



Short and decadal impacts of seafloor physical perturbation on the abundances of *Lebensspuren* ‘traces of life’ in the Peru Basin manganese nodule province

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Abstract

Interest in deep-sea mining for polymetallic nodules as an alternative source to onshore mines for various high-technology metals has risen in recent years, as demands and costs have increased. The need for studies to assess its short- and long-term consequences on polymetallic nodule ecosystems is therefore also increasingly prescient. Recent image-based expedition studies have described the temporal impacts on epi-/megafauna seafloor communities across these ecosystems at particular points in time. However, these studies have failed to capture information on large infauna within the sediments or give information on potential transient and temporally limited users of these areas, such as mobile surface deposit feeders or fauna responding to bloom events or food fall depositions. This study uses data from the Peru Basin polymetallic nodule province, where the seafloor was previously disturbed with a plough harrow in 1989 and with an epibenthic sled (EBS) in 2015, to simulate two contrasting possible impact forms of mining disturbance. To try and address the shortfall on information on transient epifauna and infauna use of these various disturbed and undisturbed areas of nodule-rich seafloor, images collected 6 months after the 2015 disturbance event were inspected and all *Lebensspuren*, ‘traces of life’, were characterized by type (epi- or infauna tracemakers, as well as forming fauna species where possible), along with whether they occurred on undisturbed seafloor or regions disturbed in 1989 or 2015. The results show that epi- and endobenthic *Lebensspuren* were at least 50% less abundant across both the ploughed and EBS disturbed seafloors. This indicates that even 26 years after disturbance, sediment use by fauna may remain depressed across these areas.

Keywords Deep-sea mining · Physical seafloor disturbance · Resilience of deep-sea seafloor ecosystems · Deep-sea monitoring · *Lebensspuren* · Traces of life · Infauna · Polymetallic nodules

Introduction

The ongoing boom in computer electronics is driving an increasing global demand for critical raw materials such as ‘high-tech metals’. The need for a scalable economical resource base for these widely used minerals (cobalt, zinc, copper, nickel, and rare-earth elements (REEs)) has reached a historical maximum and will in the future most likely exceed the capabilities of common terrestrial mines, promoting the ongoing search for alternative sources (Hein et al. 2013; Toro et al. 2020). Potential sources of these elements include metal-rich marine mineral resources, such as ferromanganese crusts and polymetallic nodule fields, formed naturally by a range of processes on the deep-sea seafloor (Hein et al. 2013). Polymetallic nodules are potato-shaped aggregations of minerals that occur in large quantities in the abyssal plain of the Pacific, the Atlantic, and the Indian

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Oceans at depths of 4000 to 6000 m (Kuhn et al. 2017). They are characteristically dark in colour and oblate spheroid in shape, with diameters of up to 25 cm. These nodules are rich in metals such as lithium, nickel, copper, cobalt, zirconium, molybdenum, and REEs (Hein et al. 2013). The exact process of nodule formation remains unknown, but nodules are believed to form through the deposition of minerals around a small hard focus (e.g. a shark tooth or shell fragment) at a very slow growth rate of approximately 2 to 20 mm per million years (Guichard et al. 1978; Hein et al. 2013).

Although areas of potentially commercially viable nodule abundances are known, commercial extraction has yet to commence, though experimental works with nodule-gathering vehicles and on investigating the potential disturbance impacts on seafloor structure and communities are ongoing. The topic remains controversial as it is assumed that mining will have negative impacts on the deep-sea ecosystem, at least on the local scale, with the hard substrate provided by the nodules being wholly removed from the seafloor/ocean interface (Amon et al. 2016; Jones et al. 2017; Stratmann et al. 2018; Smith et al. 2020). In general, soft sediments form much of this interface across the abyssal plains, though in regions where polymetallic nodules occur, these nodules provide a hard substrate, creating a complex which supports a highly diverse range of sessile fauna (Vanreusel et al. 2016), as well as adding complexity to the local hydrodynamic regime on the local scale. For some larger filter-feeding organisms, such as a number of species of stalked sponge or soft coral, these nodules are essential for existence, and their removal would most likely result in the loss of these species in impacted areas (Gollner et al. 2017; Tilot et al. 2018). Some generally mobile fauna, such as octopods, also use these nodule-based fauna as habitat niches for brooding within their life cycle (Purser et al. 2016). These vertically extended fauna further provide access to the faster flowing, higher waters for additional sessile filter feeders, as well as elevated positions for mobile scavengers and predators, such as amphipods. It is also likely that any nodule mining would remove nutrient-rich surface sediments from the seafloor, causing further impacts to endemic ecosystems via food source removal, while simultaneously subjecting fauna to a potentially harmful resuspended particle cloud, both during particle transport following resuspension and as a subsequent settling particle blanket (Simon-Lledó et al. 2019). Toxic metals may potentially be released together with the creation of sediment plumes (Hauton et al. 2017), and noise and light pollution be generated by the mining equipment (Weaver et al. 2018). There remains a lack of studies on the full temporal extent of any long-term consequences of deep-sea mining and recovery of the exploited sites. To address some of these outstanding questions, and to support appropriate regulations for future deep-sea mining endeavours, a number of simulated mining tests and

