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Surface lebensspuren and their tracemakers in Arctic fjords of Spitsbergen: Patterns, diversity, and environmental controls

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Abstract: This study presents a comprehensive analysis of epibenthic lebensspuren, *i.e.*, biogenic surface traces, and their tracemakers in the fjords of Svalbard. Data were collected over six Arctic summer seasons (2015–2017, 2019, 2020, and 2023) and one winter season (2016), across 206 stations, 57% of which exhibited lebensspuren. Nineteen distinct lebensspuren morphotypes were identified, including eight newly described forms. Tracemakers were identified for 18 of these types, and specific species or genera determined for 10. Echinoderms were the dominant group, responsible for 55% of all traces, followed by decapods (20%) and gastropods (17%). The study documents lebensspuren morphology and ethology along with their associated tracemakers, offering insights into their abundance and spatial distribution within fjord ecosystems. Notable findings include the high frequency of lebensspuren produced by the sea star *Urasterias lincki*, along with significant contributions from brittle stars, shrimps, and gastropods. Distribution patterns were influenced by environmental factors such as proximity to glaciers and river mouths; however, non-metric multidimensional scaling analysis revealed no clear community separations. This dataset can serve as a valuable resource for the interpretation and classification of trace fossils (*i.e.*, fossil analogues of lebensspuren), while highlighting the ecological and paleoenvironmental importance of lebensspuren in Arctic marine systems.

Keywords: Arctic, glacial bays underwater imagery, biogenic surface traces, epibenthic megafauna, bioturbation.

Introduction

Benthic organisms, through activities such as locomotion and burrowing, bioturbate sediments and consequently produce a variety of traces. These traces, known as lebensspuren, are defined as any biogenic structures resulting from the interaction of living organisms with the substrate, primarily sediment (Ewing and Davis 1967). One of the pioneering classifications of lebensspuren was based on the organism behavior during their formation (Seilacher 1953). Resting traces are imprints left by temporarily stationary organisms, with the most common examples being those of asteroids (sea stars) and ophiuroids (brittle stars). Crawling traces result from movement across the sediment surface and are often marked by impressions of limbs or podia, such as the tube feet of sea stars or the appendages of mobile crustaceans. Grazing traces are surface trails that reflect both locomotion and feeding activity, typically produced by snails or sea urchins. Dwelling traces are burrows that serve as domiciles for their tracemakers and are represented the burrow openings of polychaetes, anemones, or fish. These structures arise from the interactions of both epifauna and infauna with the sediment; however, the most readily observable and morphologically distinctive are those produced by epibenthic megafauna (Young *et al.* 1985). A separate category of lebensspuren includes digestion traces, also referred to as defecation traces (Miguez-Salas *et al.* 2024c), which encompasses fecal casts and pellets, such as the coiled castings of lugworms (*Arenicola marina*) or the fecal deposits of holothurians.

According to new classification proposed by Miguez-Salas *et al.* (2024c), marine lebensspuren are categorized based on three components: morphology, ethology, and tracemaker identity. For the latter two components, the use of open nomenclature is possible when precise identification is uncertain. This classification framework is adopted in the present study.

Current knowledge of lebensspuren primarily stems from the analysis of photographs or various types of casts (Bell *et al.* 2013; Ishida *et al.* 2022; Miguez-Salas *et al.* 2023b). Neoichnological studies remain limited due to high operational costs and observational challenges (Kaufmann *et al.* 1989; Przeslawski *et al.* 2012; Miguez-Salas *et al.* 2024b). Much of the existing research has focused on more accessible shallow marine environments or has been carried out under experimental conditions (Uchman and Pervesler 2006; Brom *et al.* 2018). In contrast, relatively few studies have addressed lebensspuren in deep-sea environments (Wheatcroft *et al.* 1989; Przeslawski *et al.* 2012; Miguez-Salas *et al.* 2022, 2024a, 2024c; Brandt *et al.* 2023).

Identifying the organisms responsible for producing lebensspuren remains a significant challenge (Ewing and Davis 1967). In the deep-sea environment, only a limited number of tracemakers have been definitively associated with the structures they produce (Miguez-Salas *et al.* 2024b). A well-known example is *Paleodictyon,* a trace fossil whose maker has long eluded discoveries despite considerable effort (Rona *et al.* 2009; Przeslawski *et al.* 2012; Miguez-Salas *et al.* 2023b). In some cases, similar traces may be produced by multiple taxa, complicating identification. For instance, the crawling lebensspuren of holothurians and echinoids are often difficult to distinguish (Dundas and Przeslawski 2009; Bell *et al.* 2013). In this context, photographs that capture both the trace and the trace-making organism are particularly valuable for improving identification accuracy and advancing neoichnological studies.

The ability to directly identify the trace-making organism and observe its behavior is one of the key distinctions between lebensspuren and trace fossils (Miguez-Salas *et al.* 2022, 2023a). These traces can provide valuable insights into the relationship between organisms and environmental conditions, such as the availability and distribution of organic matter (Miguez-Salas *et al.* 2022). Such observations allow for the inference of environmental factors in both modern settings (neoichnology) and past environments through comparison with trace fossils (Buatois and Mángano 2011). Documenting and cataloging new examples of lebensspuren plays a crucial role in bridging the fields of neoichnology and paleoichnology (Bromley 1996).

The fjords of Svalbard (the high Arctic archipelago), unique in many aspects, offer an excellent natural laboratory for collecting and study of lebensspuren. This is particularly relevant in the current era of climate change, as increased sedimentation due to glacial melt is altering fjords ecosystems. Notable trends include the influx of new species and the northward shift of species ranges (Deja *et al.* 2016). A key question remains whether there is a correlation between the abundance and diversity of lebensspuren, and the abundance and biodiversity of megafauna. Current studies have not reached a definitive conclusion, suggesting instead that a complex interplay of biotic and abiotic factors influences this relationship (Kitchell *et al.* 1978; Young *et al.* 1985; Wheatcroft *et al.* 1989; Turnewitsch *et al.* 2000; Hughes and Gage 2004; Miguez-Salas *et al.* 2024b). The link between lebensspuren and benthic fauna suggests that these traces can serve as useful proxies for assessing species richness and community structure, particularly in patchy environments where megafauna may not be visible and traces may be the only indicators of biological activity (Heezen and Hollister 1971; Mauviel *et al.* 1987; Kaufmann *et al.* 1989).

This study is based on the hypothesis that the prevailing abiotic and biotic conditions in the fjords of Svalbard favor the preservation of lebensspuren. Building on this premise, it presents the most frequently observed lebensspuren in these fjords and, where possible, identifies their tracemakers. In addition, it describes several new types of lebensspuren, not previously reported in the literature. The resulting dataset is particularly valuable, as high-resolution video observations enabled the assignment of traces to their producers and even documented the process of trace formation *in situ*. Furthermore, the study investigates potential correlations between the number and diversity of lebensspuren and the composition of epibenthic megafauna. The findings highlight the importance of incorporating neoichnological analysis into studies on benthic biodiversity and behavior.

Study area

Spitsbergen, the largest island of the Svalbard archipelago, is located in the high Arctic and is characterized by a dynamic interplay of various water masses, including the warm Western Spitsbergen Current and the colder Sørkapp Current (Walczowski *et al.* 2012; Promińska *et al.* 2017). These currents play a crucial role in shaping the island's climate, sea ice conditions, and marine ecosystems (Cottier *et al.* 2007; Walczowski and Piechura 2011; Carmack *et al.* 2015). The island hosts a complex network of fjords, each exhibiting distinct hydrological and geological features influenced by their proximities to glacial inputs and exposure to ocean currents. Variability in water mass influence and the presence or absence of underwater sills create diverse ecological niches that support rich and varied marine communities (Svendsen *et al.* 2002; Nilsen *et al.* 2008). Spitsbergen a key research area for studying interactions between Arctic marine and glacial systems, offering critical insights into the impacts of climate change on polar environments. This unique geographic and oceanographic settings make Spitsbergen an essential location for understanding Arctic ecological dynamics and their broader climatic implications. The data presented in this study were collected from several fjords and adjacent marine areas around Spitsbergen, each offering distinct environmental settings shaped by oceanographic and glacial influences.

Hornsund

Recognized as the coldest fjord, Hornsund is primarily influenced by the Sørkapp Current. It is distinguished by a high rate of glacial retreat and plays a notable role in regional carbon sequestration (Promińska *et al.* 2017; Węsławski *et al.* 2017).

Van Mijenfjord

This fjord is characterized by a stratified water column due to the presence of a sill and is subjected to significant glacial inflows. It also experiences pronounced seasonal freezing, making it an unique Arctic system (Støylen and Fer 2014).

Isfjorden

The largest fjord in the region, Isfjorden lacks a sill at the mouth, allowing for extensive advection of Atlantic waters. Its multiple glacier-fed branches contribute to diverse physical conditions and a rich mosaic of benthic and pelagic communities (Nilsen *et al*. 2008).

Kongsfjord

Known for substantial Atlantic water influence, Kongsfjord's hydrography and biological communities are shaped by the interplay between warm Atlantic inflows and glacial meltwater, which enhances Arctic conditions in the inner fjord (Hop *et al.* 2006; Cottier *et al.* 2007).

Additional data were collected near the Torellbreen glacier and on the adjacent shelf (nine stations), as well as from isolated stations located in Magdalenfjorden, Raudfjorden, Smerenburgfjorden, and Rijpfjorden. These varied locations collectively provide a comprehensive representation of Svalbard's fjord ecosystems and contribute to understanding spatial patterns of lebensspuren and their environmental drivers.

Methods

Field sampling

The photographic material presented in this study comprises of 206 video transects recorded in the fjord regions of Svalbard (Fig. 1). Most of the data were collected from the deck of the RV *Oceania* during six Arctic summer expeditions (2015–2017, 2019, 2020, 2023). One additional video transect (station GR7_2023) was conducted from a small boat *Gavia Immer*. These summer stations are complemented by 10 stations recorded in 2016 aboard the R/V *Helmer Hansen* (Supplementary Material, available from https://opendap.iopan.pl/opendap/data/csv/Lebensspuren/contents.html).

