucaria</i> (Linnaeus, 1758)	-	-	--	--	--	--	--	--
<i>Proboscina</i> cf. <i>incrassata</i> Smitt, 1867					--	--		
<i>Stomatopora</i> sp.	--	--	--	--	--	--		
<i>Amphiblestrum septentrionalis</i> (Kluge, 1906)	--							
<i>Aquiloniella orientalis</i> (Kluge, 1955)				--				--
<i>Callopora craticula</i> (Alder, 1856)	--	+	--	-	--		--	-
<i>Doryporella spathulifera</i> (Smitt, 1868)	-	+	-	--	-	--	+	+
<i>Einhornia arctica</i> (Borg, 1931)	--	--	-	-	-	--	--	--
<i>Ramphonotus gorbunovi</i> Kluge, 1946					--	--		
<i>Tegella arctica</i> (d'Orbigny, 1853)	-	-	-	-			--	-
<i>Celleporella hyalina</i> (Linnaeus, 1767)	--							
<i>Cylindroporella tubulosa</i> (Norman, 1868)	-	-	--	-	-		--	--
<i>Cylindroporella tubulosa</i> (Norman, 1868)	--	--	--	--	--			
<i>Cystisella saccata</i> (Busk, 1856)		--			--	--		
<i>Escharella dijmphnae</i> (Kluge, 1929)								--
<i>Hemicyclopora emucronata</i> (Smitt, 1872)	--		--					
<i>Hippodiplosia obesa</i> (Waters, 1900) <i>sensu</i> Kluge, 1962	--	-	-	+	+	-	-	-
<i>Hippoconella hipopus</i> (Smitt, 1868)	--	-	--	--				
<i>Hippothoa arctica</i> Kluge, 1906	-	--	-	-	+	+	--	--
<i>Lepraliella contigua</i> (Smitt, 1868)			--	--				
<i>Microporella klugei</i> (Kuklinski & Taylor, 2008)				--	--			
<i>Myriozoella plana</i> (Dawson, 1859)			--					
<i>Porella acutirostris</i> (Smitt, 1868)							--	--
<i>Porella</i> cf. <i>concinna</i> (Busk, 1854)	--	--	--	--	--		--	--
<i>Porella</i> sp.	-	-	-	--			--	-
<i>Ragionula rosacea</i> (Busk, 1856)			--	--	--	--	--	--
<i>Raymondcia majuscula</i> (Smitt, 1867)	--							
<i>Rhamphostomella</i> cf. <i>hincksi</i> Nordgaard, 1906			--				--	--
<i>Schizomavella porifera</i> (Smitt, 1868)	--	--		--		--		--
<i>Smittina bella</i> (Busk, 1860)	--		-	--	--	--	--	
<i>Smittina</i> cf. <i>mucronata</i> (Smitt, 1868)	-	-	--	--				
<i>Stomacrustula producta</i> (Packard, 1863)	--	-	--	--	--		--	-
Serpulids								
<i>Circeis armoricana</i> Saint-Joseph, 1894	+	+	-		--	--	+	+
<i>Circeis spirillum</i> (Linnaeus, 1758)		--					--	-

(Continues)

TABLE 1 (Continued)

Calcifier group and species (biotaxon)	46-m platform				127-m platform			
	Up PVC	Up L	Down PVC	Down L	Up PVC	Up L	Down PVC	Down L
<i>Paradexiospira (Spirorbides) vitrea</i> (Fabricius, 1780)	++	+	+	+	+	+	-	+
<i>Paradexiospira (Paradexiospira) violacea</i> (Levinsen, 1884)	+	-	+	+	-	-	--	-
<i>Paradexiospira (Spirorbides) cancellata</i> (Fabricius, 1780)	--		--	+				
<i>Bushiella (Jugaria) similis</i> (Bush, 1905)	+	+	+	--	-	-	+	+
<i>Bushiella (Jugaria) quadrangularis</i> (Stimpson, 1854)		--						
<i>Spirorbis (Spirorbis) sp.</i>	+	+	+	-	--	--	+	+
<i>Chitinopoma serrula</i> (Stimpson, 1854)	-	--	+	+	--	--	-	-
<i>Protula tubularia</i> (Montagu, 1803)				+			-	-
<i>Placostegus tridentatus</i> (Fabricius, 1779)								--
Foraminiferans								
<i>Lobatula</i> (Walker & Jacob, 1798)	+	-	+	+	++	++	+	+
<i>Ammopemphix quadrupla</i> (Wiesner, 1931)					--	--		
<i>Diffusilina humilis</i> Heron-Allen & Earland, 1924					--	--		
<i>Lituotuba lituiformis</i> (Brady, 1879)	--	--		--	+	+		--
<i>Hemisphaerammina bradyi</i> Loeblich & Tappan, 1957	-	-	+	-	++	++		
<i>Dendrophyra sp.</i>					--	-	--	--
Barnacles								
<i>Balanus balanus</i> (Linnaeus, 1758)	+	+	-	-	-	-	-	-
Bivalves								
<i>Pododesmus patelliformis</i> (Linnaeus, 1761)							--	--
Rhodophytes								
<i>Lithothamnion glaciale</i> Kjellman, 1883	++	++	+	+				
Species richness <i>S</i>	37	34	36	36	34	29	31	35
Species richness <i>S</i> total per platform	47				45			
Relative overall abundance of calcareous encrusters	High	Medium	Medium	Medium	High	High	Low	Low
Simpson index of dominance <i>D</i>	0.23	0.29	0.09	0.09	0.29	0.31	0.13	0.10
Shannon index <i>H'</i>	1.98	1.96	2.62	2.60	1.67	1.54	2.32	2.54
Pielou's equitability <i>J</i>	0.55	0.56	0.73	0.73	0.47	0.46	0.68	0.72

exhibiting the characteristic pair of brood chambers. The largest among all serpulid species was *Protula tubularia* (up to about 10 cm in tube length) that was found restricted to down-facing substrates at both depth stations. The rarest among the serpulids was the vitreous *Placostegus tridentatus*, of which only a single specimen was found down-facing at 127 m water depth.

3.1.3 | Foraminiferans

Numerous sessile epibenthic foraminiferans were found settling on both types of substrate, most common of which *Lobatula lobatula* (= *Cibicidoides lobatulus*) with a high morphological variability in size,

chamber inflation and direction of coiling. The highest abundance of this species was encountered on the up-facing substrates at the 127-m station, but it occurred at both depths and in both substrate orientations. This species formed shallow attachment etchings that by far outnumbered the recorded tests sitting on the limestone substrates, implying that actual rates of colonisation by this species were much higher. All the other recorded foraminiferans were agglutinating forms that did withstand the hydrogen peroxide treatment. The most abundant species at both depth stations were the very small and purely white *Hemisphaerammina bradyi* and the conspicuous brownish/orange curled *Lituotuba lituiformis*. All other species were rare to very rare and with one exception restricted to up-facing substrates at the 127-m station.

3.1.4 | Cirripeds

Balanus balanus was the only cirriped found on the experimental substrates. It was found most common on up-facing substrates at the 46-m station but also at the 127-m station in both orientations.

3.1.5 | Bivalves

The only bivalve (and only mollusc) that was found encrusting the experimental substrates was the saddle oyster *Pododesmus patelliformis*, only few specimens of which were found on the down-facing substrates at the 127-m station.

3.1.6 | Rhodophytes

Lithothamnion glaciale, the key ecosystem engineer in the dysphotic zone at Mosselbukta, was the sole crustose coralline alga found on the experimental substrates, although molecular genetics would be needed to confirm that monospecific nature (Peña et al., 2021). Up-facing substrates at the 46-m station were densely colonised by thin crusts of this species, whereas the shaded down-facing substrates at this depth were colonised by minute patches only. The aphotic 127-m station was, expectedly, devoid of this phototrophic calcifier.

3.2 | Bioerosion traces

A total of 30 different bioerosion traces were identified (Table 2, Figure 3), 28 at the 46-m station and 24 at the 127-m station. Most of these traces are microborings (19), followed by attachment traces (9) and traces of grazing activity (2). When including also those bioerosion traces that were recorded in barnacle shells sampled at roughly the same water depth (ca. 50 and 125 m) and analysed by Meyer et al. (2020), two additional microborings can be added to this list, while the other nine bioerosion traces documented in that study were found in common. Considering the entire bathymetrical transect analysed by Meyer et al. (2020), including seven depth stations from the intertidal to 125 m water depth, yet another six ichnotaxa add to the suite of known bioerosion traces recorded in Mosselbukta, resulting in a total ichnospecies richness of 38 ichnotaxa and informal forms.