research programmes have been conducted and are ongoing. One of the most extensive long-term projects was started in 1989 with the 'DISturbance and reCOLonization' (DISCOL) experiment (Thiel et al. 1989). This project aimed at simulating possible future commercial deep-sea mining impacts through small-scale sediment disturbance in the Peru Basin nodule province in the South-east Pacific, and subsequently observe the system's recovery. For this, an 8-m-wide plough-harrow was used to diametrically trawl a large circular area of 10.8 km² a total of 78 times. During this process, the upper layer of seafloor sediments was disturbed, killing, overturning, or displacing the majority of surface sessile megafauna, creating a sediment plume, and removing nodules from the surface by ploughing them to depths below the upper 10–20 cm of sediment, thus mimicking the lack of nodules on the seafloor which will be the situation after mining (Thiel and Schriever 1990). To date, the DISCOL site in the Peru Basin remains the most extensively experimentally disturbed nodule ecosystem seafloor region. During the last three decades, this area was revisited multiple times to examine post-disturbance conditions and faunal communities: in March 1989 (right after conducting the initial disturbance experiment), in September 1989, in January 1992, in February 1996, and, most recently, in September 2015 (Boetius 2015; Greinert 2015). These follow-up cruises aimed at monitoring the ecosystem recovery with special focus on the recolonization of benthic communities. Through physical sampling as well as video and image surveys, densities of macrofauna and invertebrate megafauna as well as sparsity of meiofaunal and microbial communities were assessed (Boetius 2015). Nearby reference areas not impacted by the simulated mining were used for comparison. In 2015, a further physical disturbance event was conducted in the area, with an epibenthic sled (EBS) being towed several times across the seafloor to actually remove the upper sediments and nodules from the seawater sediment interface (Greinert 2015). This physical disturbance is perhaps more comparable to the latest generation of polymetallic nodule devices currently undergoing testing, where heavy vehicles compact sediments as they scoop up the upper 10 cm or so of sediments and all nodules resting on the seafloor surface.

In 2001, Bluhm (2001) reported that the initial short-term effects of the mining were apparent immediately following ploughing. Fauna living attached to nodules was either mechanically removed or destroyed as the nodules were ploughed under the upper soft sediments. Re-sedimentation of particle plumes was apparent not only within the directly ploughed tracks, but also across the adjacent areas of seafloor, where settling particles led to a general decline in surrounding faunal densities. The first signs of recovery, or at least an increase in local biomass, were observed shortly after the experiment was conducted, with highly motile scavenging organisms starting to repopulate the ploughed areas. In 1996, 7 years post-disturbance, hemi-sessile

animals had returned to ploughed areas, whereas the number of soft-bottom animals was still lower in the ploughed area than were present before ploughing. Even 26 years after the disturbance experiment, in September 2015, macrofauna and megafauna densities were still significantly depressed within the disturbance area (Stratmann et al. 2018). Sediment porewater chemistry had recovered, but the microbial biogeochemical activities still showed negative impacts and also metal distributions within the sediments continued to differ from those at undisturbed reference sites.

In general, faunal groups in the DISCOL area have shown varying degrees of recovery (Bluhm 2001; Stratmann et al. 2018; Simon-Lledó et al. 2019). Mobile species were found to recover faster than sessile species with large individuals, which either did not recover at all or only recovered at comparably slow rates (Jones et al. 2017). Impacts across all ecosystem components have not been satisfactorily investigated however, such as the effects of mining disturbances on the infauna community and transient mobile surface deposit feeding fauna, which may be missed by occasional seafloor monitoring expeditions. Small infauna abundances have been investigated, with monitoring suggestions for any future commercial disturbance presented (Lins et al. 2021).