All footage was captured using an underwater imaging system referred to here as a drop camera. The device con-

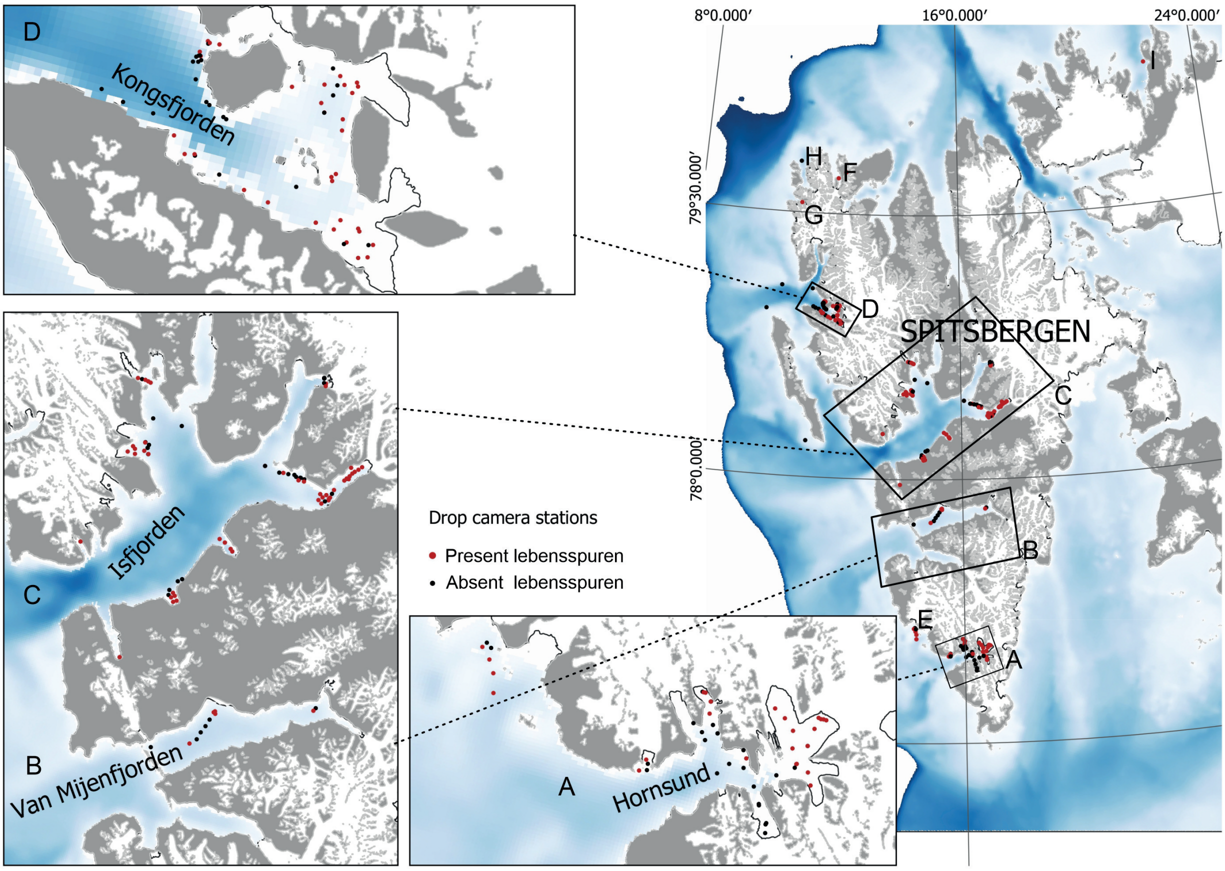

Fig. 1. Map of the Svalbard archipelago showing the locations of stations surveyed using a drop camera. Red dots indicate stations where lebensspuren were recorded, while black dots represent stations where no traces were observed. Letter symbols correspond to the following regions: **A** – Hornsund Fjord; **B** – Van Mijenfjorden Fjord; **C** – Isfjorden Fjord; **D** – Kongsfjorden and a fragment of Krossfjorden; **E** – Torellbreen and shelf; **F** – Raudfjorden; **G** – Magdalenfjorden; **H** – Smeerenburgfjorden; **I** – Rijpfjorden.

sists of a metal frame housing two cameras: an analog camera with a resolution of 700 TV lines (TVL) for live monitoring, and a digital Panasonic HX-A500 camera that recorded high-resolution video (1280×720 px) to a memory card. The system is also equipped with two batteries, each powering an independently operated lamp, and a pair of parallel-mounted lasers used for scale calibration.

Each transect recorded approximately 10 min of seabed footage while the camera was towed at a speed of approximately 0.3 knots (0.15 m s^{-1}) and maintained at an average height of 50 cm above the seafloor. In stations near glacier fronts, the camera height was reduced to 10–30 cm due to poor visibility caused by high concentration of suspended glacial particulates. The height of the camera above the seabed was estimated using visible referencing objects of known size, such as sponges and sea anemones, as well as with the spacing of laser points – a method consistent with approaches used by other researchers (Gutt and Siegel 1994; Hirche *et al.* 2016).

The surveyed depth range extended from 22 m at the shallowest location to 280 m at the deepest, with a median depth of 70 m (Supplementary Material, see above). Video footage from the digital camera was recorded in fourfold slow motion, which facilitated detailed post-processing and minimized blurring and out-of-focus frames. This is especially important in turbid areas affected by glacial discharge, where water clarity and camera drift often posed challenges to capturing high-quality imagery.

Video analysis

Each station was then analyzed for the abundance and biodiversity of megafauna, as well as for the presence of lebensspuren preserved on the seabed – primarily resting lebensspuren, locomotion lebensspuren, and grazing traces. Due to the considerable variability in water transparency and occasionally unfavorable sea conditions during video acquisition, *e.g.*, swaying of research vessel's hull, all footage was analyzed manually. Each video was reviewed multiple times using VLC media player, an open-source software licensed under the GPL.

At certain stations, the usable portion of the footage, and consequently the analysis duration, was slightly reduced due to poor visibility or recording artifacts. The exact duration of the analyzed footage for each transect along with the estimated area of the seafloor surveyed (expressed in m²) was calculated based on the vessel's average drift speed and the camera's field of view. The values are provided in Supplementary Material (see above).

Additionally, bottom turbidity at each station was visually assessed using a four-level scale (0–3): (*i*) 0 (No Suspension): no visible particles suspended of in the water column; the water appeared clear; (*ii*) 1 (Low Suspension): minimal particle suspension of observed; water remained predominantly clear with slight turbidity and good visibility; (*iii*) 2 (Moderate Suspension): noticeable particle suspension resulted in moderate turbidity, with a marked reduction in visibility; (*iv*) 3 (High Suspension): a high concentration of suspended matter was visible, often significantly disrupting the image quality; at some stations, lowering the camera closer to the seafloor was required to improve visibility.

Due to the extensive volume of material collected, the analysis excluded certain types of traces, such as openings of burrows and various surface traces. These included depressions or openings produced by anemones of the family Cerianthidae, tube openings of polychaetes from the families Terebellidae and Sabellidae, probable fish burrow openings, likely produced by species from the family Lumpenidae, and fecal mounds produced by polychaetes of the family Arenicolidae.

Representative examples of the most common recorded lebensspuren, along with their tracemakers, are shown in Figs. 2–5. In these still frames, image contrast was enhanced to compensate for poor water clarity and to reduce the visual effect of backscatter caused by suspended particles. All illustrations were produced using QGIS and Corel Draw software. For statistical analyses, PRIMER 7 software with the PERMANOVA+ add-on was employed. Spearman's rank correlation coefficient was used to assess the significance of the relationships among the measured variables. The data collected were divided into three subsets: (*i*) "Lebensspuren": this subset consists of data from 117 stations where traces were recorded. Each trace was counted and identified to the lowest possible ethological and taxonomic category (Table 1); (*ii*) "All Megafauna": this subset comprises all benthic fauna identified at the same 117 stations where lebensspuren were observed; (*iii*) "Tracemakers": this subset also draws from the same 117 stations but includes only mobile species capable of producing the analyzed traces. A list of these potential tracemakers is provided in Supplementary Material, see above.

Distances from each station to the nearest glacier front or glacial river mouth were measured using QGIS software. Based on this information, stations were categorized under the factor "Station Type" into one or three groups: "Glacier Influence" "River Influence" or "No Direct Influence".

Results

Spatial distribution and multivariate patterns of lebensspuren

Out of the 206 analyzed stations, clear examples of lebensspuren were identified at 117 stations, representing 55% of total (Table 1). The recorded traces were assigned to 19 distinct types. For 18 of them, still-frame examples and corresponding tracemakers were documented. Each trace was assigned a morphotype, a taxonomic identification of the trackmaker, where possible, and behavioral category.

In ten types of lebensspuren, the tracemakers could be confidently identified to the genus or species level. For the remaining types, precise taxonomic identification was not