3.2.1 | Microborings

Only three of the observed microborings can be attributed to phototrophic microendoliths, as there are the very abundant *Ichnoreticulina elegans* (produced by the chlorophyte alga *Ostreobium quekettii*; Radtke, 1991) and two morphotypes of *Scolecia filosa*

(produced by species of the cyanobacterium *Plectonema*; Radtke, 1991; Wisshak et al., 2011). Meyer et al. (2020) had additionally reported *Conchocelichnus seilacheri*, a trace formed by bangialean rhodophyte algae (Radtke et al., 2016). All these inferred trace makers are low-light specialists, confirming the dysphotic light regime at 46 m water depth, for which the co-occurrence of the key ichnotaxa *I. elegans* and *S. filosa* and the absence of other traces produced by chlorophytes or cyanobacteria is considered indicative (Glaub, 1994; Glaub et al., 2001; Vogel et al., 2008). Unfortunately, the 11-m platform in the euphotic zone was lost, so that we can only refer to the barnacle substrates analysed by Meyer et al. (2020) from shallower depths, who additionally recorded *Cavernula pediculata* (produced by the chlorophyte alga *Gomontia polyrhiza*; Radtke, 1991), as well as *Planobola* cf. *microgota* and *Fascichnus* spp. (produced mainly by cyanobacteria of the genus *Hyella*; Radtke, 1991). All other microborings were also found in the tube-legs or at the deeper 127-m station, identifying them as the work of organotrophic trace makers, albeit the specific biological identity remains largely unknown. Three traces presumably produced by marine fungi (Radtke, 1991; Wisshak et al., 2018; Wisshak & Porter, 2006) were most abundant, namely *Flagrichnus baiulus*, *Orthogonum tubulare*, and *Saccomorpha guttulata*. Additional microborings in this category were another two ichnospecies and two morphotypes of the ichnogenus *Orthogonum*, all of which rare to very rare. Among the larger microborings were three dendrinids, foremost the occasionally dominant *Nododendrina europaea* (produced by the foraminiferan *Globodendrina monile*; Plewes et al., 1993), complemented by the common to very rare *Pyrodendrina* ichnospecies *P. arctica* and *P. villosa* (both tentatively considered also foraminiferan traces; Wisshak, 2017). In addition, the two micro-entobians *Entobia mikra* and *Entobia nana* were documented, both of which common to very rare and interpreted as the work of micro-sponges (Wisshak, 2008). Finally, several specimens of previously unknown morphologies were documented and referred to by informal names, their biological affinity remaining enigmatic.

3.2.2 | Macroborings

In contrast to studies from lower latitudes, no borings of excavating sponges were found in this study, except for the putative micro-sponge borings *Entobia mikra* and *Entobia nana*, as noted above. In fact, to the best of our knowledge, there are no unequivocal reports of any polar clionaid sponges or their macrobioerosion traces (ichnogenus *Entobia*) in the literature (see also the discussion in Meyer et al., 2021). Hence, while bioeroding sponges are among the most destructive macrobioeroders in tropical and temperate environments (Schönberg, Fang, Carreiro-Silva et al., 2017; Schönberg, Fang, & Carballo, 2017), they appear to play only a marginal role, if any, in the polar regions. There were also no other macroborings recorded, neither in our settlement experiment, nor in the barnacles studied from the same site (Meyer et al., 2020). Not even the usual suspects in cold-temperate



FIGURE 2 Calcareous encrusters (a selection of the more common ones) recorded on the experimental substrates, including bryozoans (blue; all in same scale), serpulids (green), foraminiferans (red), a barnacle (yellow), a bivalve (brown) and a rhodophyte alga (purple)

waters were found, as there are spionid polychaete borings (ichnogenera *Caulostrepsis* and *Maeandropolydora*), pouch-shaped borings of acrothoracican barnacles (ichnogenus *Rogerella*), or

bivalve borings (ichnogenus *Gastrochaenolites*). However, a very common bioeroding or chasmoendolithic bivalve is found in the Mosselbukta rhodolith beds, *Hiatella arctica*, which seems to

TABLE 2 Abundances and ichnodiversity indices of bioerosion traces identified in the experimental substrates of the two settlement platforms, semi-quantified per orientation using the abundance classes ++ = very common, + = common, - = rare, and -- = very rare; results from barnacle shells collected at the same depth and reported by Meyer et al. (2020) are provided for comparison

Bioerosion type and trace	Known or inferred tracemaker	46-m platform			Meyer et al. (2020)	127-m platform			Meyer et al. (2020)
		Top	Bottom	Legs	50 m	Top	Bottom	Legs	125 m
Microborings									
<i>Ichonoretulina elegans</i> (Radtke, 1991)	<i>Ostreobium quekettii</i> (chlorophyte alga)	++	++	-	++				
<i>Conchocelichnus seilacheri</i> Radtke et al., 2016 ^a	Bangialean rhodophyte algae				-				
<i>Scolecia filosa</i> Radtke, 1991 (thin morphotype)	<i>Plectonema terebrans</i> (cyanobacterium)	++	-	--					
<i>Scolecia filosa</i> Radtke, 1991 (thick morphotype)	<i>Plectonema endolithicum</i> (cyanobacterium)	-							
<i>Scolecia serrata</i> Radtke, 1991 ^a	Bacterium?				-				-
<i>Flagrichnus baiulus</i> Wisshak & Porter, 2006	Fungus?		+	++	--	+	++	++	+
<i>Orthogonum tubulare</i> Radtke, 1991	Fungus?	--	+	-	--	++	-	-	-
<i>Orthogonum lineare</i> Glaub, 1994	Fungus?			--	--	-	--		--
<i>Orthogonum giganteum</i> Glaub, 1994	Fungus?			--					--
' <i>Orthogonum</i> form I' sensu Wisshak et al., 2005	Fungus?					-	-	--	
' <i>Orthogonum</i> form II'	Fungus?	--	-	--		-	-		
<i>Saccomorpha guttulata</i> Wisshak et al., 2018	Fungus?	--	+	+	--	++	--	--	-
<i>Nododendrina europaea</i> (Fischer, 1875)	<i>Globodendrina monile</i> (foraminiferan)	++	+	+	-	+	-	+	-
<i>Pyrodendrina arctica</i> Wisshak, 2017	Foraminiferan?	--		-	--	+	-	-	--
<i>Pyrodendrina villosa</i> Wisshak, 2017	Foraminiferan?	--	-	+	--	-	-	-	--
<i>Entobia mikra</i> Wisshak, 2008	Microsponge?		--	--	--	+	-	+	-
<i>Entobia nana</i> Wisshak, 2008	Microsponge?	-	-	-		+	+	--	
'large tongue form'	Unknown organotroph		--	--		-			
'small ear form'	Unknown organotroph		--				--		
'large ear form'	Unknown organotroph		--			--			
'nidus form' sensu Meyer et al., 2021	Unknown organotroph		+	-					
Attachment traces									
<i>Finichnus dromeus</i> (Taylor et al., 1999)	Uniserial bryozoans			+		- ^b		- ^b	

(Continues)

TABLE 2 (Continued)

Bioerosion type and trace	Known or inferred tracemaker	46-m platform			Meyer et al. (2020)	127-m platform			Meyer et al. (2020)
		Top	Bottom	Legs	50 m	Top	Bottom	Legs	125 m
<i>Finichnus peristoma</i> (Taylor et al., 1999)	Multiserial bryozoans		+	- ^b			+	-	
<i>Kardopomorphos</i> isp. (round morphotype)	Foraminiferans		+	-		+	+	+	
<i>Kardopomorphos</i> isp. (spiral morphotype)	Foraminiferans		-	-		-	-	-	
<i>Centrichnus concentricus</i> Bromley & Martinell, 1991	Cirripeds	--	- ^b						
<i>Centrichnus eccentricus</i> Bromley & Martinell, 1991	<i>Pododesmus patelliformis</i> (bivalve)						--		
'bunched whips form' sensu Wisshak et al., 2011	?		+	-		-	+	-	
<i>Renichnus</i> cf. <i>arcuatus</i> Mayoral, 1987	Spirorbid and serpulid worms	--	--	- ^b		-	--	-	
<i>Ophthalmichnus lyolithon</i> Wisshak et al., 2014	Diatoms			-					
Grazing traces									
<i>Gnathichnus pentax</i> Bromley, 1975	<i>Strongylocentrotus</i> spp. (echinoid)	++ ^b	- ^b	- ^b		- ^b	+		
<i>Radulichnus transversus</i> Lopes & Pereira, 2019	<i>Tonicella rubra</i> (chiton)	+ ^b	-	-		--	-		
Ichnospecies richness <i>S</i>		14	22	24	11	20	20	15	10
Ichnospecies richness <i>S</i> total per platform		28				24			
Ichnospecies richness <i>S</i> total per depth		30				25			
Relative overall abundance of bioerosion traces		High	Medium	Medium	Medium	High	Medium	Medium	Low
Simpson index of dominance <i>D</i>		0.24	0.30	0.45	0.93	0.28	0.41	0.54	0.44
Shannon index <i>H'</i>		1.51	1.83	1.39	0.22	1.68	1.47	1.11	1.30
Pielou's equitability <i>J</i>		0.57	0.59	0.44	0.09	0.56	0.49	0.41	0.56

^aIchnotaxon documented in barnacle shells by Meyer et al. (2020) only.