The main aim of this study was to assess the impacts of historic (1989) and recent (2015) physical disturbance of the nodule-rich seafloor within the DISCOL experimental area, as indicated by any change or reduction in visible surface sediment usage by mobile epibenthic fauna, and on the traces left by emergent endobenthic infauna. By analysing images collected from the impacted region, the present study, by identifying and quantifying the visible *Lebensspuren*, was to additionally assess the potential for monitoring long-term effects of deep-sea mining with this comparatively inexpensive, un-invasive methodology, as a tool for future routine impact assessment (Danovaro et al. 2020). Image data from the most recent visit to the DISCOL area in 2015 were analyzed by logging the various sorts of *Lebensspuren*, or ‘traces of life’, that can be observed in towed camera images from disturbed and undisturbed areas of the seafloor. These *Lebensspuren* are formed by infauna living within the seafloor making disturbances on the surface layers (endobenthic *Lebensspuren*) or by mobile epifauna on top or above the seafloor surface disturbing the sediments (epibenthic *Lebensspuren*). Images from the original plough tracks made in 1989, as well as images from undisturbed local reference areas and from freshly disturbed seafloor areas—disturbed by an epibenthic sled (EBS) during the SO242-1 expedition—were compared. The abundances of the various traces, both of surface deposit feeder waste, emergent burrows, etc., were statistically compared across seafloor categories, and how any differences in abundance may relate to ecosystem fitness and recovery discussed.