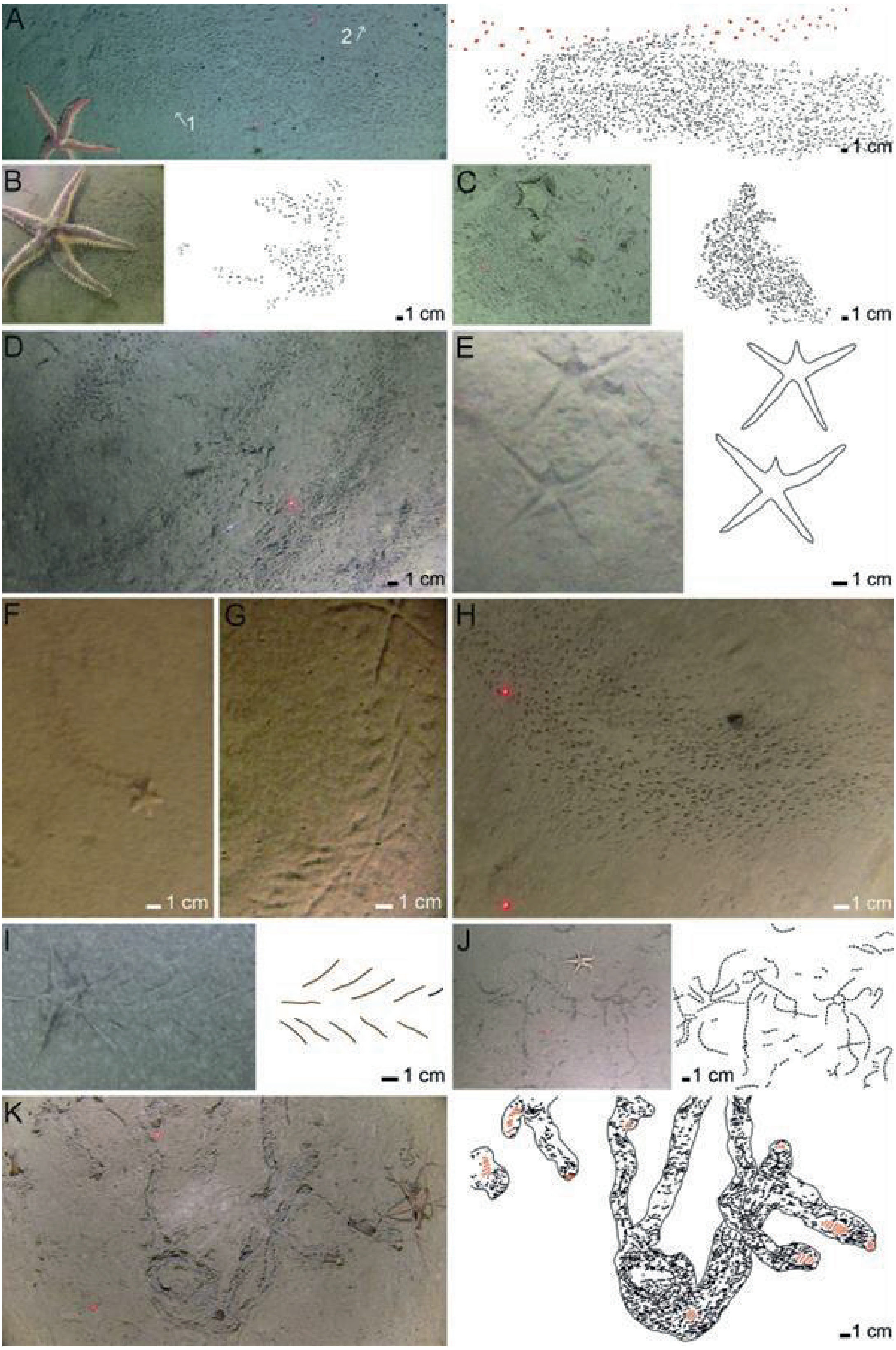

Fig. 2. Recorded lebensspuren – part one. High-density punctuated trail produced by the sea star *Urasterias lincki*, shown both with its tracemaker (**A$_1$, B**) and without (**D, H**). (**C**) High-density punctuated trail produced by *Ctenodiscus crispatus,* shown with its tracemaker. (**E**) Sea star impression of an unidentified sea star with an arm undergoing regeneration. (**F**) High-density punctuated trail produced by of juvenile, indeterminate asteroid, shown with its tracemaker. (**G, I**) Herringbone trails produced by *Ophiuridae* spp., both with visible tracemakers. (**J**) Discontinuous, winding trail produced by *Ophiuridae* spp., shown with its tracemaker. (**K**) Irregular M-ridged trail attributed to the sea cucumber *Myriotrochus rinki* (indicated with red shading), along with well-developed associated lebensspuren. (**A$_2$**) Step trail produced by *Pagurus* spp.

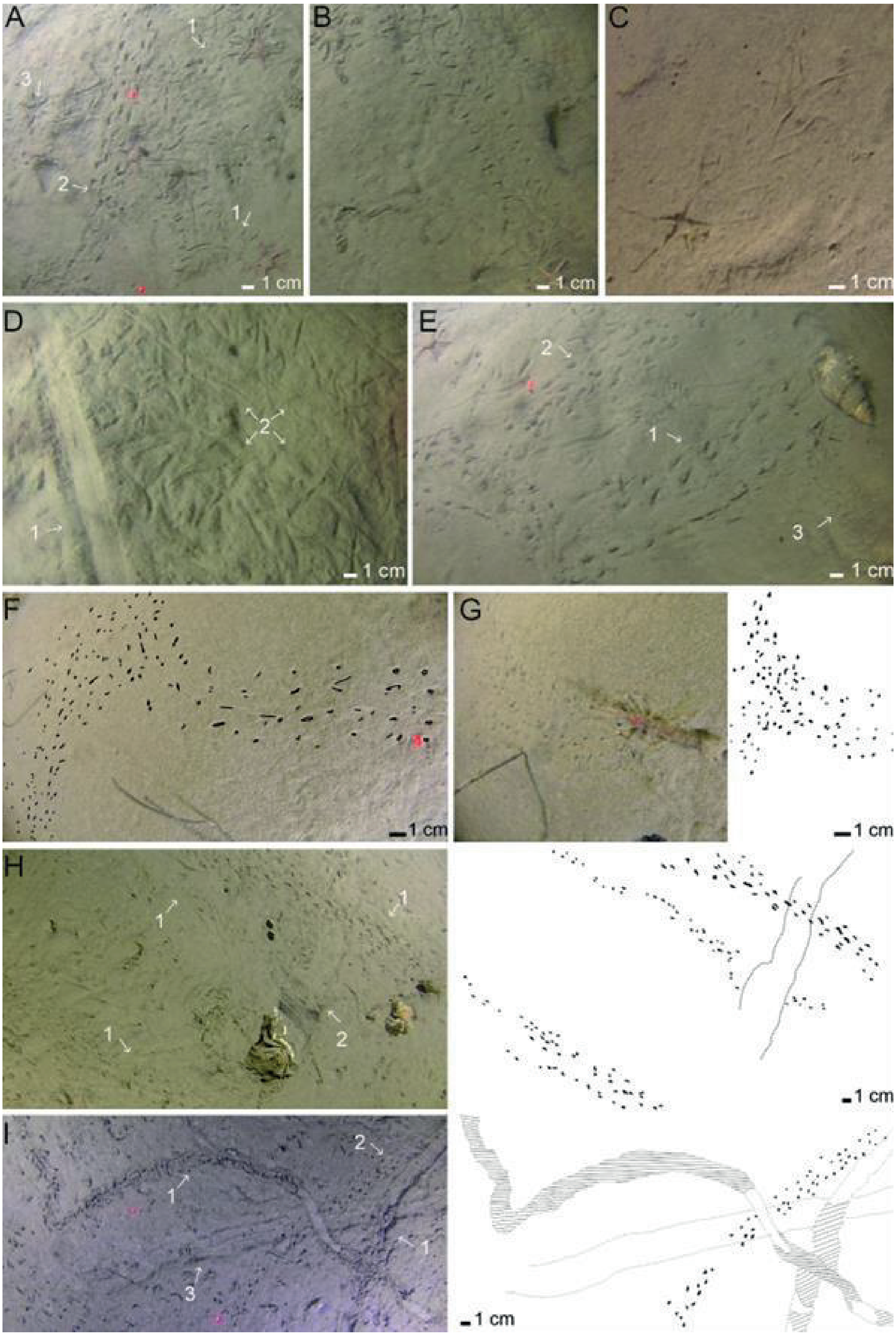

Fig. 3. Recorded lebensspuren – part two. (**A$_1$, B, E$_3$**) Railroad trail produced by the brittle star *Stegophiura nodosa*, shown with the tracemaker. (**A$_3$**) Ophiuroid impression left by *Stegophiura nodosa*. (**C**) Herringbone trail attributed to Ophiuridae spp., with a visible tracemaker, likely *Ophiura robusta*. (**D$_2$**) Irregular intersecting trail formed by Ophiuridae spp. (**D$_1$**) Flat, shallow trail produced by Gastropoda. (**A$_2$, E$_2$, I$_2$**) Step trails produced by *Pagurus* spp., shown without visible tracemakers. (**H$_1$**) Step trail of *Pagurus* spp. with visible tracemaker. (**F, G**) Step trail created by Caridea, with and without visible tracemakers. (**I$_3$**) Furrow trail produced by indeterminate *Pagurus* spp., shown with the tracemaker; this type of trail results from the hermit crab dragging its shell across the sediment (**H$_2$**). (**E$_1$**) Bilateral step trail produced by *Pagurus* spp., also resulting from shell dragging, shown with the tracemaker. (**I$_1$**) Composite sinuous fractured-flat trail formed by Naticidae spp.