^bIchnotaxon documented via stereo microscopy only.

prefer clathrostomes and rhodoliths as substrate (Adey et al., 2013; Teichert, 2014).

3.2.3 | Attachment traces

Traces formed by means of attachment etching were common to very rare constituents of the Mosselbukta bioerosion trace assemblages. Most common and conspicuous of these were *Finichnus*

dromeus and *Finichnus peristoma* (attachment traces of uniserial and multiserial bryozoans, respectively; Taylor et al., 1999) as well as a round and a spiral morphotype of *Kardopomorphos* isp. (formed by epilithic foraminiferans; Beuck et al., 2008). Only few specimens were found of *Centrichnus concentricus* (formed by cirripeds; Bromley & Martinell, 1991) and *Centrichnus eccentricus* (etched by the foot of anomiid bivalves; here probably *Pododesmus patelliformis*; Bromley & Martinell, 1991). Large spiral etchings, assigned as *Renichnus* cf. *arcuatus*, were found below some spirorbid and

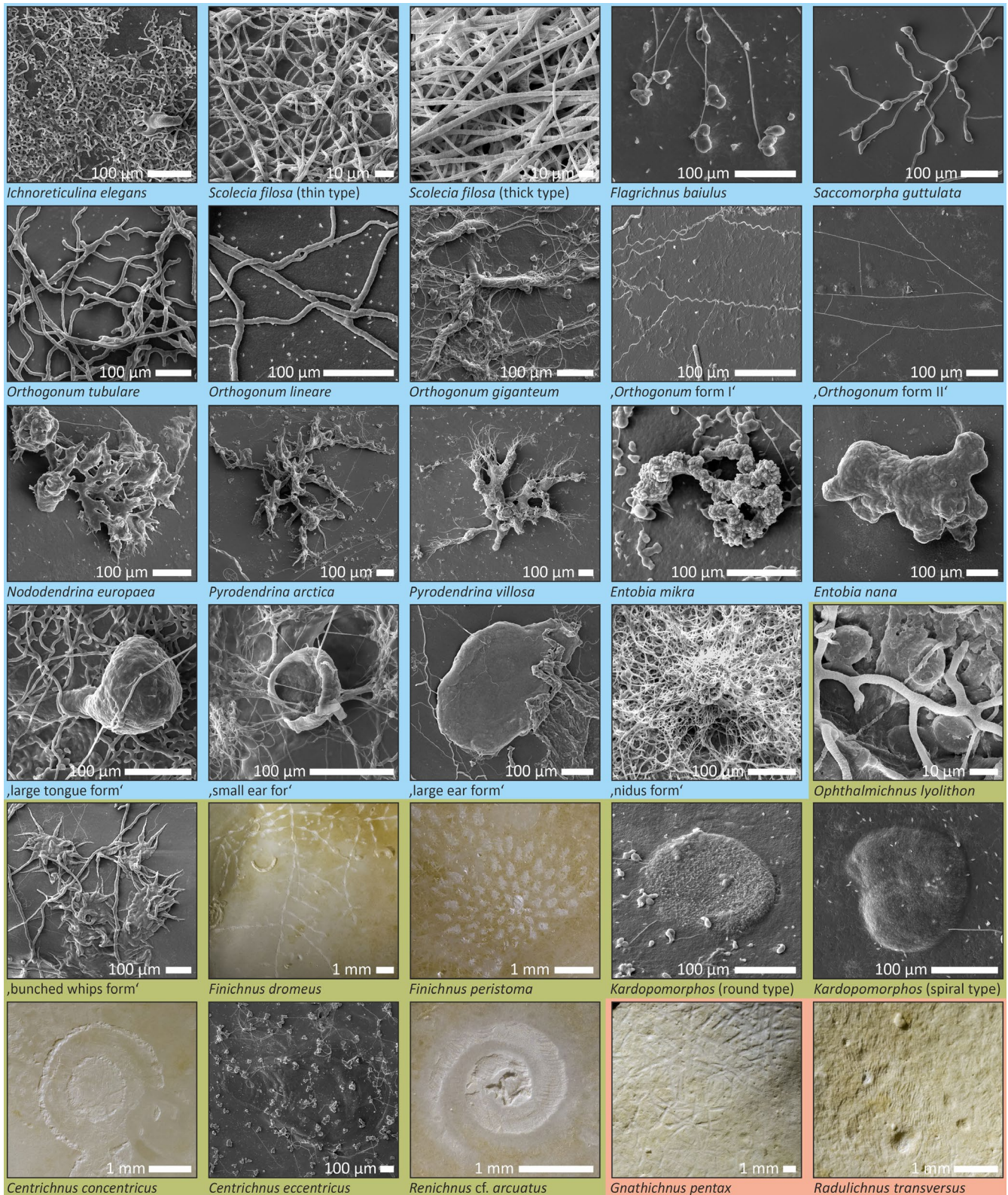


FIGURE 3 Bioerosion traces recorded in the experimental substrates, as visualized via scanning electron microscope of epoxy-resin casts (b&w photos) or stereo microscopy of original substrates (colour photos), including microborings (blue), attachment etchings (green) and grazing traces (red)

serpulid worms, and another trace that was commonly associated with serpulids (producer unknown) was the 'bunched whips form' sensu Wisshak et al. (2011). In addition, ring-shaped micro-etchings

of the ichnospecies *Ophthalmichnus lyolithon* were found, representing traces produced by attachment of sessile diatoms (Wisshak et al., 2014).

3.2.4 | Grazing traces

The most common grazing trace and particularly dominant on the upward-facing substrates of the shallower platform was *Gnathichnus pentax*, the pentaradiate sets of scratches left behind by grazing echinoids such as *Strongylocentrotus* sp. (Bromley, 1975). An additional grazing trace much smaller in dimension was *Radulichnus transversus*, produced by the radula of grazing chitons such as the local species *Tonicella rubra* (Lopes & Pereira, 2019). The abundance of these two kinds of grazing traces is in close accordance to the observation that *Strongylocentrotus* spp. and *Tonicella rubra* are the principal grazers in the Mosselbukta rhodolith beds (Wisshak et al., 2019).

3.2.5 | Predation traces

No predation traces were found in the experimental substrates (other than *Gnathichnus pentax*, which is mainly a grazing trace) and neither were they found in the balanid background samples. This is little surprising, though, as they are more commonly found in skeletons of mobile epibenthos.

3.3 | Biodiversity

The overall biodiversity of calcareous encrusters is similar at the two depth stations, with 47 taxa (out of 56 in total) recorded in the rhodolith bed at 46 m water depth and 45 taxa found settling on the substrates in 127 m depth (Table 1). Although the overall variability is low, there is a consistently higher species richness at the 46-m station when looking at the two types of substrates (PVC and limestone) and substrate orientations (up- and down-facing).

The degree of dominance/evenness in the species composition of calcifiers varies little between water depths, substrate types and substrate orientations. Dominance is generally low, as reflected in a Simpson index D ranging from as low as 0.09 (down-facing substrates at 46 m) to 0.31 (up-facing limestones at 127 m). Accordingly, values of the Pielou's equitability J are relatively high, with a range of 0.46 (up-facing limestones at 127 m) to 0.73 (down-facing substrates at 46 m).

The analyses of similarity (ANOSIM) show that overall, there are only low to moderate differences in calcifier community composition between the two depth stations, substrate orientations and substrate types. Depth is the only factor where the difference was found statistically significant ($p = 0.029R = 0.552$) (Table S1). Accordingly, PVC and limestone substrates cluster closest in the NMDS plot (Figure 4a) and the cluster analyses (Figure 4b; similarity >75%). Substrate orientations cluster more closely for the 46-m station compared to the 127-m station, where the differences are as pronounced as for the two depth stations. The number of permutations was relatively low (35), so these statistics need to be interpreted with some reservation, albeit being in good agreement with the descriptive statistics and qualitative observations. The relevance

of the factors water depth versus orientation versus substrate type is the same as found in the Azores experiment (Wisshak et al., 2015; see discussion therein), underlining that hard-bottom calcifier communities appear to have little preference for PVC versus limestone and are more strongly controlled by the orientation of the substrate and particularly by water depth.

3.4 | Ichnodiversity

Bioerosion traces were found diverse at both depth stations and for all three substrate orientations (up-facing, down-facing, within tube-legs), the ichnospecies richness varying between 14 and 24 ichnotaxa (Table 2). The lowest ichnospecies richness (14) was found for the up-facing substrates of the 46-m platform, which show also the highest overall abundance of bioerosion traces. However, the dense 'carpet' of *Ichnoreticulina elegans* and *Scolecia filosa* in the epoxy casts and the intense grazing abrasion, reflected in the high abundance of *Gnathichnus pentax* and *Radulichnus transversus*, had complicated recognition of other bioerosion traces. Hence, the comparatively low ichnodiversity is probably partly an observational artefact. This is in accordance to the observation that the ichnodiversity at the other up- and down-facing substrates is higher and very similar (20–22). Surprisingly, this applies also to the cryptic substrates in the tube-legs at the 46-m platform (24) while those at the 127-m station show a lower ichnodiversity (15). This pattern may reflect the circumstance that the 46-m platform was placed on the bio- and lithoclasts of the rhodolith beds, thus prohibiting the tube-legs from sinking into the sediment and allowing access even of some phototrophic endoliths and grazers, while at the 127-m station dropstones were mixed with soft sediment, so that there was more contact to the sediment. However, this pattern could also reflect a generally higher abundance and diversity of bioeroders preferring cryptic substrates, as this is a common ecological niche in the rhodolith beds only (e.g. hollow rhodoliths).

