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Small topographical variations controlling trace maker community: Combining palaeo- and neoichnological data at the Porcupine Abyssal Plain

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ABSTRACT

Ichnological research has generally assumed that abyssal plains are dominated by quiescent, homogenous environmental conditions. Thus, deep-sea trace fossil assemblage changes have been usually linked to significant spatial and temporal environmental variations. Here, we conducted a comparative ichnological analysis between a small abyssal hill (50 m elevation) and the surrounding abyssal plain; this modest bathymetric variation is known to generate substantial environmental heterogeneity for the benthic fauna community of the Porcupine Abyssal Plain (c. 4850 m depth), Northeast Atlantic. Based on X-ray data from a 5 × 5 core grid emplaced in two box cores, we compared hill and plain bioturbational sedimentary structures, including trace fossil assemblages (e.g., ichnotaxonomy) and biodeformational structures (e.g., mixed-layer depth). We observed that topographically-enhanced near-bottom currents over the hill likely produce significant changes in depositional dynamics and sediment properties (e.g., grain size, organic matter content and degradation), and control specificities of bioturbational sedimentary structures (e.g., trace fossils, mixed layer attributes such as thickness, mottled background, discrete traces). Palaeoichnological data suggested that the abyssal plain had experienced consistent conditions during the last thousands of years while the abyssal hill recorded improving environmental conditions for the trace maker community. Our results highlight the complexity of the deep-sea environment, demonstrating that small changes in bioturbated sedimentary assemblages appear even within the same box core (m-scale), and that substantial changes can occur due to environmental heterogeneity (e.g., subtle topographic variations) at the local scale (km-scale). Considering the vast global extent of abyssal hill terrain, we suggest that their influence on the bioturbational sedimentary record may be significantly under-appreciated and require more attention in palaeoenvironmental reconstructions.

1. Introduction

The deep sea is the largest environment on Earth and is far more varied and dynamic than has been historically assumed (Ramirez-Llodra et al., 2010). Several studies have shown that deep seafloor heterogeneity (e.g., sediment and hard-substratum availability) influences geographic patterns of species richness (Riehl et al., 2020; Simon-Lledó et al., 2019). Additionally, bathymetric gradients are known to affect benthic community diversity and body size (Rex et al., 2006), with locally elevated terrain, such as abyssal hills, seamounts, and ridges, being important in driving change in the community structure and function (e.g., Durden et al., 2020b; Durden et al., 2015). The deep-sea benthic community interacts with the sedimentary environment through bioturbational processes (Kristensen et al., 2012) which are essential to ecosystem function through modification of physicochemical characteristics including the redistribution of seafloor food resources (Meysman et al., 2006). These processes can be sometimes preserved through biogenic structures, i.e., *lebensspuren* created by the present benthic community and their trace fossils equivalents, such as burrows, trails, mounds, or faecal casts produced by past organisms (Ewing and Davis, 1967; Przeslawski et al., 2012; Bell et al., 2013; Brandt et al., 2023; Miguez-Salas et al., 2024a, 2024b, Miguez-Salas

et al., 2023a, Miguez-Salas et al., 2023b).

Ichnology, the study of present (neo-) and past (palaeo-) bio-turbational processes and their associated traces, initially investigated large-scale bathymetric variations at intervals of hundreds to thousands of metres with the purpose of establishing links between trace fossil associations and depositional environments (Seilacher, 1967a, 1967b). Further research concluded that trace fossil distribution reflects sets of environmental factors rather than sedimentary environments and specific bathymetric zones, with bathymetry being an indirect limiting factor for trace makers communities (Frey et al., 1990). Consequently, trace fossil bathymetric interpretations should be examined with caution. In modern environments, many of the ecological variations noted with water depth may not be directly related to variations in depth or pressure per se, being primarily caused by other environmental parameters, such as temperature, oxygen concentration or nutrient supply, all of which typically vary systematically from shallow- to deep-sea settings (Gage and Tyler, 1991).