Materials and methods

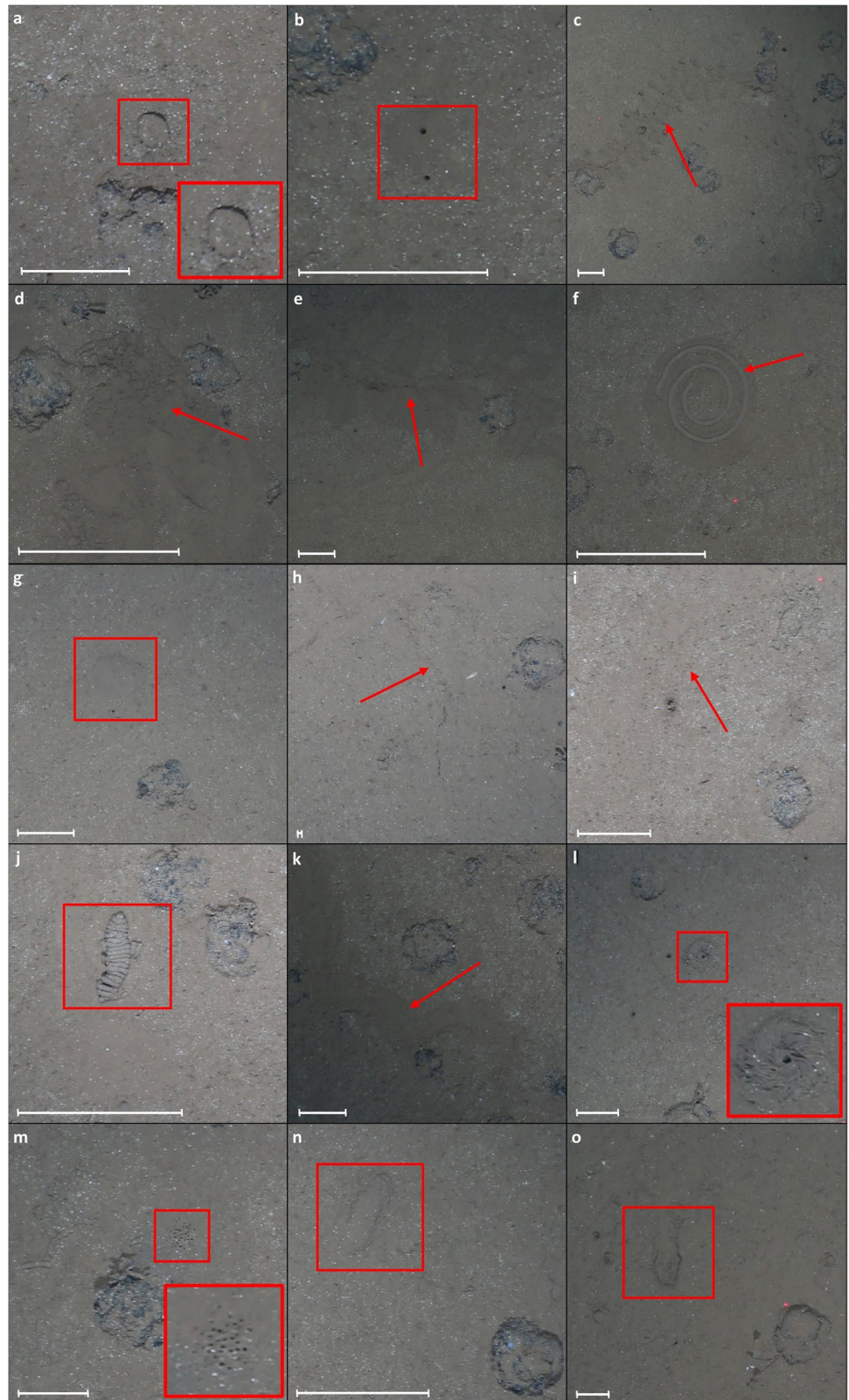
Image data

All images analysed were collected as part of the two-leg expedition of the RV SONNE (SO242-1 and SO242-2) in 2015. The expedition revisited the DISCOL disturbance site, 26 years after the experiment was conducted, to collect imagery for assessing short- and long-term recovery of local fauna. During the first leg of the expedition (SO242-1), an additional mining event was mimicked by towing an epibenthic sled (EBS) across the seafloor, removing the upper 30 cm of sediments (Greinert 2015). Following this, the second leg of the expedition (SO242-2) started 6 weeks later, with the main aim being to survey the seabed (Boetius 2015). An advanced towed camera system, the Ocean Floor Observation System (OFOS) consisting of a 24-megapixel camera, an HD video camera, three lasers with a 50-cm spacing, multiple lights, and an altimeter as well as a positioning beacon, was used to collect high-quality seafloor images. At an altitude of about 1.5 to 1.7 m and with a ship speed of 0.2 to 0.5 kn, the OFOS was towed across the seafloor for eight transects, taking images of roughly 5 m² in area every 15 s. In this way, data was collected from three seafloor categories, representing different levels of physical disturbance: undisturbed (abundant in nodules), recently disturbed (EBS tracks), and historically disturbed (ploughed in 1989). In total, 1345 images were analysed from across these categories within the study. All image data is available from the PANGAEA data repository (Purser et al. 2018).

Image annotation

The open-source image annotation program PAPARA(ZZ) I (Marcon and Purser 2017) was used to annotate the images within this study. This program has been designed specifically for the purpose of studying benthic megafauna on photo footage, and was therefore also suitable for analysing the dataset from the DISCOL seabed with respect to infaunal traces (Fig. 1). Each image was identified as representing one particular seafloor type, namely undisturbed (‘Undisturbed nodules’), historically disturbed (‘Ploughed’), or recently disturbed (‘EBS’) (Fig. 2). Following categorization of seafloor type, traces of life (*Lebensspuren*) were logged onto each image as belonging to one of 15 categories, based on classification in the literature (e.g. Bell et al. 2013; Dundas and Przeslawski 2009): ‘Circular impression’, ‘Paired burrow’, ‘Ploughed trail’, ‘Unknown source’, ‘Complex trail’, ‘Acorn worm spiral’, ‘Small mound’, ‘Thin trail’, ‘Perforated trail’, ‘Coiled faecal cast’,

Fig. 1 Examples of the differing *Lebensspuren* identified in the current study, and whether they are considered to be the traces of epibenthic fauna or endobenthic infauna: **a** circular impression, epibenthic; **b** paired burrow (polychaete or bivalve formation), endobenthic; **c** ploughed trail, epibenthic; **d** unknown source; **e** ‘Complex trail’, epibenthic; **f** acorn worm spiral, epibenthic; **g** small mound, endobenthic; **h** thin trail, epibenthic; **i** perforated trail, epibenthic; **j** coiled faecal cast, epibenthic; **k** wide trail, epibenthic; **l** faecal nest cast, endobenthic; **m** *Paleodictyon*, endobenthic; **n** coiled faecal cast (degraded), epibenthic; **o** oblique burrow, endobenthic. The scale bars equal 10 cm in situ



‘Wide trail’, ‘*Paleodictyon*’, ‘Coiled faecal cast (degraded)’, and ‘Oblique burrow’. Examples of these traces are shown in Fig. 1. Roundish, shallow imprints in the soft sediments of the

seafloor were considered ‘Circular impression’, classed among the epibenthic *Lebensspuren* (Fig. 1a), with this trace category including perfectly circular but more oval hole shapes, most