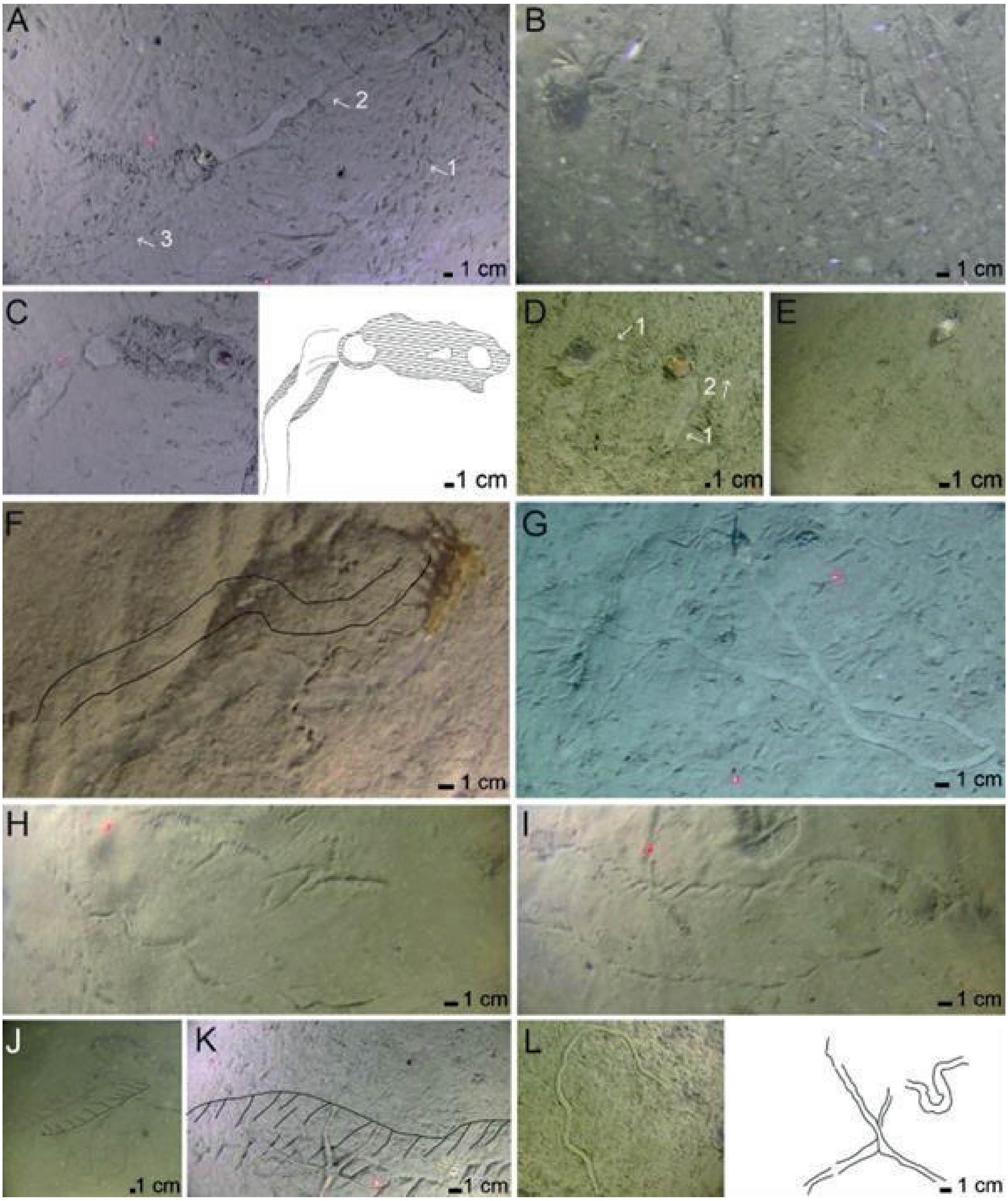

Fig. 4. Recorded lebensspuren – part three. (**A₁, D₂**) Step trail produced by *Pagurus* spp.; the tracemaker is visible only in panel **D₂**. (**A₃**) Bilateral step trail left by *Pagurus* spp., formed by shell dragging. (**A₂**) Flat, shallow trail produced by an indeterminate Gastropoda. (**B**) Step trail produced by the crab *Hyas* sp. (**C**) Composite, winding, fractured-flat trail produced by a gastropod of the family Naticidae spp., shown with its tracemaker. (**D₁, E, G**) Flat, shallow trails produced by *Buccinum* sp., each accompanied by the tracemakers. (**F**) Flat, shallow trails of the nudibranch *Dendronotus frondosus*, with the tracemaker present. (**J, K**) Ribbed, curved trails attributed to Pleuronectinae spp., with the tracemaker visible in panel **J**. (**H, I**) Segmented, winding twin trails produced by Pleuronectinae spp. (**L**) Irregular shallow trail formed by *Phyllodoce* sp., accompanied by its tracemaker.

possible due to limitations in visual resolution. For instance, within Naticidae, two snail species, *Euspira pallida* and *Cryptonatica affinis*, are morphologically similar and indistinguishable in the video material. Similarly, Caridea indet. includes members of the families Pandalidae and Thoridae. While most observed individuals are likely *Pandalus borealis*, conclusive identification would require specimen collection and laboratory analysis. This is also true for individuals of Nemertea indet. Other ambiguous categories include juvenile representatives of Asteroidea and Ophiuridae, which comprise three species – *Ophiura sarsi*, *Ophiura robusta*, and *Ophiocten sericeum*. Although

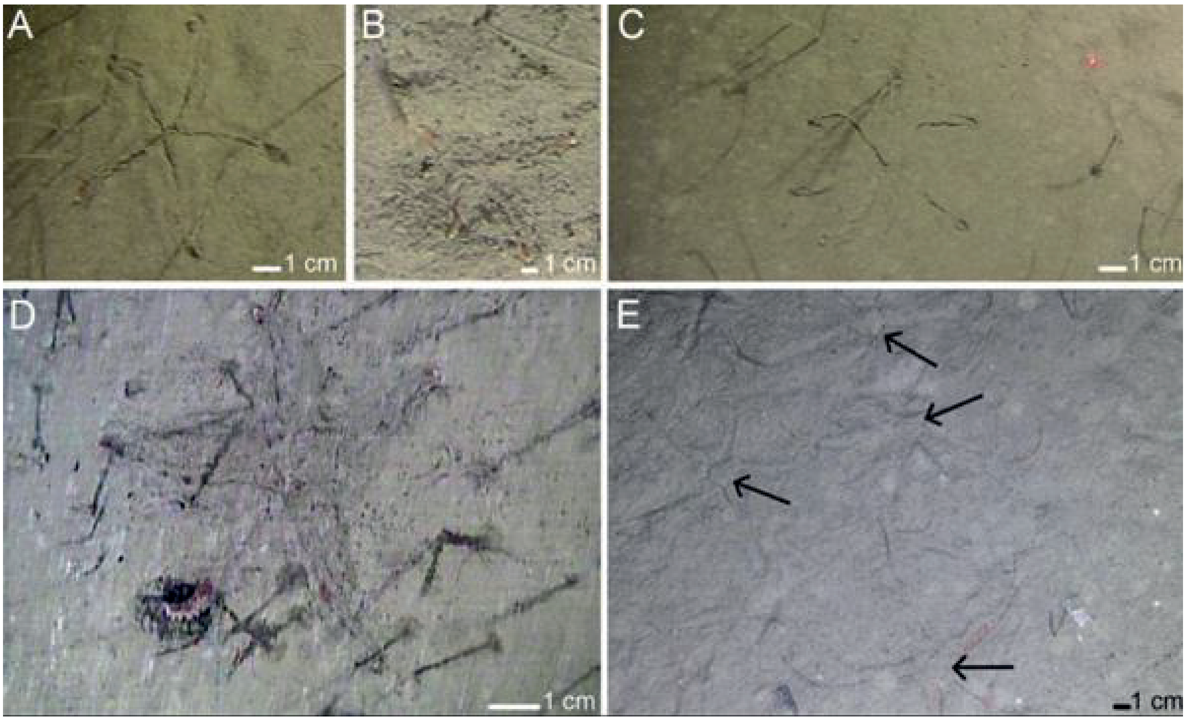

Fig. 5. Resting traces produced by nearly completely buried echinoderms. (**A–D**) Sea star impressions left by individuals of *Urasterias lincki* almost entirely buried beneath the sediment surface. (**E**) Impression created by a nearly completely buried, undetermined brittle star.

these species are morphologically distinct under laboratory conditions, they are difficult to differentiate in video footage and were therefore grouped under a single general category.

Identified lebensspuren were further grouped into four major biological categories based on the likely tracemakers. The most numerous group was Echinodermata, responsible for 691 traces, accounting for 55% of all recorded lebensspuren. Decapoda formed the second largest group with 249 occurrences (20%), followed by Gastropoda with 207 occurences (17%). The remaining 8% (105 traces) included those produced by *Phyllodoce* sp., Nemertea indet., Pleuronectinae (*Hippoglossoides platessoides* and *Reinhardtius hippoglossoides)*, and unidentified traces (Table 1). Notably, no fecal casts attributable to holothurians were observed in the analyzed video material, despite the confirmed presence of species such as *Myriotrochus rinkii* and occasional occurrences of *Cucumaria frondosa*. This absence may reflect species-specific defecation behavior, rapid degradation of fecal structures, or limitations of the video resolution

Non-metric multidimensional scaling (NMDS) analysis conducted for lebensspuren, epibenthic megafauna and tracemaker subset did not reveal distinct community groupings. Instead, the stations in all three datasets appear to form a single, continuous community. However, a clear spatial organization is evident when considering environmental factors, particularly proximity to glaciers and glacial rivers. Stations are distinguishably structured according to the predefined station-type categories: River Influence, Glacier Influence, and No Direct Influence (Fig. 6).

Figure 7 illustrates the percentage distribution of individual lebensspuren types across the studied locations. In the inner parts of the fjords, traces attributed to the sea star *Urasterias linckii* predominate. In the immediate vicinity of the most active glacier fronts, such as Kongsfjorden (Kronebreen) and in Hornsund (Hornbreen), *Urasterias* traces remain dominant, but traces attributed to the *Caridea* group also represent a significant portion of the total. *Ophiuridae* are commonly observed near glacier-affected sites, including Austreburgerbukta and Hornbreen (Hornsund), Yoldiabukta (Isfjorden), and Blomstrandhamna (Kongsfjorden).

Statistical analysis revealed a statistically significant positive correlation between the abundance of lebensspuren and their morphological diversity ($\rho = 0.62$, $p < 0.05$), as well as between lebensspuren richness and the number of distinct tracemaker taxa ($\rho = 0.27$, $p < 0.05$) (Fig. 8). A moderate and statistically significant positive correlation was also observed between lebensspuren abundance and the abundance of identified tracemaker organisms ($\rho = 0.37$, $p < 0.05$), suggesting that areas with a higher density of potential tracemakers tend to exhibit more biogenic surface traces. Conversely, a moderate negative and statistically significant correlation was found between station type and bottom turbidity ($\rho = -0.58$, $p < 0.05$), with glacier-influenced stations exhibiting elevated levels of suspended sediment. Additionally, a moderate negative and statistically significant correlation between the species richness of benthic fauna and bottom turbidity ($\rho = -0.53$, $p < 0.05$) suggests that high turbidity—particularly near glacier fronts—may suppress overall faunal diversity (Fig. 8).

Table 1. Number of stations and occurrences of identified lebensspuren by individual fjords and for the entire dataset. The label "Others" includes Smeerenburgfjorden, Rijpfjorden, and Krossfjorden, each represented by a single seafloor recording. A corresponding table presenting the densities of each lebensspuren type (n m^{-2}) is available in Supplementary Material (link in Methods).