The overall abundance and ichnospecies richness are similar at both depth stations (28 vs. 24). The small difference is resulting from the presence of four bioerosion traces produced by phototrophic euendoliths exclusively at the shallower station (Table 2). In contrast, the ichnospecies richness in the barnacles sampled at the same depths, as studied by Meyer et al. (2020), was low (10–11). This can be explained by the focus of the latter study on microborings only and by the fact that bioerosion traces are more difficult to recognise in barnacle substrate when compared to the very smooth experimental bivalve substrates. Notwithstanding, the composition of the microboring trace assemblages in the experimental and natural substrates were found very similar at both depth stations, underlining that the experiment has yielded representative results.

As far as the degree of dominance/evenness in the composition of the bioerosion trace assemblages is concerned, there is little variation between water depths and substrate orientations (Table 2). That is, dominance and evenness are balanced, as expressed by medium values for the Simpson index D of 0.24–0.54 and the Pielou's

equitability J of 0.41–0.59 respectively. In comparison to the biodiversity of calcareous encrusters, the bioerosion traces show a lower (ichno)species richness, higher dominance, and lower values for evenness.

According to the analyses of similarity (ANOSIM) there are moderate albeit not statistically significant differences in the bioerosion trace assemblages between the two depth stations ($p = 0.200$; $R = 0.370$) and only very minor differences between the three substrate orientations ($p = 0.939$; $R = -0.278$) (Table S1). Down-facing substrates and those in the tube legs cluster closest in the NMDS plot (Figure 4c) and the cluster analysis (Figure 4d; similarity >65%). For the 127-m station they cluster together with the up-facing substrates at this depth station and the down-facing substrates at the 46-m station next. The up-facing substrates at the 46-m station show the strongest dissimilarity (Figure 4d; similarity >65%), a result that mirrors the observation that microborings produced by phototrophic chlorophytes were restricted to these substrates. The number of permutations was very low (10–15), so these statistics again need to be interpreted with some reservation, albeit being in good accordance to the descriptive statistics and the bioerosion trace inventory. The relevance of the factors water depth versus orientation is the same as found in the Azores experiment (Wisshak et al., 2011; see discussion therein), underpinning that bioerosion trace assemblages are most strongly controlled by the photic zonation and secondarily by the availability of light governed by different substrate orientations at a given water depth.

3.5 | Do the rhodolith beds promote local biodiversity or ichnodiversity?

It has been demonstrated that the higher habitat complexity offered by the occurrence of rhodoliths (particularly hollow ones) promote benthic biodiversity at Svalbard shelf sites with rhodolith beds

(Teichert, 2014). This pattern was found particularly pronounced for bryozoans, polychaetes and molluscs (Teichert, 2014: figure 3). While that study did not consider bathymetrical trends in biodiversity, preliminary results of a series of beam trawls undertaken in 25-m depth intervals from 25 to 150 m water depth in Mosselbukta show that the biodiversity of sessile as well as mobile macrobenthos and some bottom-dwelling fish was markedly elevated at 50 m water depth (38–43 taxa), compared to shallower as well as deeper waters (18–28 taxa), thus coinciding with the peak in rhodolith abundance and suggesting that their occurrence might also promote a bathymetrical peak in biodiversity (Wisshak et al., 2017). The present experiment provides a solid basis to further assess this line of reasoning and to test the hypothesis of increased diversity in the sessile hard-bottom communities recorded in the experimental substrates deployed in the Mosselbukta rhodolith bed at 46 m water depth compared to the adjacent seafloor at aphotic 127 m water depth, both in respect to biodiversity of calcareous encrusters as well as ichnodiversity of bioerosion trace assemblages (i.e. reflecting the biodiversity of bioeroders): As outlined above, the species richness S (Tables 1 and 2) is higher at the 46-m station, but this difference is minor, and the same applies for the ichnospecies richness. Looking at the Shannon index H' as another diversity measure (Tables 1 and 2), values are also higher at the 46-m station, but the difference is again low for the calcareous encrusters as well as the bioerosion traces. Accordingly, none of the Mann-Whitney U-tests performed for the species or ichnospecies richness S , the Simpson index of dominance D , the Shannon index H' , or the Pielou's equitability J , showed any statistically significant difference between the two depth stations (Table S2). Hence, in contrast to the results obtained for sessile and mobile macrobenthos from beam trawls (Wisshak et al., 2017), there is no statistically significant elevation of encruster biodiversity or bioerosion ichnodiversity in the rhodolith beds, compared to aphotic deeper waters. Our data do show, however, a marked and statistically significant increase in the per

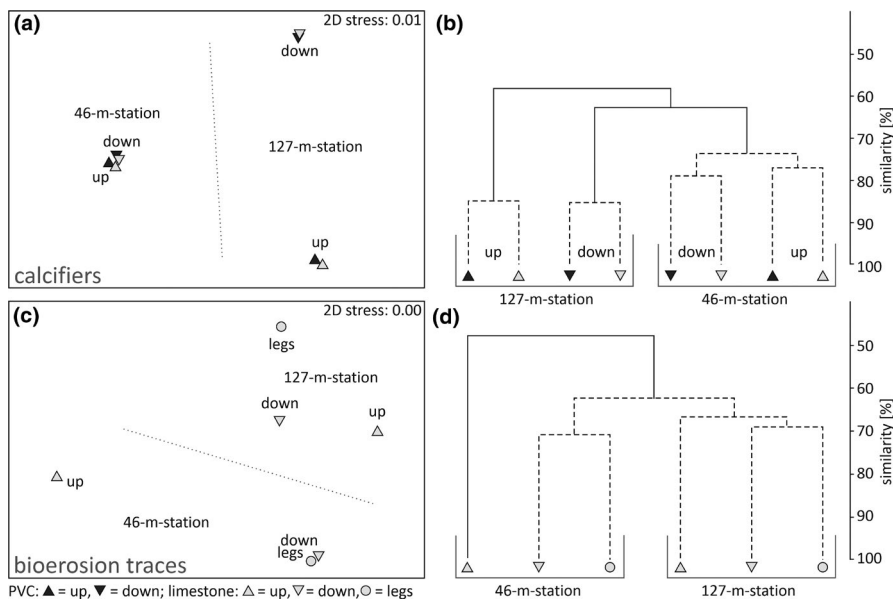


FIGURE 4 Non-metric multidimensional scaling plots (NMDS; left) and cluster analyses with similarity profiles (SIMPROF; right) of calcifiers (a, b) and bioerosion traces (c, d); dashed lines indicate differences with no statistical support

cent surface coverage and carbonate as well as bioerosion rates, as presented in the following sections.

3.6 | Carbonate accretion densities

Settlement densities of calcareous encrusters, expressed as per cent surface cover, on first sight appear to vary strongly between the two depth stations, types of substrate and substrate orientations, but they vary only little within each sub-set of substrates (Figures 5 and 6, Table S3). By far the highest density ($78.2 \pm 4.9\%$; mean \pm SD) was observed for the up-facing PVC substrates at the dysphotic 46-m station (Figure 6a), with most of the available space occupied by thin crusts of *Lithothamnion glaciale*. The respective limestone substrates, in contrast, show much stronger signs of grazing bioerosion that has eroded into the experimental substrate and limited, or reduced, the colonised surface area, resulting in much lower densities ($20.9 \pm 3.3\%$). For the down-facing substrates (Figure 6b), which show only initial crustose algae crusts and comparatively few grazing traces, the colonised area is similarly low and the difference between the two substrate types is small ($15.8 \pm 5.5\%$ and $22.3 \pm 11.1\%$, respectively). At the aphotic 127-m station (Figure 6c, d), with no encrustation by crustose algae, both substrate types and orientations have similar accretion densities with mean values between 11.3% and 19.3% surface coverage. Hence, overall this pattern reflects a relatively homogenous colonisation density of calcareous invertebrates that over the course of the 10-year exposure have occupied only about a tenth to a fifth of the available substrate, while the dominant colonisation by the local ecosystem engineer *Lithothamnion glaciale* strongly varies depending on the available light and the grazing pressure by chitons and echinoids (compare also substrates in Figure 5).