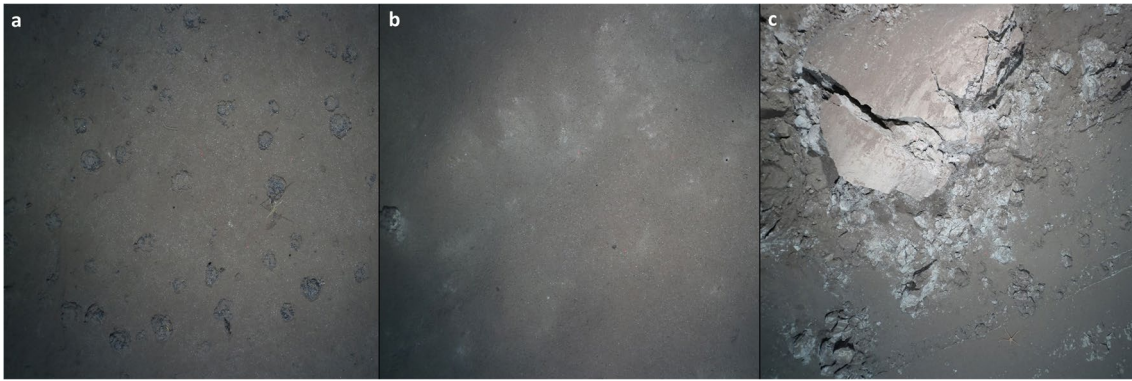


Fig. 2 The three degrees of disturbance of the seafloor in the DISCOL area: **a** undisturbed (undisturbed nodules); **b** historically disturbed (ploughed); and **c** recently disturbed (EBS)

likely produced by Actiniaria. ‘Paired burrows’—also categorized as epibenthic *Lebensspuren*—were marked wherever a distinct and deep hole could be observed which appeared to have been used recently, i.e. it did not seem to be old or partially destroyed (Fig. 1b). Commonly, these ‘Paired burrows’ were characterized by freshly accumulated sediments around them and were considered to be definite ‘Paired burrows’ since this was assumed to be a sign of recent usage. ‘Ploughed trail’ were traces characterized by a wriggling wide path with small roundish imprints on its rim, here identified as being epibenthic *Lebensspuren*, produced by holothurians of the genus *Psychropotes* (Fig. 1c). Other traces classified as epibenthic *Lebensspuren* included dark areas in the sediment that looked like the sediment had been stirred up recently, marked as ‘Unknown source’ (Fig. 1d), and traces of distinct feather-like patterns, categorized as ‘Complex trail’ (Fig. 1e). The category ‘Acorn worm spiral’ was used for the distinct sand spirals left by foraging Enteropneusta, and was therefore also counted among the epibenthic *Lebensspuren* (Fig. 1f). These traces were logged even if they were slightly covered by sediments or partially destroyed (but still recognizable). ‘Small mounds’ were piles of sediment which seemed to not have been created by water movements, and which often showed a darker colouration than the surrounding sediments; such traces were identified as endobenthic *Lebensspuren* (Fig. 1g). ‘Thin trail’ and ‘Wide trail’ categories were marked whenever (mostly) consistent clear lines of roughly 0.5-cm and 6.5-cm widths, respectively, appeared that indicated animal movements, for ‘Wide trail’ potentially by echinoids. Both trail types were classified as epibenthic *Lebensspuren* (Fig. 1h and k). Traces of asteroids, potentially of the genus *Hymenaster*, were logged as ‘Perforated trail’ (Fig. 1i), and coiled sediments, most likely being produced by holothurians of the genus *Psychropotes* coils, were logged as ‘Coiled faecal cast’ (Fig. 1j). These categories belong to the epibenthic *Lebensspuren*. The ‘Faecal nest cast’ category represented small helical sediment formations, mostly associated with an emerging burrow in the centre, counted among the endobenthic *Lebensspuren* (Fig. 1l).

An array of hexagonal hole patterns was observed and categorized as ‘*Paleodictyon*’, i.e. *Paleodictyon nodosum* (Fig. 1m) (Rona et al. 2009), which are part of the endobenthic *Lebensspuren*. ‘Coiled faecal cast (degraded)’ were marked for any distinct degraded faecal shape and categorized as epibenthic *Lebensspuren*. The final category was ‘Oblique burrow’, marking burrows not clearly recognizable as originating from a particular animal (mostly big and oval-shaped), and belonging to the endobenthic *Lebensspuren* (Fig. 1o).

Statistical evaluation

The average densities (per m²) per faunal trace category and the average densities for epibenthic *Lebensspuren* and endobenthic *Lebensspuren* overall, as well as respective standard deviations, were computed across each seafloor disturbance type (Undisturbed nodules, Ploughed, EBS). These densities were then compared with one-way ANOVAs to determine whether significant differences in traces were present across disturbance categories. Given the large variance in sample sizes across the three substrates, and the skewness in the data associated with the zero values common for some trace types in some images, the robust Welch’s *p*-value was computed and reported for each test.