Location	Number of stations	Station with lebensspuren in percentage		Echinodermata lebensspuren																Decapoda lebensspuren						Gastropoda lebensspuren								Other lebensspuren							
				Ophiuroidea lebensspuren						Asteroidea lebensspuren								Holothuroidea																					
				Number of stations *Stegophiura nodosa*		Number of stations Ophiuridae spp.		Number of stations Ophiuroidea imprints		Number of stations Asteroidea indet., juv.		Number of stations Asteroidea imprints		Number of stations *Urasterias lincki*		Number of stations *Ctenodiscus crispatus*		Number of stations *Myriotrochus rinkii*		Number of stations *Pagurus* spp.		Number of stations *Hyas* sp.		Number of stations Caridea indet.		Number of stations *Buccinum* sp.		Number of stations Naticidae spp.		Number of stations *Dendronotus frondosus*		Number of stations Gastropoda indet.		Number of stations *Phyllodoce* sp.		Number of stations Nemertea indet.		Number of stations Pleuronectinae spp.		Number of stations Unidentified	
Hornsund	44	20	47	-	-	8	68	1	12	-	-	2	4	14	72	-	-	-	-	1	10	-	-	6	23	-	-	-	-	-	-	3	9	-	-	-	-	2	3	2	4
Kongsfjorden	58	33	58	-	-	-	-	1	5	-	-	4	12	25	112	-	-	-	-	2	2	-	-	6	22	2	2	-	-	-	-	8	20	-	-	-	-	3	3	2	3
Isfjorden	77	49	64	1	96	5	24	7	57	1	2	-	-	24	136	1	2	2	53	10	138	2	4	3	30	3	5	9	24	5	26	19	78	1	3	3	3	6	8	26	74
Van Mijenfjorden	11	5	45	-	-	-	-	-	-	-	-	-	-	5	22	-	-	-	-	-	-	-	-	-	-	-	-	3	6	-	-	1	1	-	-	-	-	-	-	1	2
Shelf/ Torellbreen	9	4	44	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	3	-	-	-	-	1	1	2	8	-	-	4	17	-	-	-	-	-	-	1	1
Raudfjorden	2	2	100	-	-	-	-	1	2	-	-	-	-	2	12	-	-	-	-	1	1	-	-	-	-	1	1	1	1	-	-	1	2	-	-	-	-	-	-	1	1
Magdalenefjorden	2	2	100	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	3	-	-	-	-	-	-	-	-	-	-	2	5	-	-	-	-	-	-	-	-
Others	3	2	67	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	13	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-
Total	206	117	57	1	96	13	92	10	76	1	2	6	16	70	354	1	2	2	53	16	157	2	4	16	88	7	9	15	39	5	26	39	133	1	3	3	3	11	14	33	85
				55% (691) lebensspuren																20% (249) lebensspuren						17% (207) lebensspuren								8% (105) lebensspuren							

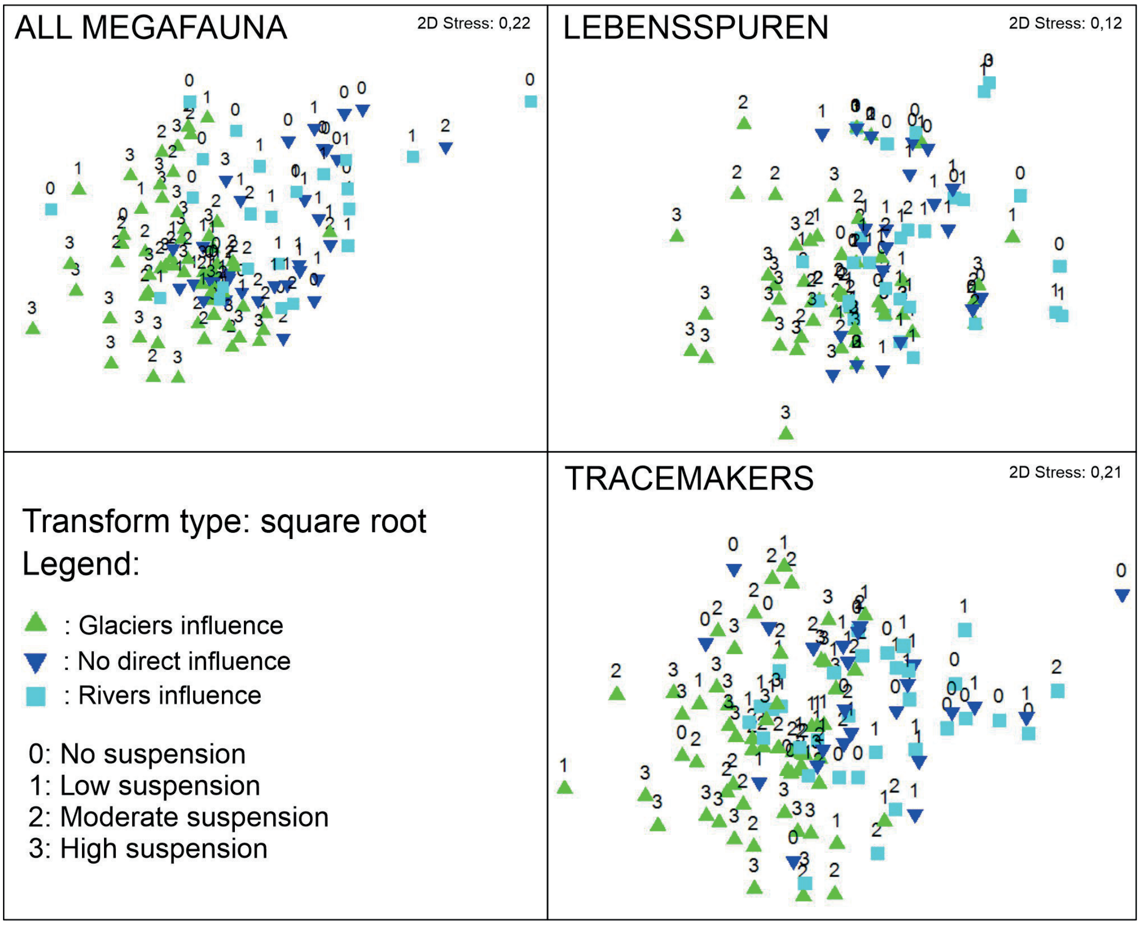

Fig. 6. Results of the n-MDS analysis showing patterns in lebensspuren, epibenthic megafauna, and identified tracemakers.

Lebensspuren and their tracemakers

Following the classification system proposed by Miguez-Salas *et al.* (2024c), the names of the lebensspuren presented in this study are based on three components/labels: (*i*) morphological characterization, (*ii*) inferred behavior, and (*iii*) tracemaker taxonomy. For clarity and consistency, these components are separated by semicolons.

This study introduces eight new morphological components: Herringbone trail, Discontinuous irregular winding trail, Irregular intersecting trail, Ribbed curved trail, Bilateral step trail, Composite sinuous fractured-flat trail, Irregular shallow trail, and Segmented sinuous twin trail. In several cases, direct video documentation of the tracemaker responsible for these traces is provided, offering rare and valuable evidence for linking morphology to behavior and producer identity.

Star-shaped depression; resting; Asteroidea indet. (Figs. 2E and 5A–D)

This is a typical resting trace of sea stars (Miguez-Salas *et al.* 2024a), with in 91 examples recorded in the entire dataset. One of the identified tracemaker is *Urasterias lincki,* which was observed to be partially buried in the sediment. Two twin traces captured in the same image (Fig. 2A) likely may reflect both arm regeneration processes of the arms (as one arm appears shorter) and a change in position by the sea star.

High-density punctuated trail; locomotion;* Urasterias lincki *(Asteroidea) (Fig. $2A_1$, B, D, H)

Lebensspuren left by the sea star *Urasterias lincki* (Asteroidea) are the most commonly encountered traces in the collected material. Like other sea stars, this species uses its water vascular system for locomotion, resulting in distinct trace pattern in areas where it is present. These traces are broad, corresponding to the maximum arm span of the individual, and consist of numerous small holes, which represent impressions of tube feet in the sediment. These impressions are elliptical rather than circular, with the longer axis aligned in the direction of movement. The holes occur at nearly uniform density, except in the central part of the lebensspuren, where a characteristic smooth strip is typically observed. This strip forms behind the oral opening during locomotion, as tube feet are absent around the mouth, resulting in a gap in the trace. These traces were primarily recorded in the inner parts of fjords, particularly in the areas of glacial bays (Fig. 6). A total of 354 occurrences of this high-density punctuated trail were identified across 70 stations (Table 1).

High-density punctuated trail; locomotion; Asteroidea indet., juv. (Fig. 2F)

This group includes the lebensspuren of juvenile sea star. These traces are of the same type as those produced by adult individuals but are noticeably more delicate and