Permutational analysis of variance (PERMANOVA) for the carbonate accretion densities shows significant differences for the two depth stations, substrate orientations and substrate types, as well as the three pairwise comparisons (Table S4). Differences are most pronounced for the factor water depth (pseudo- $F = 45.2$; $p = 0.001$), followed by substrate orientation (pseudo- $F = 19.7$; $p = 0.001$) and substrate type (pseudo- $F = 3.9$; $p = 0.046$), mirroring the relative order of these three factors seen in the calcifier biodiversity.

3.7 | Carbonate accretion and bioerosion rates

Rates of carbonate accretion and bioerosion vary markedly with depth and substrate orientation (Figures 5 and 6, Table S3), and are in good accordance to the observed carbonate accretion densities. Both the carbonate accretion and the bioerosion rates are to be considered conservative estimates, because our gravimetric approach does not account for calcifiers that have settled on the substrates and were then partly bioeroded. Hence, accretion and bioerosion rates are residual rates.

The highest accretion rates ($24.6 \pm 18.3 \text{ g m}^{-2} \text{ year}^{-1}$; mean \pm SD) were recorded for the up-facing PVC substrates at the 46-m station (Figure 6a), whereby the large range results from patchy settlement of heavy balanids (e.g. Figure 5 upper left). Respective rates on the limestone substrates are somewhat lower ($16.4 \pm 18.0 \text{ g m}^{-2} \text{ year}^{-1}$) because of the removal or inhibition of calcifiers by intense grazing activity of echinoids and chitons. Accordingly, these limestone tiles also show the highest recorded bioerosion rates ($-35.1 \pm 2.8 \text{ g m}^{-2} \text{ year}^{-1}$), resulting in net bioerosion ($-18.7 \pm 19.2 \text{ g m}^{-2} \text{ year}^{-1}$) for the up-facing substrates at the 46-m station. At the down-facing substrates (Figure 6b), all rates are considerably lower and less variable. In contrast to the up-facing substrates, accretion outweighs bioerosion, resulting in net accretion ($5.7 \pm 4.7 \text{ g m}^{-2} \text{ year}^{-1}$). At the 127-m station, up- (Figure 6c) and down-facing substrates (Figure 6d) show comparable low rates ($<10 \text{ g m}^{-2} \text{ year}^{-1}$) and variability ($<3 \text{ g m}^{-2} \text{ year}^{-1}$). In accordance to the 46-m station, there is a slight net bioerosion ($-3.3 \pm 1.1 \text{ g m}^{-2} \text{ year}^{-1}$) at the up-facing substrates and net accretion ($6.4 \pm 2.6 \text{ g m}^{-2} \text{ year}^{-1}$) at the down-facing substrates, likely because of a higher grazing pressure on up-facing substrates. When considering both depth stations, substrate types and orientations together (Figure 6e) the overall accretion is very similar on the PVC versus the limestone substrates (10.4 ± 12.0 vs. $9.9 \pm 9.8 \text{ g m}^{-2} \text{ year}^{-1}$) and in the same range than the inverse bioerosion rates ($-12.4 \pm 13.6 \text{ g m}^{-2} \text{ year}^{-1}$). In consequence, carbonate accretion and bioerosion appears overall nearly in balance ($-2.5 \pm 13.9 \text{ g m}^{-2} \text{ year}^{-1}$). It must be stressed, however, that these low rates of net carbonate production refer to the initial 10 years of settlement on bare substrate and not to the standing hard-bottom community with a large surface coverage of the primary carbonate producer *Lithothamnion glaciale* (see also discussion in Section 3.8 below). Also, our experiment does not account for carbonate production by the abundant motile calcifiers, especially echinoids and large gastropods or clams (Wisshak et al., 2019), that contribute to the total net carbonate production and support a positive carbonate budget of the rhodolith carbonate factory.

PERMANOVA for the carbonate accretion rates shows significant differences for the two depth stations, whereas differences between substrate orientations and substrate types are insignificant (Table S5). Accordingly, differences are most pronounced for the factor water depth (pseudo- $F = 13.0$; $p = 0.003$), followed by substrate orientation (pseudo- $F = 0.9$; $p = 0.369$) and substrate type (pseudo- $F = 0.1$; $p = 0.886$), thus mirroring the relative order of these three factors seen in the calcifier biodiversity. In the case of the bioerosion rates, both water depth (pseudo- $F = 34.1$; $p = 0.001$) and substrate orientation (pseudo- $F = 119.5$; $p = 0.001$) show significant differences (Table S6). In contrast to the accretion rates, here the substrate orientation has the highest influence, reflecting the intensively-grazed illuminated versus the little-grazed shaded substrates. Accordingly, the same applies to the net rates for depth (pseudo- $F = 3.7$; $p = 0.025$) and substrate orientation (pseudo- $F = 6.2$; $p = 0.007$) (Table S7).

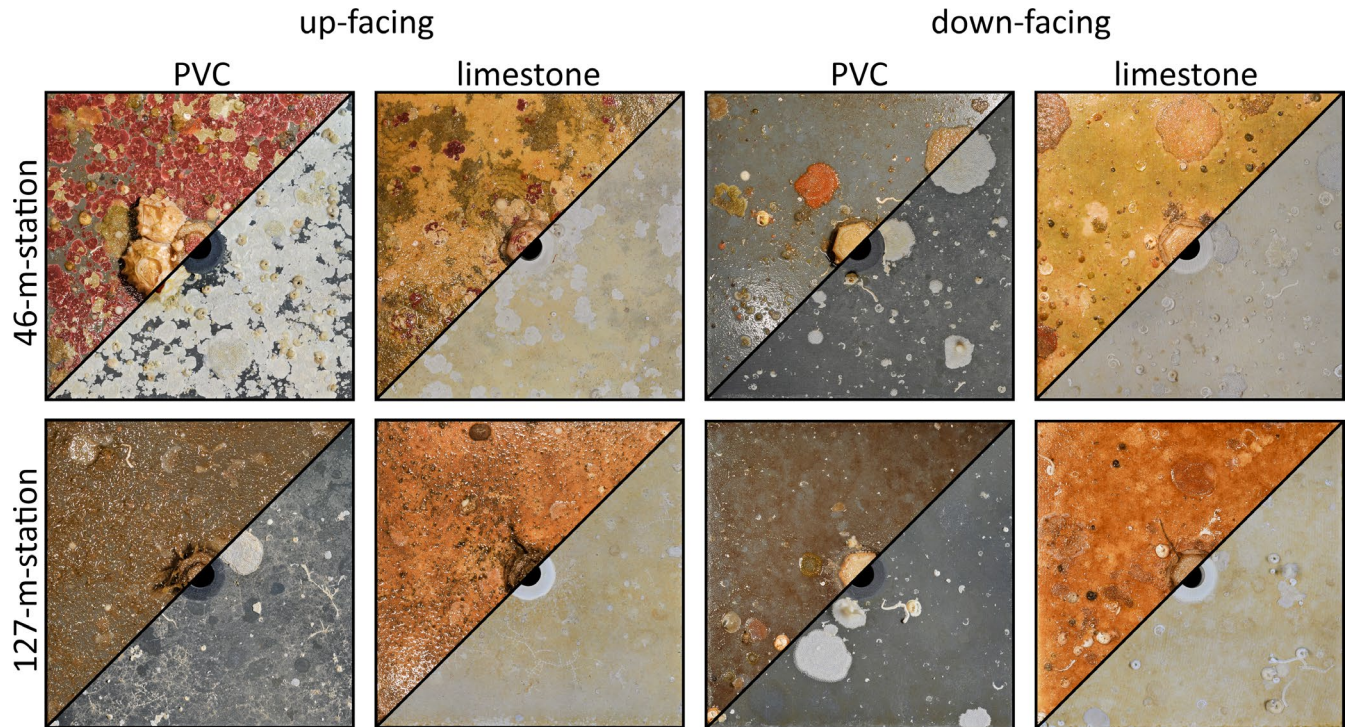


FIGURE 5 Representative examples of the experimental PVC and limestone substrates at the two depth stations and substrate orientations, photographed immediately upon recovery (upper left triangle) and after bleaching with hydrogen peroxide (lower right triangle)

3.8 | Carbonate accretion rates in relation to rhodolith growth rates

The carbonate accretion rates recorded for the up-facing PVC substrates at the 46-m station are, at least at first sight, considerably lower than those estimated by Teichert & Freiwald (2014) for Svalbard rhodoliths. On the experimental substrates, rates of $24.6 \pm 18.3 \text{ g m}^{-2} \text{ year}^{-1}$ were recorded, whereby substrates without large balanids show rates of only $12.5 \pm 1.5 \text{ g m}^{-2} \text{ year}^{-1}$ ($n = 3$). Because other calcifiers also contributed to this carbonate accretion rate, these rates are a maximum estimate for what crusts dominated by *Lithothamnion glaciale* have contributed to the carbonate accretion on those substrates (see Figure 5 upper left). Their actual contribution is likely well below $10 \text{ g m}^{-2} \text{ year}^{-1}$. The rhodolith carbonate production rates obtained from several Svalbard rhodolith beds by Teichert & Freiwald (2014) range from 119.8 to $200.3 \text{ g m}^{-2} \text{ year}^{-1}$, with a rate of $119.8 \text{ g m}^{-2} \text{ year}^{-1}$ determined for rhodoliths sampled in Mosselbukta in 44 m water depth. However, these rates refer to 100% coverage of established algae colonies and thus cannot readily be compared to our rates that reflect the initial settlement of *L. glaciale* crusts on pristine substrate. These are not, and cannot be, normalised for *L. glaciale* surface area, because we do not have data on the temporal increase in per cent surface coverage. This also means that the actual carbonate production by *L. glaciale*, and the resulting net carbonate accretion of the standing community (see Section 3.7), are to be expected higher than recorded by our experimental design.