Results

Of the images analysed for levels of physical disturbance, 1137 were identified as being ‘Undisturbed nodules’, 30 as ‘Ploughed’, and 167 as ‘EBS’. Average densities and standard deviations of the fauna traces observed across the images are given in Table 1. For almost all trace categories investigated, densities were higher on the ‘Undisturbed nodules’ seafloor category than on either the ‘Ploughed’ or ‘EBS’ categories. ‘Paired burrows’ and ‘Circular impressions’ were the most abundant traces observed, across all seafloor

categories. The ‘Complex trail’, ‘Ploughed trail’, ‘Small mound’, ‘Oblique burrow’, and ‘Faecal nest cast’ categories of traces were not observed on any of the disturbed substrates, only being observed in images classified as ‘Undisturbed nodules’. Figure 3 shows the total trace abundances observed across the seafloor categories investigated.

Discussion

The most immediate conclusion apparent from the results of this study is that *Lebensspuren*, ‘traces of life’, are far less abundant on areas of the polymetallic nodule abundant deep-sea seafloor that has been physically disturbed than on areas which have not been physically disturbed. Perhaps surprisingly, the traces were generally as scarce on seafloor areas disturbed in 1989 and examined in 2015 than on surfaces disturbed 6 months prior to examination in 2015—i.e. effects on trace abundance seem to be long-lasting in such areas exposed to upper sediment perturbation, possibly partly due to reduced microbial degradation of sediments reduced in labile organic matter (Vonnahme et al. 2020). The fact that *Lebensspuren* abundances remain reduced even decades after simulated mining impacts has a wider ranging significance for the seafloor/bottom water ecosystem than just being indicative of reduced epibenthic and endobenthic fauna abundances. *Lebensspuren* formation is the result of sediment bioturbation by fauna, a significant factor in transporting settling organic matter into the upper sediments for non-emergent endobenthic fauna, playing a role in grain sorting and porosity maintenance, transporting oxygen below the seafloor surface, and biomineralization and determining the redox state of the buried sediment layers (Durdin et al. 2020). The reduced vigour of the naturally occurring bioturbation of these seafloor sediments will therefore likely have a profound effect on meio- and macrofauna communities within the seafloor, as well as the bacterial communities. Possibly this reduced bioturbation will also have an effect on the seafloor sediment resuspension cycle, further impacting filter feeding epibenthic fauna (Graf and Rosenberg 1997).

Endobenthic *Lebensspuren*

Although visible on photographs taken from the water column, the trace categories ‘Circular impression’, ‘Paired burrow’, ‘*Paleodictyon*’, and ‘Faecal nest cast’ are indicative of fauna activity within the upper sediments of the seafloor. Generally, for these traces, abundances were at

least 50% lower across disturbed seafloor areas than those undisturbed. The reasons for this are not immediately clear, though it can be assumed that much of the more labile carbon within the upper sediments was removed by the disturbance action, rendering the sediments less attractive to some sediment feeding epi- and endobenthic fauna. Three additional factors may well be at play in driving the observed reduction in abundances of these infauna traces. Firstly, it is possible that the now exposed sediments, from 10 or 20 cm below the initial seafloor surface, were rendered more compacted than the naturally occurring sediments found between the nodules in the ‘Undisturbed nodules’ category images by the disturbance action. This compaction could be partially the result of burial by resuspended material but may have been further increased with the passage of heavy disturbing equipment. The EBS, in particular, has a large intrinsic weight further increased with the collected content of nodules and sediments, compressing underlying material during a tow. These compacted sediments may deter fauna looking for a suitable substrate into which to build their residence or forage for food. A second factor is the removal of the nutrient-rich, or at least less nutrient-poor, sediment/seawater interface sediments. This removal may deter fauna responsible for the ‘Paired burrow’ and ‘Faecal nest cast’ in particular. Thirdly, it is possible that endobenthic infauna populations were directly impacted by the simulated mining events, either leaving the area in response to the perturbation or being directly killed by the activity. Potentially the few traces visible were made rapidly following disturbance, and represent the re-establishment of survivors, rather than the reoccupation or comparably vigorous and successful use of the seafloor by fauna as pre-disturbance. This rapid reformation of the *Paleodictyon* patterns has been noted in the north Pacific Clarion-Clipperton Fracture zone following similar simulated mining disturbances (Boehringer et al. 2021). Should these direct impacts have occurred, recovery from reduced standing stocks or migration into the area had not allowed recovery to the pre-impact levels after 26 years.