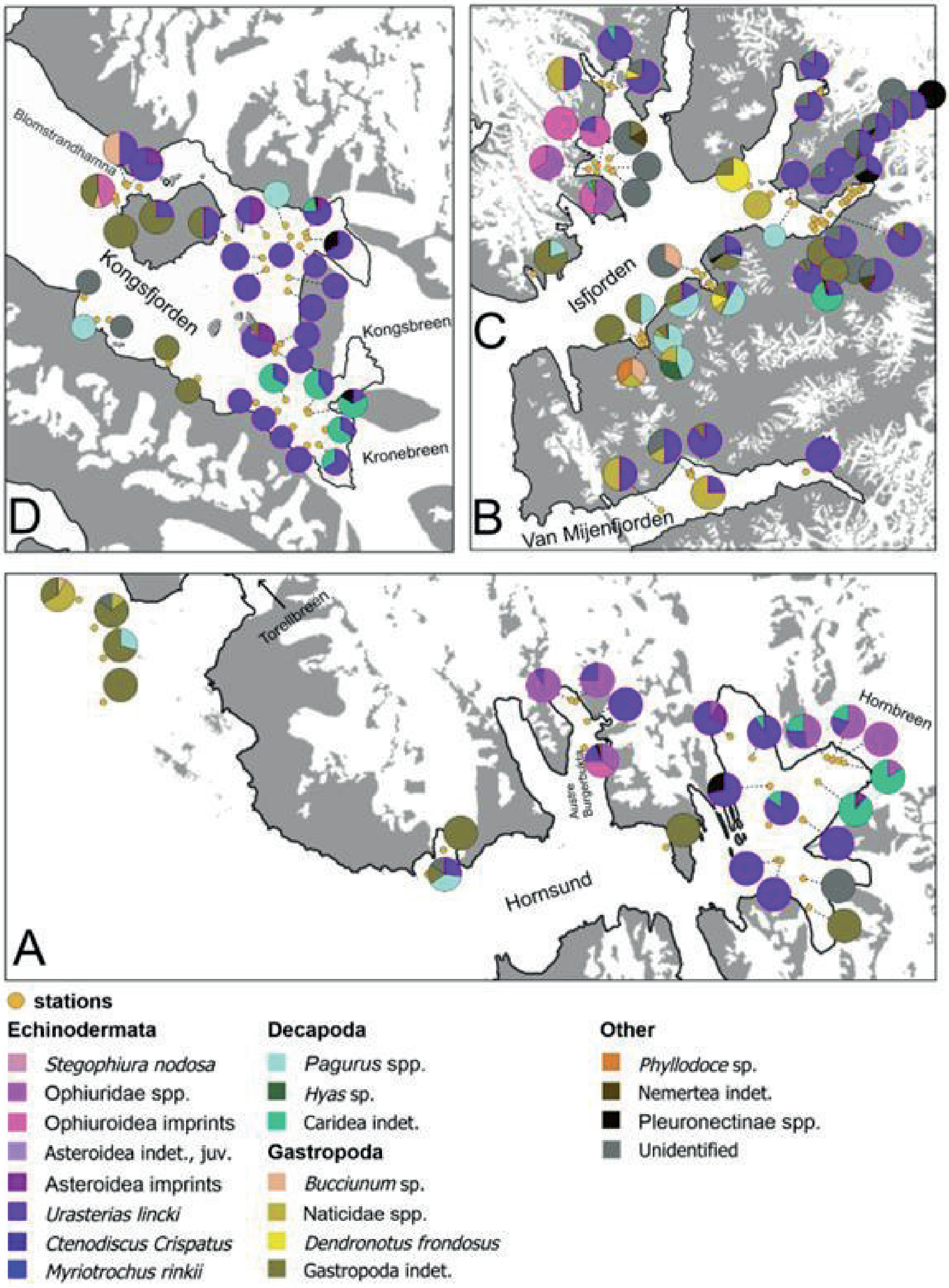

Fig. 7. Percentage distribution of identified lebensspuren across the four most extensively sampled fjords.

smaller in scale. The illustrated juvenile specimen of Asteroidea, measuring just over 1 cm in diameter, was nonetheless capable of leaving visible imprints of its tube feet on the sediment surface. Across the entire analyzed material, only two such cases were recorded, both at a single station in Isfjorden (Table 1).

High-density punctuated trail; locomotion;* Ctenodiscus crispatus *(Asteroidea) (Fig. 2C)

Ctenodiscus crispatus, a relatively common sea star, was rarely observed in the recordings. This non-selective deposit feeder (Shick *et al.* 1981) typically remains buried in the sediment for extended periods. Its trace is somewhat similar to that produced by *Urasterias lincki,* but the spacing between tube foot impressions is smaller, and their density per unit area appears higher. This difference may reflect the generally smaller body size of *C. crispatus*. However, only two such traces were identified in the entire dataset, both from a single station (ISF26-2019), which limits the possibility for detailed comparisons.

Irregular M-ridged trail; locomotion and feeding;* Myriotrochus rinkii *(Holothuroidea) (Fig. 2K)

Traces of *Myriotrochus rinkii* were discovered at only two stations. These characteristic lebensspuren are deeply incised into the sediment, forming looping and overlapping patterns. The disturbed sediment often displays longitudinal cracking. In some cases, up to eight living specimens

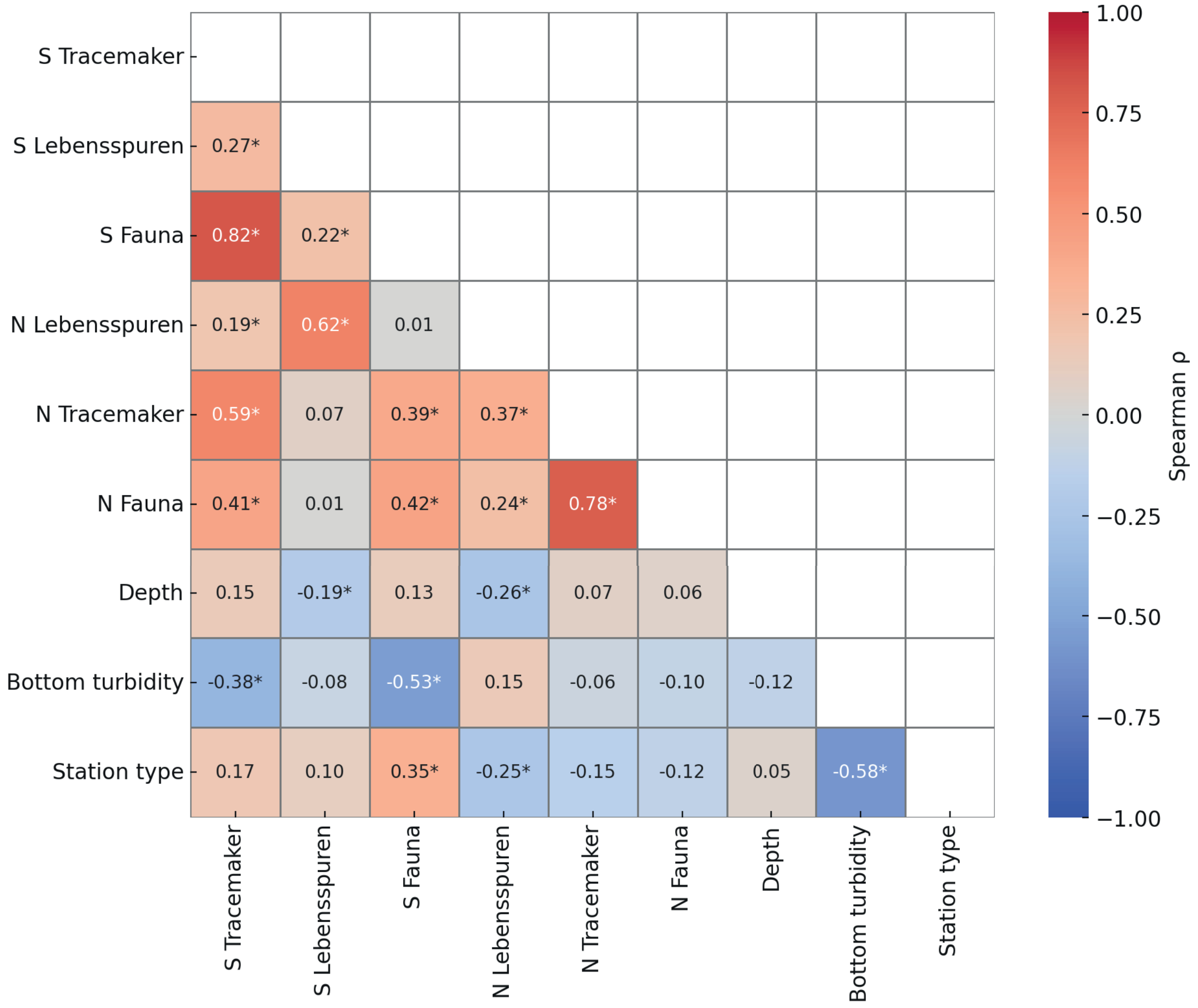

Fig. 8. Spearman correlation matrix showing relationships among the number of species (types) of lebensspuren, megafauna, tracemakers (prefixed with S), their abundance (prefixed with N), depth, bottom turbidity, and station type (Glacier Influence, River Influence, No Direct Influence). Statistically significant correlations ($p < 0.05$) are marked with an asterisk.

of this species were observed along the traces within a single field of view of the camera (Fig. 2K, red hatching indicates individuals of *M. rinkii*).

Ophiuroid-shaped depression; resting; Ophiuroidea indet. (Figs. 3A$_3$ and 5E)

This is a typical resting trace of brittle stars (Miguez-Salas et al. 2024a). It consists of a central disc-shaped depression with radiating arm impressions, reflecting the characteristic body plan of ophiuroids. A total of 76 such traces were recorded across ten stations. One of the most clearly defined examples (Fig. 3A$_3$) was created by a living individual of *Stegophiura nodosa*. Another case (Fig. 5E) shows a nearly buried, unidentified ophiuroid within the depression.

Railroad trackway; locomotion;* Stegophiura nodosa *(Ophiuroidea) (Fig. 3A$_1$, B, E$_3$)

Stegophiura nodosa, along with its distinctive lebensspuren, was recorded exclusively at a single station (GR7). During locomotion, this species produces relatively deep grooves in the seabed using only tips of its arms. Along the longer axis of symmetry, a distinct depression extends beyond the central disc of the organism. As a surface deposit feeder, *S. nodosa* is likely to produce this depression through sediment intake during feeding activity. Notably, such a depression is not produced by other recorded representatives of Ophiuroidea. This brittle star is highly distinctive due to short arms and small body size. However, because of the small scale of both the organism and its trace, the movement pattern could not be accurately reconstructed due to the limited resolution of the video material.

Herringbone trail; locomotion; Ophiuridae spp. (Figs. 2G, I and 3C)

This is a locomotion trace is produced by three species of Ophiuridae (*Ophiocten sericeum*, *Ophiura sarsii*, and *Ophiura robusta*) when the organism is elevated above the substrate and "walks" using its arms. Although these species exhibit notable morphological differences under laboratory conditions, their small size in the video footage makes it impossible to assign traces to individual species with complete certainty. In total, 92 such traces were identified across 13 stations.

Discontinuous irregular winding trail; locomotion; Ophiuridae spp. (Fig. 2J)

The tracemakers are the same as for the previous trace. This type of trace likely was produced in environments with high sedimentation rates, where the individual remains elevated on its arms for extended periods and shifts its position at irregular intervals.

Irregular intersecting trail; locomotion; Ophiuridae spp. (Fig. 3D$_2$)

The tracemakers are the same as for the previous two traces. Unlike the previously described patterns, this trace typically covers a much larger area, with the seabed appearing uniformly disturbed across a localized zone.

Step trail; locomotion;* Pagurus *spp. (Malacostraca) (Figs. 3A$_2$, E$_2$, H$_1$, I$_2$ and 4A$_1$, D$_2$)

This trace was recorded 157 times at 16 stations. It is produced by a complex of hermit crab species from the genus *Pagurus*, specifically *Pagurus pubescens* and *P. bernhardus*. The trace consists of fairly regularly spaced limb impressions left as the organism moves across the substrate. The width of the trace varies depending on the size of the individual.