Linear extension rates of *L. glaciale* determined in protuberances from various rhodoliths sampled at 46 m in Mosselbukta were in average $75 \pm 24 \mu\text{m}$ ($n = 1031$) per annual increment Schlüter et al. (2021). This is in good accordance to the observation that the *L. glaciale* crusts observed on our experimental substrates were less than a millimetre thick and still partly in the progress of expanding laterally. This suggests that initial settlement and the early crustose life stage of *L. glaciale* before developing protuberances and reaching equilibrium growth rates are a matter of at least a decade (see also Freiwald, 1995). Together with the low rhodolith carbonate production rates these observations underline the slow pace of rhodophyte carbonate production in the carbonate factory of Svalbard rhodolith beds.

3.9 | The Mosselbukta experiment in relation to other Svalbard experiments

Only few settlement experiments, investigating various aspects of biodiversity of calcifiers (but none investigating bioerosion traces), have previously been undertaken in the Svalbard area. Barnes & Kuklinski (2005) were the first to study colonisation on settlement panels in Isfjorden, the largest fjord on the western side of Spitsbergen, and recorded 20 taxa on substrate tiles (plastic) deployed at 12 m water depth for up to a year of exposure. Kuklinski et al. (2013), in a study focusing on seasonality of recruitment of benthic invertebrates, listed 22 taxa settling on panels (plastic)

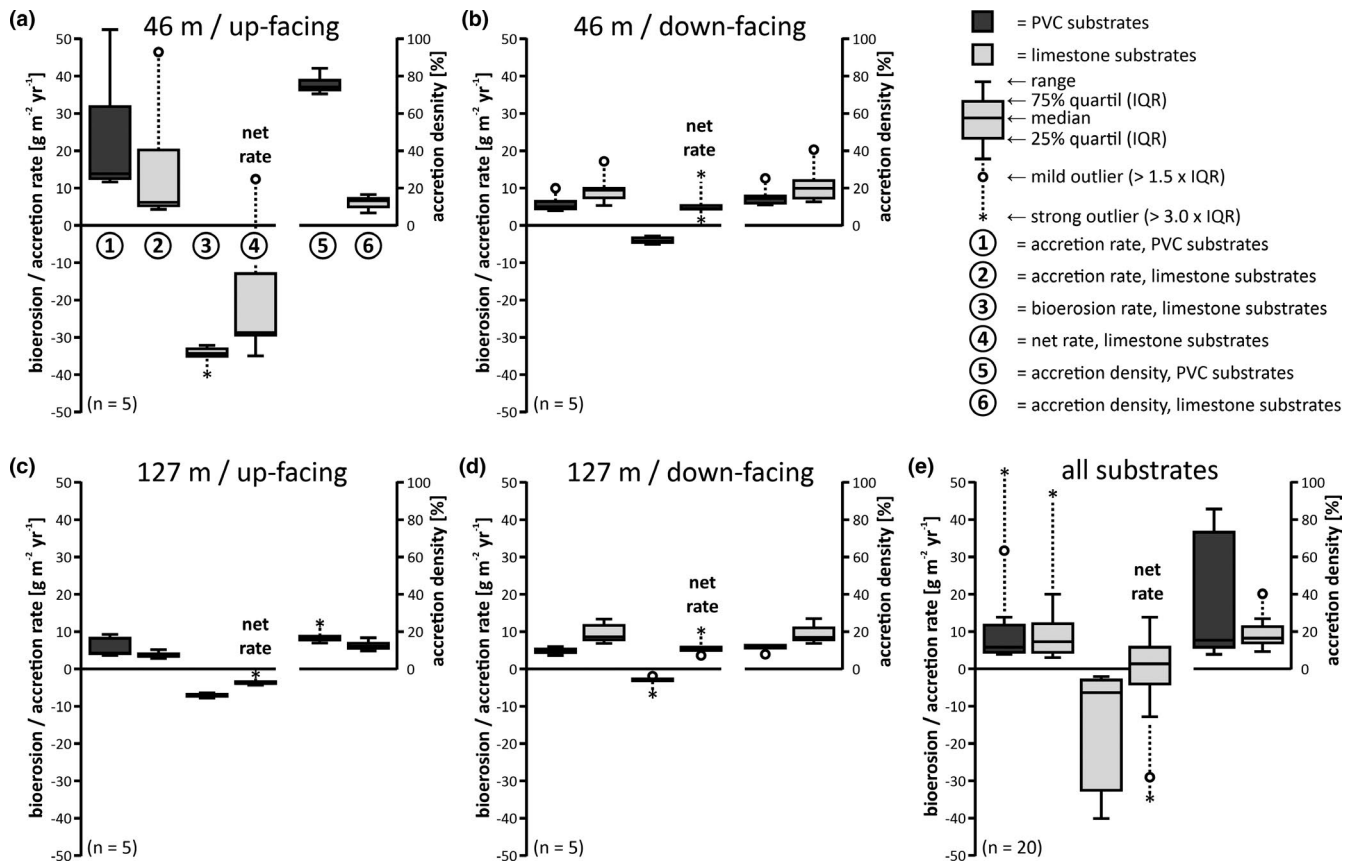


FIGURE 6 Box-plots of carbonate accretion and bioerosion rates as well as carbonate densities for the PVC and limestone substrates at the two depth stations and for the two substrate orientations. From left to right, boxes refer to accretion on PVC and limestone substrates (positive values), bioerosion of limestone substrates (negative values), net rate of limestone substrates (accretion minus erosion), and per cent coverage of carbonate accretion on PVC and limestone substrates

deployed for up to a year at about 6 m water depth in Adventfjorden (a branch of Isfjorden). Most recently, Meyer et al. (2017) focused on recruitment of benthic invertebrates on experimental substrates (acrylic) in relation to temperature, depth and seasonality at five different sites in Svalbard fjords at 7–215 m water depth for 1 year of exposure and revealed 48 species and morphotypes, including also macrophytes. Hence, the present study, with a total species richness of 56 calcifier taxa, has recorded a high biodiversity in comparison to the previous experiments. However, this high biodiversity could, at least partially, be an effect of the significantly longer exposure period of 10 years, compared to only 1 year in the previous studies. In this coherence, the earlier experiments would have primarily recorded the most opportunistic species only. Also, the total substrate surface (40 tiles of 10×10 cm) was relatively high and we were looking at both up- and down-facing surfaces and two types of substrates, all being factors that might have increased the number of taxa recorded. Nevertheless, it is remarkable that the species richness in Mosselbukta is even higher than the total biodiversity found in the study by Meyer et al. (2017), who had deployed an even larger number of substrates (44 tiles of 15×15 cm) in a much larger bathymetrical range and spatial scope. Despite the limited comparability, this could well suggest that the biodiversity in Mosselbukta is high for Svalbard standards, a finding that would be in good accordance

to the observation of Teichert (2014), who concluded that benthic biodiversity is enhanced at shelf settings with prominent rhodolith beds (see Section 3.5). Such local differences in biodiversity is in good accord to the findings of Meyer et al. (2017), who reported a high spatial and temporal variability in recruitment of hard-ground communities. At sites with a high local species pool, more species can be observed on experimental substrates (Kuklinski et al., 2017). Given the very similar species richness found at 46 and 127 m water depth, our data does not support the observation of an exponential decrease in species richness with water depth, as reported by Meyer et al. (2017) for depths between 7 and 215 m. In any case, the high overall species richness recorded by the Mosselbukta experiment clearly underlines the conclusion put forth already by Barnes & Kuklinski (2005) in that Arctic colonisation is slow but it is not poor in species.

3.10 | Latitudinal trends

Setting the results of the Svalbard experiment into the context of latitudinal trends, we can draw comparisons to earlier settlement experiments in lower latitudes, expanding the discussions put forth in Wisshak et al. (2010,2011,2015). In the North Atlantic, these

include experiments in equatorial Caribbean (Scoffin et al., 1980; Stearn et al., 1977), the tropical Bahamas (Hoskin et al., 1986; Vogel et al., 1996, 2000), the warm-temperate Azores (Wisshak et al., 2010, 2011, 2015) and the cold temperate coastal waters of the Kosterfjord in SW Sweden (Wisshak, 2006; Wisshak et al., 2005; Wisshak & Rüggeberg, 2006).