Epibenthic *Lebensspuren*

The trace categories ‘Complex trail’, ‘Ploughed trail’, ‘Acorn worm spiral’, ‘Coiled faecal cast’, and ‘Perforated trail’ represent the surface activities of fauna which either feed directly on seafloor/ocean interface sediments for the most labile of settling material or forage in the upper centimetre of sediment for small infauna to consume. As such, the lower abundances of these traces on the disturbed sediment surfaces likely indicate that these sediments are less attractive than the undisturbed nodule abundant sediments in the surrounding area. From the current

Table 1 Trace type mean abundance estimates (per m²), and standard deviations of counts given for all images examined in the current study, as defined by seafloor type. The output of the one-way ANOVA to compare means between seafloor categories for each trace type is also given, with the robust Welch *p* statistic reported

Trace type	Type	Seafloor_type	<i>N</i>	Mean	std_dev	std_error	sum sq	df	<i>F</i>	Welch <i>p</i>
Circular impression	Epibenthic	Nodule rich	1137	0.8266	0.652	0.019	30.03	2	39.07	<0.001
		Ploughed	30	0.48	0.377	0.069				
		EBS	167	0.3916	0.378	0.029				
Unknown source	Epibenthic	Nodule rich	1137	0.087	0.139	0.004	1.112	2	33.4	<0.001
		Ploughed	30	0.4	0.969	0.0179				
		EBS	167	0.012	0.016	0.001				
Paired burrow	Endobenthic	Nodule rich	1137	1.522	1.01	0.03	103.3	2	56.67	<0.001
		Ploughed	30	0.647	0.582	0.11				
		EBS	167	0.756	0.496	0.037				
Complex trail	Epibenthic	Nodule rich	1137	0.003	0.26	0.0008	0.002	2	1.333	0.264
		Ploughed	30	0	0	0				
		EBS	167	0	0	0				
Ploughed trail	Epibenthic	Nodule rich	1137	0.02	0.065	0.002	0.066	2	9.06	<0.001
		Ploughed	30	0	0	0				
		EBS	167	0	0	0				
Acorn worm spiral	Epibenthic	Nodule rich	1137	0.507	0.101	0.003	0.391	2	22.29	<0.001
		Ploughed	30	0.02	0.061	0.011				
		EBS	167	0	0	0				
Small mound	Endobenthic	Nodule rich	1137	0.11	0.155	0.046	2.03	2	49.26	<0.001
		Ploughed	30	0	0	0				
		EBS	167	0	0	0				
Paleodictyon	Endobenthic	Nodule rich	1137	0.067	0.122	0.004	0.299	2	11.068	<0.001
		Ploughed	30	0.04	0.081	0.149				
		EBS	167	0.023	0.067	0.005				
Coiled faecal cast	Epibenthic	Nodule rich	1137	0.29	0.304	0.009	11.45	2	71.608	<0.001
		Ploughed	30	0.2	0.21	0.038				
		EBS	167	0.014	0.052	0.004				
Perforated trail	Epibenthic	Nodule rich	1137	0.019	0.063	0.002	0.03	2	4.095	0.02
		Ploughed	30	0.02	0.061	0.011				
		EBS	167	0.0048	0.031	0.002				
Oblique burrow	Endobenthic	Nodule rich	1137	0.002	0.006	0.001	0.001	2	0.872	0.418
		Ploughed	30	0	0	0				
		EBS	167	0	0	0				
Faecal nest cast	Endobenthic	Nodule rich	1137	0.008	0.052	0.002	0.011	2	0.005	0.917
		Ploughed	30	0	0	0				
		EBS	167	0	0	0				
Coiled faecal cast (degraded)	Epibenthic	Nodule rich	1137	0.031	0.16	0.005	0.148	2	3.39	0.091
		Ploughed	30	0.013	0.073	0.013				
		EBS	167	0	0	0				
Thin trail	Epibenthic	Nodule rich	1137	0.17	0.202	0.006	0.787	2	0.368	<0.001
		Ploughed	30	0.14	0.211	0.039				
		EBS	167	0.1	0.181	0.014				
Wide trail	Epibenthic	Nodule rich	1137	0.171	0.214	0.006	0.838	2	9.65	<0.001
		Ploughed	30	0.187	0.203	0.037				
		EBS	167	0.096	0.17	0.013				