Step trail; locomotion;* Hyas *sp. (Malacostraca) (Fig. 4B)

This trace is attributed to crabs of the genus *Hyas*. It consists of irregularly spaced and disorganized limb impressions formed during locomotion across the substrate. It clearly differs from trails produced by *Pagurus* spp., which are typically more linear and regularly patterned. The width of the trace varies depending on the size of the individual. This lebensspuren was recorded only four times at two stations within the entire dataset.

Bilateral step trail; locomotion;* Pagurus *spp. (Malacostraca) (Figs. 3E$_1$ and 4A$_3$)

Visible modifications of the step trail trace, resulting from the dragging of adapted snail shells, primarily from the family Buccinidae, by the hermit crab were observed. The attached shell can alter the trace by smearing the sediment or creating additional longitudinal grooves and forms. This type of lebensspuren often co-occurs with traces left by gastropods.

Step trail; locomotion; Caridea indet. (Malacostraca) (Fig. 3F, G)

This group includes traces from two families of shrimps: Pandalidae and Thoridae. These organisms are difficult to distinguish in camera images. The lebensspuren are long, typically winding trackways composed of a series of depressions left by the walking limbs. Observations by the author indicate that these shrimps frequently change direction, moving backward, sideways, or forward, which can result in larger areas densely limb impressions. Such traces were only recorded at stations with very soft, malleable sediments (Fig. 7).

Flat shallow trail; locomotion;* Buccinum *sp. (Gastropoda) (Fig. 4D$_1$, E, G)

Unlike the lebensspuren produced by gastropods of the family Naticidae, this trace lacks distinctive features that would allow confident attribution to the genus *Buccinum* without direct observation of the organism creating it. The trace remains clearly visible on the sediment surface, with its width corresponding to the size of the individual's foot.

Composite winding, fractured-flat trail; locomotion; Naticidae spp. (Gastropoda) (Figs. 3I and 4C)

The tracemakers include two co-occurring species found in the Svalbard region: *Euspira pallida* and *Cryptonatica affinis*. These gastropods produce a distinctive trace by ploughing deeply into the seabed, resulting in characteristic sediment disturbances. The surface of the trace is often coated with mucus. These features help distinguish it from lebensspuren left by other snails, such as those of the family Buccinidae. A total of 39 occurrences of this trace were recorded across fifteen stations (Table 1).

Flat shallow trail; locomotion;* Dendronotus frondosus *(Gastropoda) (Fig. 4F)

These are very delicate traces, similar in appearance to those left by gastropods of the family Buccinidae. However, these are much more subtle, disturbing only a very thin layer of sediment. The affected area is typically coated with mucus.

Winding shallow trail; locomotion;* Phyllodoce *sp. (Polychaeta) (Fig. 4L)

This trace is similar to those produced by Gastropoda and Nemertea but exhibits notable variation in width, which may help distinguish it from the lebensspuren of those groups. Nevertheless, it remains relatively subtle, and accurate identification is not possible without direct observation of the tracemaker. Across the entire analyzed material, this trace was recorded only three times, all at a single station (Table 1).

Ribbed curved trail; locomotion Pleuronectinae spp. (Teleostei) (Fig. 4J, K)

This trace is produced by fins of flatfish species belonging to the *Hippoglossoides platessoides* and *Reinhardtius hippoglossoides* complex. These species create long linear traces, which are likely characteristic of other members within the family Pleuronectidae.

Segmented winding twin trail: locomotion: Pleuronectinae spp. (Teleostei) (Fig. 4H, I)

The tracemakers are the same as in the previous trace. The trace is produced when the individual attempts to bury itself in the upper sediment layer of the sediment or moves in a "jumping" motion across the seabed surface. A total of 14 such traces were identified across 11 stations (Table 1).

Discussion

The region of the Svalbard fjords described in this study exhibits a high abundance and diversity of lebensspuren (Table 1; Figs. 2–5), supporting the hypothesis that prevailing abiotic and biotic factors in this area promote their production, even by relatively small tracemakers such as shrimp (Fig. 3F, G), sea stars (Fig. 2A$_1$, B–D, H), and nudibranchs (Fig. 4F). These traces are primarily concentrated in the inner parts of the fjords (Figs. 1 and 7). On the shelf areas, traces were recorded only near the Torellbreen glacier and were predominantly associated with gastropod activity.

Trace resident time

The Svalbard fjords exhibit a notably low rate of sedimentation – two orders of magnitude lower than fjords of a comparable size in Greenland or Alaska (Zaborska *et al.* 2006). This extended "trace resident time", the period during which a trace remains visible on the seabed before being destroyed (Wheatcroft *et al.* 1989) or buried, likely contributes to the preservation of lebensspuren in this region. As a result, traces are less rapidly degraded.

Trace resident time is influenced by both abiotic and biotic factors. Abiotic influences include sedimentation rate, hydrodynamics, substrate consistency, and grain size, while biotic factors involve microbiological degradation and the erasure of traces by other mobile organisms (Wheatcroft *et al.* 1989). For instance, meiofauna can smooth and ultimately obliterate lebensspuren by shifting individual sediment grains (Cullen 1973), while infauna may impact surface traces through horizontal movement within the sediment (Wheatcroft *et al.* 1989).

Some authors (Bell *et al.* 2013) have suggested that abiotic processes degrade lebensspuren at a uniform rate. However, more recent studies (Miguez-Salas *et al.* 2020) demonstrate that sudden events, such as benthic storms, can entirely erase traces from the seabed. In the studied Svalbard region, iceberg scouring may also disrupt the seabed, though such events are typically evident in the sedimentary record.

No single factor can be identified as dominant in determining the preservation potential or duration of trace visibility. For example, in the Adolfbukta (a small glacial bay in Isfjorden) high densities of brittle stars, primarily *Ophiocten sericeum* (unpublished data from dredge and video surveys), were observed, yet no distinct ophiuroid lebensspuren were documented. In contrast, in Hornbukta – a glacial bay in the Hornsund with lower brittle star densities, ophiuroid traces were abundant. Kitchell *et al.* (1978) explained such paradoxes by suggesting that trace resident time may be longer in areas with lower biomass, implying a negative correlation between the lebensspuren and faunal density.

In the current study, analyses revealed a positive correlation between the abundance and diversity of lebensspuren ($\rho = 0.62$), indicating that higher trace density tends to co-occur with greater morphological variability. A moderate negative correlation was also found between station type and bottom turbidity ($\rho = –0.58$), with glacially influenced stations showing higher suspended sediment levels (Fig. 8). Additionally, bottom turbidity was negatively correlated with benthic species richness ($\rho = –0.53$). A moderate positive correlation was observed between the abundance of lebensspuren and the abundance of identified tracemakers ($\rho = 0.37$), suggesting that greater numbers of known trace-producing taxa are associated with more traces.

Previous studies have reported mixed results regarding the relationship between lebensspuren and benthic megafauna. Kitchell *et al.* (1978) suggested an inverse relationship, while Young et al. (1985) and Wheatcroft *et al.* (1989) attributed weak correlations to the rapid erasure of traces by deposit feeders. Similarly, Jumars and Wheatcroft (1989) proposed that no consistent (monotonic) relationship existed between trace abundance and faunal density. More recently, Miguez-Salas *et al.* (2024b) recommended limiting such analyses to confirmed tracemakers rather than the entire benthic community. This distinction is crucial, as comparisons involving all megafauna may be confounded by the presence of non-trace-making species. The difficulty in defining clear correlations also stems from the fact multiple organisms can produce morphologically similar trace types, while a single species may produce a variety of lebensspuren (Miguez-Salas *et al.* 2024b).

The relationship between benthic fauna and lebensspuren appears more complex than originally postulated by Kitchell *et al.* (1978) and Young *et al.* (1985). Later studies reported no significant correlation (Turnewitsch *et al.* 2000; Miguez-Salas *et al.* 2024b), while emphasizing the multitude of factors that influence trace preservation and interpretation (Przeslawski *et al.* 2012; Miguez-Salas *et al.* 2024b). The connections between traces and epibenthic megafauna are clearly multifaceted, making it difficult to identify a single controlling parameter. Continued identification of new trace types and their associated tracemakers is essential for improving our understanding of benthic ecosystems and drawing more accurate conclusions about their dynamics.

Tracemakers and their lebensspuren

The dominant group of tracemakers in the study area is Echinodermata (55%, 691 trace occurrences) (Fig. 7; Table 1 for occurrences; Table 2 for frequency and dominance). This dominance of echinoderms in in tracemaker assemblages is consistent with additional findings from other regions worldwide (Hollister *et al.* 1975; Gage and Tyler 1991; Smith *et al.* 1993; Lauerman and Kaufmann 1998; Turnewitsch *et al.* 2000; Vardaro *et al.* 2009). In contrast to deep-sea environments, where the most common sea star trace is the resting impression, often referred to as star-shaped traces (Fig. 2E) (Kitchell *et al.* 1978; Wheatcroft *et al.* 1989; Durden *et al.* 2020; Miguez-Salas *et al.* 2020, 2024a), the most frequently observed lebensspuren in the studied Svalbard region is the trace left by a moving sea star, specifically *Urasterias lincki* (Fig. 2A$_1$, B, D, H). This trace showed a frequency of 60% and dominance of 28% across all stations where lebensspuren were recorded (Table 2).

Sea stars produce not only resting traces related to stationary behavior or feeding but also distinctive traces associated with locomotion on the seabed. Examples of such traces have been described as trace fossils by Mángano *et al.* (1999), with neoichnological and experimental studies documenting these patterns (Gingras *et al.* 2008; Ishida *et al.* 2017). Przeslawski *et al.* (2012) also discussed perforated traces created by sea stars. The closest analogues to the traces presented here are those recorded in the Aleutian Trench (Miguez-Salas *et al.* 2024a), where tube feet impressions are clearly visible.

Star resting impressions of this type have been observed relatively infrequently. However, several near-complete burials of *Urasterias lincki* (Fig. 5A–D) and brittle stars (Figs. 3A$_3$ and 5E) have been documented, all exclusively in the inner fjord areas near glaciers (Fig. 7). This distribution may reflect fundamentally different environmental conditions in these zones, notably high sedimentation rates during the Arctic summer. Species inhabiting environments, *e.g.*, *Alcyonidium disciforme*, often exhibit special adaptations (Kvitek 1989; Kukliński and Porter 2004) or increased mobility, as seen in brittle stars and sea stars.