Despite the harsh environmental conditions in the polar environment of Mosselbukta, the biodiversity of the calcifying hard-bottom communities was found similar or even higher than at comparable depth in the Azores. Taking the bryozoans as most specious group as an example, 32 species at the 46-m station compare to 21 species at 60 m in the Azores, and 28 species at the 127-m station to 30 species at 150 m in the Azores. For the serpulid worms the diversity was found about twice as high in Svalbard, with 10 species at the 46-m station comparing to only five at 50 m in the Azores and nine species at the 127-m station comparing to six at 150 m in the Azores. A comparable diversity in benthic foraminiferal species is documented at the cold-temperate coastal waters of the Kosterfjord in SW Sweden with seven species at 50 m and five species at 85 m water depth, compared to three species at the 46-m station and six species at the 127-m station in Svalbard, respectively (at the Azores only the most abundant foraminiferans were identified, thus prohibiting a comparison). Only in respect to molluscs and calcifying algae, the biodiversity was higher in the Azores. However, these comparisons need to be interpreted with some reservation as the Azores archipelago is biogeographically more isolated than Svalbard and because in Mosselbukta the experimental exposure was longer, allowing also less opportunistic species to settle.

With respect to ichnodiversity of bioerosion traces in the experimental substrates and the additional background samples (Meyer et al., 2020), we see a depletion in the spectrum or traces produced by phototrophic microphytes. This is interpreted as resulting from a combination of environmental factors, namely the condensed photic zonation, the long spell of the polar night (ca. 4 months), the additional shading by seasonal sea ice, and the very low seawater temperatures. In addition, calcareous substrates are very scarce in the shallowest subtidal and the intertidal range due to sea ice scour. The most specious group of bioerosion traces are microborings formed by organotrophic bioeroders. These were found more diverse than in the cold-temperate Kosterfjord (Wisshak et al., 2005) and about as diverse as in the warm-temperate Azores (Wisshak et al., 2011). The same holds true also for attachment and grazing traces. Solely in respect to macroborings the trend is reversed, given an almost complete lack of macroborings so far documented from Svalbard waters. For a more detailed discussion on latitudinal trends in bioerosion ichnodiversity see Wisshak et al. (2011).

Looking at carbonate accretion rates, this 10-year settlement experiment clearly demonstrates the slow pace at which hard-bottom calcifier communities contribute to the carbonate production in the polar carbonate factory of the Svalbard rhodolith beds. While rates were found significantly higher in the rhodolith beds compared to adjacent aphotic waters as well as compared to rates found at a similar water depth in the cold-temperate (non-carbonate factory)

setting at the Kosterfjord (Wisshak, 2006), they are far lower than what was observed in the warm-temperate Azores (Wisshak et al., 2010). Expressed in numbers, the platform at 46 m water depth in the Mosselbukta rhodolith bed had recorded a mean of $24.6 \text{ g m}^{-2} \text{ year}^{-1}$ (up-facing) and $5.9 \text{ g m}^{-2} \text{ year}^{-1}$ (down-facing PVC substrates), whereas accretion rates recorded at 60 m in serpulid/oyster bioherms in the Azores surpassed these rates by one to two orders in magnitude, yielding a mean of $463.1 \text{ g m}^{-2} \text{ year}^{-1}$ (up-facing) and $896.9 \text{ g m}^{-2} \text{ year}^{-1}$ (down-facing PVC substrates). Yet, these high rates are still to be considered an order in magnitude lower than rates of carbonate production found in shallow-water tropical coral reef environments, such as the total carbonate production rate of $9000 \text{ g m}^{-2} \text{ year}^{-1}$ assessed for a fringing reef at Barbados (Stearn et al., 1977) and census-based coral carbonate production rates of up to $12,070 \text{ g m}^{-2} \text{ year}^{-1}$ calculated for reef sites around Bonaire (Perry et al., 2012), although the dramatic ecological decline of most Caribbean reefs has reduced carbonate production rates by at least 50% (Perry et al., 2013). In any case, the Svalbard carbonate factory marks the low end of a latitudinal gradient in the carbonate production of hard-bottom communities, even though rates are higher than in environments without calcifying ecosystem engineers that support local carbonate factories.

With respect to bioerosion rates, a contrasting picture is evident in that the observed rates were similar or in some cases even higher than at the same water depth at the other experimental sites. Specifically, the platform at 46 m water depth in the Mosselbukta rhodolith bed had recorded a mean of $-35.1 \text{ g m}^{-2} \text{ year}^{-1}$ (up-facing) and $-4.0 \text{ g m}^{-2} \text{ year}^{-1}$ (down-facing substrates), compared $-1.9 \text{ g m}^{-2} \text{ year}^{-1}$ (up-facing) determined at 50 m in the cold-temperate Kosterfjord (Wisshak, 2006) and $-21.0 \text{ g m}^{-2} \text{ year}^{-1}$ (up-facing) and $-3.7 \text{ g m}^{-2} \text{ year}^{-1}$ (down-facing) found in the Azores experiment (Wisshak et al., 2010). Even the rates of tropical bioerosion determined in the Bahamas at these depths were not much higher, with rates at around 50 m depth to be interpolated between $-40.0 \text{ g m}^{-2} \text{ year}^{-1}$ (all orientations) found at 32 m depth and $-2.0 \text{ g m}^{-2} \text{ year}^{-1}$ at 79 m depth (all orientations), as reported by Hoskin et al. (1986), and between $-105 \text{ g m}^{-2} \text{ year}^{-1}$ at 30 m depth and $-13.0 \text{ g m}^{-2} \text{ year}^{-1}$ at 100 m depth (all orientations), determined by Vogel et al. (1996, 2000). Accordingly, the low rates of $-7.1 \text{ g m}^{-2} \text{ year}^{-1}$ (up-facing) and $-3.5 \text{ g m}^{-2} \text{ year}^{-1}$ (down-facing substrates) found at the aphotic 127-m station in Mosselbukta are similar or higher than in similar water depths at the other experimental sites. When comparing not the actual water depth but the respective dysphotic and aphotic zones, then the rates of the Svalbard platforms are higher than at any of the above experimental sites. Unfortunately, the 11-m platform was lost due to winter storms or ice scour, so at present we cannot include the euphotic zone in that comparison, where usually peak bioerosion rates are found. Given the marked depletion in phototrophic microendoliths and the almost complete lack of macroborers, we would expect considerably lower rates than at lower latitudes.

Apart from the ubiquitous and diverse microbioerosion, macrobioerosion appears to play only a very minor role, apart from the bioeroding bivalve *Hiattella arctica* and its contribution to hollowing rhodoliths,

as observed in Mosselbukta (Teichert, 2014). In the contrary, grazing bioerosion by echinoids, and to a lesser degree by chitons, appears particularly relevant for the degradation of the carbonates in the Svalbard rhodolith beds. Although rates were not quantified separately, the abundance of bioerosion traces suggest that echinoids are a principal agent of bioerosion that support the highest rates of bioerosion observed on up-facing substrates at the 46-m station. Accordingly, a lander study has found high densities of *Strongylocentrotus* spp. in the rhodolith bed (13.8 ± 3.1 individuals per square metre; Wisshak et al., 2019) and video transects indicate that this density remains high also towards shallower depths (unpublished data). The density of echinoids and the abundance of their bioerosion traces were found far higher than in the Kosterfjord and Azores experiments, whereas echinoid bioerosion is a major force of grazing bioerosion in many tropical coral reef sites. There, echinoid bioerosion rates alone can reach several kilograms per square metre and year, such as $-5300 \text{ g m}^{-2} \text{ year}^{-1}$ determined for *Diadema antillarum* at a Barbados fringing reef (Scoffin et al., 1980) or $-6670 \text{ g m}^{-2} \text{ year}^{-1}$ assessed for *Echinometra lucunter* at the Bahamas (Hoskin et al., 1986). More recent, census-based carbonate budget assessments have demonstrated that in many Caribbean reef sites, echinoid bioerosion has markedly declined and parrotfish are now the dominant agents of grazing bioerosion, contributing an average of $1600 \text{ g m}^{-2} \text{ year}^{-1}$ (76% of the total bioerosion) across all reef habitats studied (Perry et al., 2012, 2014). All these very high rates of grazing bioerosion, however, concern shallow-water coral reef sites, whereas at deeper settings that correspond to the water depth or the photic regime of our Svalbard experimental platforms, grazing did not lead to higher rates of total bioerosion in tropical settlement experiments.