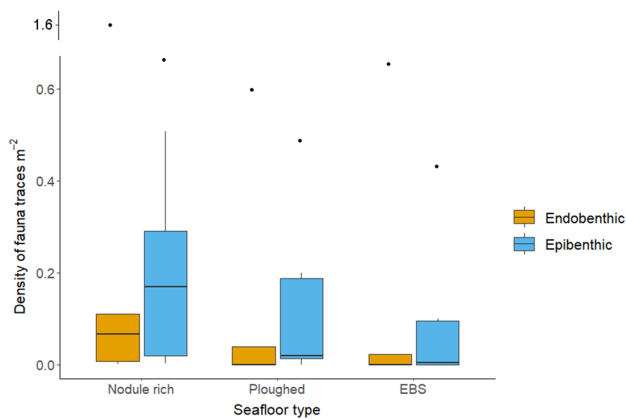


Fig. 3 Epibenthic and endobenthic *lebensspuren* abundances recorded across the ‘Undisturbed nodules’, ‘Ploughed’, and ‘EBS’ seafloor categories. Outliers are indicated by a point

study, it is not possible to determine whether the absence of labile material or the increased hardness and compaction of the exposed sediments is the reason for the preferential exclusion of these disturbed areas from foraging efforts. The ‘Coiled faecal cast’ traces were only 30% less abundant on the ‘Ploughed’ areas rather than the ‘Undisturbed nodules’ areas, perhaps indicating that spiral-deposit-leaving holothurians would pass across disturbed regions with only a reduced activity, rather than wholly avoiding the regions, as appears to be the case with the ‘Perforated trail’ produced by asteroids which leave this characteristic trace as they move and feed. Hemicordate traces, such as ‘Acorn worm spiral’ are left by fauna dropping from suspension to the seafloor to feed on the seafloor surface/ocean interface sediments (Smith et al. 2005). Though occasionally present on disturbed sediments, it seems these fauna, on encountering the disturbed sediments, do not enter their spiral foraging cycle, but likely return back to the water column for transport via bottom currents to a more favourable location for feeding.

Seafloor traces and environmental monitoring

Occasional surveys of a region with towed cameras, ROVs, or AUVs can give important information on the epibenthic megafauna communities present at the time of the survey, but offer little information on transient populations, such as large agglomerations of holothurians or other Echinodermata which may occur from time to time, or fauna gathering in response to a short duration food fall or surface bloom event. Permanent robotic presence near and on the seafloor would be a needed approach to monitor changes in the abundances of these important migrators (Huffard et al. 2016) directly (Danovaro et al. 2020; Weaver et al. 2022).

Generated traces of life may remain visible for a considerable time in the low-deposition, low-energy environments commonly associated with high polymetallic nodule abundances, and therefore indicate not only the passing or sediment interactions of both the transient surface epibenthic fauna, but also the utilization of the region by endobenthic fauna living within the sediments. Larger endo- and epibenthic fauna are missed during spatially and temporally limited box core or multi-core sediment sampling, and therefore the influence of disturbance on their abundances and their response to perturbation disruption remain unobserved. We suggest that, in addition to investigating and quantifying fauna at the surface prior, during and after a mining or simulated mining event has been conducted, a number of these ‘traces of life’ are also quantified across regions of interest, to gauge the response of these more elusive fauna to the environmental changes associated with deep-sea mining.

Numerous studies have used seafloor imagery to analyse alterations in the abundance, volume/size, distribution, and behaviour of megafaunal organisms. The current study demonstrates that image data can also be used to aid in determining whether infauna and transient surface organisms migrate away from, traverse, or utilize these impacted regions. Evaluation across both space and time is possible through the use of time-lapse imagery or repeat surveys conducted by mobile or fixed platforms. Digital imaging and illumination technology has advanced to a degree that enables the collection of images while platforms are in motion, even allowing a resolution of littoral features as small as a few millimetres in diameter from flight heights of several metres. The monitoring platform detailed in this paper is primarily composed of ‘off the shelf’ components, a design strategy that enables the rapid production of identical systems while minimising costs—an approach appealing to monitoring authorities for planning long-term monitoring efforts. When combined with AI technologies, such robust and ready-to-use technologies enable monitoring of benthic environments at an equally sophisticated level over time and therefore for developing strategies for the sustainable industrial exploitation and monitoring of potentially impacted deep-sea ecosystems, while also maintaining the preservation of deep-sea goods and services (Sustainable Development Goal 14 of the United Nations Development Programme).

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Declarations

Competing interests The authors declare no competing interests.

Ethics approval No animal testing was performed during this study.

Sampling and field studies All necessary permits for sampling and observational field studies have been obtained by the authors from the competent authorities and are mentioned in the acknowledgements, if applicable. The study is compliant with CBD and Nagoya protocols.

Data availability All images collected during the SO242-2 expedition used in the current study are open access and available from the PAN-GAEA data repository at the following URL: <https://doi.org/https://doi.org/10.1594/PANGAEA.890634>.

Author contribution AP, IV, LB, and LT conceived and designed the study. AP collected the image data. IV labelled the image data. AP conducted the statistical tests. IV and AP wrote the initial draft of the manuscript with input from LB and LT. All the authors read and approved the manuscript.

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