The observed individuals of the sea star *Urasterias lincki* may have been dead, or the traces could be linked predation or scavenging activity shallowly buried mollusks and crustaceans. Similar traces evidence was presented by Howell *et al.* (2003) and Miguez-Salas *et al.* (2024a). After prey consumption, organisms likely digest *in situ*, explaining burial by suspended sediment (Blake 1989).

In addition to echinoderms, numerous individuals of Caridea indet., likely *Pandalus borealis* (Fig. 7), were observed near glaciers. Given their sensitivity to inorganic particles (Dale *et al.* 2008), their presence in these high-sedimentation environments is somewhat unexpected but aligns with observations by Meyer and Sweetman (2015).

Table 2. Frequencies (F%) and dominance (D%) of identified lebensspuren in individual fjords and across the entire dataset. Frequencies (F%) represent the percentage of samples containing specimens of a given species, while dominance (D%) indicates the proportion of a species' abundance relative to the total megafauna abundance. The label "Others" refers to the fjords Smeerenburgfjorden, Rijpfjorden, and Krossfjorden (each with a single seafloor recording), as well as Magdalenfjorden and Raudfjorden, each with two recorded stations.

	All stations		Hornsund		Kongsfjorden		Isfjorden		Van Mijenfjorden		Schelf & Torellbreen		Other	
Lebensspuren:	F%	D%	F%	D%	F%	D%	F%	D%	F%	D%	F%	D%	F%	D%
Stegophiura nodosa	1	8	-	-	-	-	2	13	-	-	-	-	-	-
Ophiuridae spp.	11	7	40	33	-	-	10	3	-	-	-	-	-	-
Ophiuroidea imprints	9	6	5	6	3	3	14	7	-	-	-	-	17	5
Asteroidea indet., juv.	1	0.2	-	-	-	-	2	0.3	-	-	-	-	-	-
Asteroidea imprints	5	1	10	2	12	7	-	-	-	-	-	-	-	-
Urasterias lincki	60	28	70	35	76	63	49	18	100	71	-	-	33	29
Ctenodiscus crispatus	1	0.2	-	-	-	-	2	0.3	-	-	-	-	-	-
Myriotrochus rinkii	2	4	-	-	-	-	4	7	-	-	-	-	-	-
Pagurus spp.	14	13	5	5	6	1	20	18	-	-	25	10	33	10
Hyas sp.	2	0.3	-	-	-	-	4	1	-	-	-	-	-	-
Caridea indet.	14	7	30	11	18	12	6	4	-	-	-	-	17	31
Buccinum sp.	6	1	-	-	6	1	6	1	-	-	25	3	17	2
Naticidae spp.	13	3	-	-	-	-	18	3	60	19	50	27	17	2
Dendronotus frondosus	4	2	-	-	-	-	10	3	-	-	-	-	-	-
Gastropoda indet.	33	10	15	4	24	10	39	10	20	3	100	57	67	19
Phyllodoce sp.	1	0.2	-	-	-	-	2	0.4	-	-	-	-	-	-
Nemertea indet.	3	0.2	-	-	-	-	6	0.4	-	-	-	-	-	-
Pleuronectinae spp.	9	1	10	1	9	2	12	1	-	-	-	-	-	-
Unidentified	28	7	10	2	6	2	53	10	20	6	25	3	17	2

Ichnological aspect

The most well-known ichnogenus of sea stars and brittle stars in paleoichnology is *Asteriacites* von Schlotheim, 1820 (Knaust and Neumann 2017). This cosmopolitan resting trace is commonly found in the fossil record from the Cambrian to the Neogene (Crimes and Zhiwen 1986; Mikuláš 1992; Knaust and Neumann 2017). The ichnofamily Biformitidae (Knaust and Neumann 2016) includes impressions interpreted as locomotion traces produced by ophiuroids and asteroids. The locomotion traces documented in this study, from species such as *Urasterias lincki*, *Ctenodiscus crispatus* (Fig. 2C) and juvenile, unidentified individuals (Fig. 2F), further support the question rised by Miguez-Salas *et al.* (2024a): „we open the question, based on the current observations, if the inclusion of unnamed trace fossils produced by sea star podia locomotion as the ones exposed by Mángano *et al.* (1999), should be included within Biformitidae ichnofamily by erecting new ichnogenera that embrace these asterozoan locomotion traces, *i.e.*, not arcuate or hook-shaped imprints, or if they should be assigned to other established ichnofamily with similar morphological features and add asterozoan as possible tracemakers". As demonstrated in this publication, the inner parts of the Svalbard fjords (Fig. 7) are rich in such traces. With continued advances of video recording technologies, we can expect increasingly frequent documentation of these types of lebensspuren, not only in the Arctic region or the deep-sea floors of the Aleutian Trench.

Behavioral insights from lebensspuren

Studying lebensspuren provides new insights into the behavior of benthic fauna that produce these traces (Przeslawski *et al.* 2012; Miguez-Salas *et al.* 2022, 2024a; Brandt *et al.* 2023). For instance, in the case of lebensspuren produced by *Pagurus* sp., it has been observed that in two instances, individuals follow the trail of a snail (Fig. 4A$_2$, D$_1$). In one case, it is likely a snail of the genus *Buccinum*. The genus *Pagurus* is known for its highly developed chemoreceptor senses and ability to locate snails and their empty shells (Rittschof 1980; Gherardi and Tiedemann 2004). Based on the assessment of the traces alone, one can attempt to draw conclusions about species co-occurrence and behavioral interactions (Fig. 3I).

Community-level patterns and tracemaker differentiation

The n-MDS analysis did not reveal distinct clusters among stations, indicating a general lack of sharp community boundaries between different fjord zones. While this absence of clear differentiation may seem unexpected, it carries ecological significance. It suggests a relatively homogeneous distributions of tracemaker types across sites, or alternatively – a continuous gradient in community composition that is not easily captured through categorical separation. Instead of discrete groupings, the n-MDS ordination reveals a continuum of similarity among stations (Fig. 6).

Nonetheless, when n-MDS results are interpreted alongside trace composition and site metadata, certain patterns become apparent. In the glacial bays, lebensspuren are predominantly associated with Echinodermata, particularly *Urasterias lincki*. Additional notable traces in these areas include those attributed to indeterminate Ophiuroidea and Caridea. In contrast, areas near river mouths (*e.g.*, Colesbukta, Adventfjorden) and regions located outside of the fjords (such as the Torellbreen area) are primarily characterized by traces from snails (Naticidae and other indeterminate Gastropoda) and hermit crabs, including *Pagurus pubescens* and *P. bernhardus* (Fig. 7).

Glacial bays are characterized by high concentrations of suspended sediment throughout the water column (Dragańska-Deja 2024), which can serve as a limiting factor for many benthic organisms (Görlich *et al.* 1987). However, this turbidity may also function as a refuge from large predators such as Atlantic cod, a species frequently recorded in the fjord region (Bengtsson *et al.* 2024). In contrast, river mouth environments tend to exhibit higher sediment suspension near the surface than at the seabed (Zajączkowski *et al.* 2010), making them more accessible to a broader range of organisms, including large predators.

Bioturbation impact

Benthic and bentho-pelagic fauna play a crucial role in shaping sediments structure, with the extent of their impact depending on the size, abundance, and activity levels of the organisms involved (Murray *et al.* 2002). The analysis of lebensspuren offers valuable insights into bioturbation processes. While most studies on bioturbation focus on its vertical dimension (Oleszczuk *et al.* 2019; Solan *et al.* 2019), trace fossil analysis can also illuminate patterns of horizontal and near-surface bioturbation (Belley *et al.* 2010; Miguez-Salas *et al.* 2024d). Jumars and Wheatcroft (1989) even suggested that horizontal bioturbation may occur at a much higher intensity than vertical mixing.

The depth and visibility of surface disturbances in sediments vary widely depending on the tracemaker. The most subtle traces are produced by nudibranchs such as *Dendronotus frondosus* (Fig. 4F), nemerteans, and polychaetes of the genus *Phyllodoce* (Fig. 4L). In contrast, lebensspuren left by sea stars (Fig. 2A$_1$, B–F, H), caridean shrimps (Fig. 3F, G), ophiuroids (Figs. 2G, I, J, 3A$_1$, A$_3$, B, C, D$_2$, E$_3$ and 5E), and hermit crabs (Figs. 2A$_2$, 3A$_2$, E$_2$, H$_1$, I$_2$ and 4A$_1$) result in highly distinctive and often extensive surface disturbances. Snails from the family Naticidae (Figs. 3I$_1$ and 4C) and the sea cucumber *Myriotrochus rinki* (Fig. 2K) are capable to disturbing sediments to depths exceeding 1 cm. By analyzing the spatial extent of these traces, the biomass of tracemaking organisms, the thickness of sediment they ingest or displace, and their levels of mobility, we can gain a more comprehensive understanding of bioturbation processes in the fjord ecosystems of Svalbard.

Conclusions

This study presents one of the first detailed, video-based documentations of lebensspuren from shallow fjord environments in the Svalbard region, based on observations from 206 stations. Traces were identified at 57% of the sites, revealing notable diversity and abundance across fjord systems. In total, 19 distinct types of lebensspuren were described, with 18 linked to directly observed tracemakers. The majority of these traces were attributed to representatives of Echinodermata, particularly *Urasterias lincki*, whose locomotion traces dominated the dataset. The study introduces eight new lebensspuren morphotypes and provides rare *in situ* documentation of trace-producing behavior. These observations offer valuable insights into both behavioral patterns and taxonomic identities of the tracemakers. By integrating morphological, behavioral, and taxonomic data, this work advances our understanding of benthic community dynamics in Arctic fjords and contributes novel material relevant for ichnological classification and future neoichnological research.

Although statistical analyses did not reveal strong correlations between lebensspuren and megafaunal abundance, the data exhibit spatial patterns that align with environmental gradients, particularly those associated with glaciers influence. The variability observed in trace-type distribution underscores the significance of environmental factors, such as sediment properties and turbidity, in determining the preservation and visibility of traces, *i.e.*, trace resident time.

Crucially, the integration of direct video observations enabled reliable interpretation of tracemaker identity and behavior, effectively bridging a key gap between ichnological classification and ecological function. These findings demonstrate that neoichnological analysis, especially when supported by real-time imagery, offers substantial potential for reconstructing benthic activity and bioturbation processes in both modern and ancient glaciomarine settings.

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