3.11 | Implications for the preservation of polar cold-water carbonates

The slow pace of carbonate build-up by calcifying hard-bottom communities but rates of dysphotic to aphotic bioerosion comparable to temperate latitudes, as observed in our Svalbard experiment, suggest a relatively low preservation potential for these polar carbonates. However, there are also other factors that need to be considered:

Due to the very low seawater temperatures, saturation states for calcite and aragonite in Mosselbukta are low compared to lower latitudes, albeit still largely in the range of supersaturation ($\Omega > 1$; Teichert et al., 2014; Wisshak et al., 2019). While late summer measurements at Mosselbukta have shown possibly seasonal drops into undersaturation ($\Omega < 1$; Teichert et al., 2014), early summer measurements have demonstrated that the seasonal sea-ice cover in concert with phytoplankton blooms and the onset of rhodophyte photosynthesis lead to temporarily elevated saturation states ($\Omega_{\text{Ca}} > 3$; $\Omega_{\text{Ar}} > 2$; Wisshak et al., 2019). As a result, pure physico-chemical dissolution of the carbonates can be expected to play only a minor role, at least above the sediment-water interface. The low rates might well promote chemical bioerosion, though, as has been shown in acidification experiments for various bioerosion agents (see Schönberg, Fang, Carreiro-Silva, et al., 2017 for a review). This

circumstance also provides a possible line of reasoning for why bioerosion rates keep up with temperate latitudes. On the other hand, the low saturation states mean that there is no relevant precipitation of calcite biospar and early diagenetic marine cements in the voids left behind in calcareous substrates by microborers (Smith & Nelson, 2003) that would have a stabilising effect on skeletal carbonates, as can be observed in many tropical to subtropical settings (e.g. Bathurst, 1966; Smith, 1988). Consequently, even the most intricate details of the microbioerosion traces observed in the experimental substrates and background sample material were well preserved. As a rule of thumb, however, sedimentation rates are lower and retention times of skeletal carbonates on the seafloor are much higher (hundreds to thousands of years) in cold-water carbonate settings compared to low latitudes (Smith & Nelson, 2003). As a result, there is a lot of time for bioeroders to degrade cold-water skeletal carbonates that in consequence often show particularly intense signs of bioerosion (e.g. Farrow & Fyfe, 1988; Freiwald & Wilson, 1998; Wisshak, 2006; Wisshak et al., 2005). Ultimately, bioerosion in combination with mechanical abrasion breaks down most skeletal carbonates to small sediment particles that are then incorporated in shelf sediments (e.g. Farrow & Fyfe, 1988). In Svalbard, this has been further promoted by the rapid post-glacial isostatic uplift, as recorded by remnants of Quaternary rhodolith beds preserved in raised beaches (Feyling-Hanssen & Jorstad, 1950 and own observations). The future of the global climate change, in turn, predicts a eustatic rise in sea-level that may drown the present rhodolith beds to greater depths. Yet, this is only one facet of the increasing vulnerability of polar rhodolith beds. In Mosselbukta, they have already seen an alarming decline of sea-ice cover (Hetzinger et al., 2019) along with a marked increase in glacier-derived runoff (Hetzinger et al., 2021) that increases turbidity. Moreover, future ocean acidification is expected to compromise growth rates and structural integrity of the ecosystem engineer *Lithothamnion glaciale* (Büdenbender et al., 2011; Ragazzola et al., 2012, 2016; Teichert et al., 2020) and adds to an increase in other human disturbances, such as bottom trawling (Fragkopoulou et al., 2021) and adverse effects of the influx of microplastics into polar waters (Teichert et al., 2021). The combination of all the above underline the reasoning put forth by Wisshak (2006) and indeed indicate a relatively low preservation potential for polar cold-water carbonates, such as those formed in the carbonate factory of the Mosselbukta rhodolith beds.

4 | CONCLUSIONS

- A diverse calcifier hard-bottom community (56 taxa) was recorded on the experimental PVC and limestone substrates exposed for 10 years in the Mosselbukta rhodolith bed and aphotic seafloor down-slope, dominated by bryozoans (36) and serpulids (11), and complemented by foraminiferans (6), a balanid, a bivalve and the local ecosystem engineering crustose coralline alga *Lithothamnion glaciale*. Likewise, a diverse bioerosion trace assemblage (30 ichnotaxa) was documented, dominated by

microborings (19), followed by attachment traces (9) and traces of grazing activity (2).

- While all biodiversity metrics show an elevated diversity of calcifiers and ichnodiversity of bioerosion traces in the rhodolith bed, if compared to adjacent aphotic waters, these differences are statistically insignificant. Dissimilarities (determined via ANOSIM) in the community structure of calcifiers and the assemblages of bioerosion traces between the two depth stations (46 and 127 m), the two substrate orientations (up- and down-facing) and the two substrate types (PVC and limestone), decrease in that order and are moderate at most.
- In contrast, the per cent surface coverage of calcifiers as well as the carbonate accretion and bioerosion rates are significantly elevated in the rhodolith bed, reflecting higher abundance or size of calcifiers and bioerosion traces, respectively. All three measures were highest for the up-facing substrates at the 46-m station, peaking at a mean surface coverage of $78.2 \pm 4.9\%$ and carbonate accretion rate of $24.6 \pm 18.3 \text{ g m}^{-2} \text{ year}^{-1}$ on the PVC substrates and a mean bioerosion rate of $-35.1 \pm 2.8 \text{ g m}^{-2} \text{ year}^{-1}$ recorded in the limestone tiles. Differences in these metrics (addressed via PERMANOVA) decrease in significance in the same order of factors than in the case of the community structure analyses.
- Overall, carbonate accretion and bioerosion of the hard-bottom calcifier community were found nearly in balance, with a mean net rate of $-2.5 \pm 13.9 \text{ g m}^{-2} \text{ year}^{-1}$. Actual net carbonate production rates of the standing community, with a high surface coverage of *L. glaciale*, are to be expected higher than our experimental results suggest.
- Crusts formed by the rhodolith-forming crustose coralline alga *L. glaciale* on the up-facing PVC substrates at the 46-m station were less than a millimetre thick and largely still expanding laterally, supporting a maximum mean surface coverage of $78.2 \pm 4.9\%$ after 10 years of exposure. Together with the linear extension rate of in average $75 \mu\text{m}$ per year and a carbonate production rate of $119.8 \text{ g m}^{-2} \text{ year}^{-1}$ determined previously for rhodoliths sampled in Mosselbukta, these observations underline the slow pace of rhodophyte carbonate production in the carbonate factory of the Svalbard rhodolith beds.
- The recorded calcifier biodiversity of 56 taxa is considerably higher than what was found in earlier settlement experiments in Svalbard waters. While this is partly grounded on methodological differences (longer exposure, two substrate types and orientations), it could nevertheless suggest that the local biodiversity in Mosselbukta is high for Svalbard standards.
- A comparison with previous settlement experiments in different biogeographical zones of the North Atlantic suggests that there is no depletion in the diversity of hard-bottom calcifier communities in Mosselbukta, despite the harsh polar environment. The same holds true for the ichnodiversity of grazing traces, attachment etchings and those microborings formed by organotrophic bioeroders in the experimental substrates and in balanid background samples previously analysed from intertidal to aphotic

depths. The number of microborings produced by phototrophic microborers, however, is strongly reduced, primarily because of limitations in the availability of light (condensed photic zonation, 4 months of polar night, and shading by seasonal sea ice). Surprisingly, otherwise common macroborings were found absent in Svalbard waters.

- With respect to rates of carbonate production of hard-bottom communities, the studied Svalbard carbonate factory marks the low end of a latitudinal gradient, even though rates are higher than in environments lacking calcifying ecosystem engineers. Bioerosion rates, in contrast, are similar or higher than at the same water depth or photic regime at lower latitudes, although this pattern may well be reversed in shallow euphotic waters not covered in our experiment (11-m platform lost), given the depletion in phototrophic microendoliths and lack of macroborers. While grazing bioerosion by echinoids (*Strongylocentrotus* spp.) is particularly relevant for the degradation of the carbonates in the Svalbard rhodolith beds, their rates of bioerosion cannot rival those reported from tropical shallow-water coral reef environments.
- The observed low rates of carbonate accretion but relatively high rates of bioerosion are possibly promoted by low carbonate supersaturation states in these cold waters. In concert with high retention times of skeletal carbonates on the seafloor and a general lack of calcite biospar or early diagenetic cements forming in the voids left behind by microborers, this suggests a low preservation/fossilisation potential for polar cold-water carbonates, such as those formed in the carbonate factory of the Mosselbukta rhodolith beds.

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CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

AUTHOR CONTRIBUTIONS

MW conceived the study, prepared the settlement platforms, analysed the experiment, and drafted the manuscript. AF was chief scientist and fundraiser for the MSM 2–3 cruise (on which MW and AR participated). MW was chief scientist and fundraiser for the MSM 55 cruise (on which NM and AR participated) and the subsequent DFG project WI 3754/3-1. PK identified the bryozoans and discussed the respective biodiversity patterns. AR identified the foraminiferans and discussed the respective biodiversity patterns. NM supported on-board and lab preparations, analysed the carbonate accretion densities, and performed the multivariate statistics. All authors have contributed to the manuscript and approved the final submission.

DATA AVAILABILITY STATEMENT

Data available in the article supplementary material and on request from the authors.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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