Recently Durden et al. (2020b) established that even very modest topography elevations (10 m-scale) in the abyss can significantly modify the abundance, diversity, and species composition of benthic communities. We are not aware of any studies addressing similar variations in trace maker communities or trace fossil assemblages. Determining at what scale this form of deep-sea heterogeneity becomes important is key in assessing spatial and/or temporal change in both present and past trace maker communities. In this study, we examine the potential impact of modest topographic elevations on bioturbational sedimentary structures in the Porcupine Abyssal Plain Sustained Observatory area (PAP-SO; Hartman et al., 2021) where the presence of several abyssal hills introduces significant environmental variations (Morris et al., 2016; Turnewitsch et al., 2015). Two topographic settings are compared: 1) the flank of a small abyssal hill (<50 m elevation) and 2) the open abyssal plain. We aimed to, a) compare hill and plain bioturbational sedimentary structures, including trace fossil assemblages and bio-deformational structures, b) connect ichnological features with documented environmental properties, and c) infer past environmental changes based on specific trace fossil distributions. Finally, we consider how spatial heterogeneity may control trace fossil assemblages and contemporary trace maker communities at different scales.

2. Material and methods

2.1. Study area

The present study was conducted at two locations within the PAP-SO (Fig. 1): 1) the flank of a single small abyssal hill (H3 sensu Durden et al., 2015), in particular a location within an area referred to as "Area B" by Morris et al. (2016) and "Hill" by Durden et al. (2020b), and 2) an open abyssal plain location, referred to as "PAP central" in Durden et al. (2020b). The sedimentary environment and megabenthic communities of both sites have been previously studied, including determinations of total organic carbon, total nitrogen, and mud content (Durden et al., 2015, 2020b; Morris et al., 2016). No data are available on the sediment mixed layer depth for the flank of the hill, but previous studies in the PAP central area (48.50° N, 16.30° W) suggest a mixed layer depth around 6–7 cm by reference to ^{210}Pb and ^{14}C values respectively (Rabouille et al., 2001; Reyss, unpublished data). The sedimentation rates vary from 6.1 to 15.3 cm kyr^{-1} below the mixed layer (from 10 cm to 35 cm approx.) (Rabouille et al., 2001). At a location a little further north in the PAP central area (48°58′ N, 16°28′ W) a piston core estimated an average sedimentation rate of 2.1 cm kyr^{-1} for the top 50 cm (Hinrichs et al., 2001). In a more general framework, sedimentation rate and mixing layer depth data are available for the general NE Atlantic area (see Table 1 in Trauth et al., 1997), suggesting a sedimentation rate of 3–4 cm kyr^{-1} and a sediment mixed layer depth of 7–8 cm. We note that these values may not be representative for our specific study sites, particularly the abyssal hill flank where significant sediment winnowing

is evident (Morris et al., 2016), suggesting a much reduced sediment accumulation rate in that area (ongoing research). However, based on these previous results, we can assume that our boxcore samples represent more than 2000 yrs. BP.

2.2. Material

Two USNEL Mk II-type spade box core (Gage and Bett, 2005) samples were obtained during RRS *James Cook* cruise 231 (Hartman, 2022). The first, station JC231–019, was collected on 6 May 2022 from position 48° 50.401′ N, 16° 31.302′ W, water depth 4842 m, from the abyssal plain ("PAP central"). The second, station JC231–049, was collected on 9 May 2022 from position 48° 59.103′ N, 16° 33.170′ W, water depth 4795 m (i. e., c. 50 elevation above abyssal plain), from the abyssal hill ("Hill"). Both recovered 50 × 50 cm surface area cores of c. 40 cm sediment depth. Each box core was then subsampled with 25 plastic core liners (internal diameter 8 cm) emplaced in a closely spaced 5 × 5 grid, each marked to ensure common orientation. The 5 × 5 grid was designed with the idea of seeing the lateral distribution of traces on a small scale (i.e., box core dimensions) (see Fig. 1c). These subcores were maintained upright at c. 6 °C for return to the shore-side laboratory.

Subcores were scanned using a Geotek Ltd. ScoutXcan multi-angle digital 2D X-ray system at the British Ocean Sediment Core Research Facility (BOSCORF), to obtain Computed Laminography data following Dorador et al. (2024) methodology. The system uses a 65 W Thermo Kevex 130 kV Microfocus X-ray source which, for the present study, was operated at 115 kV and 425 µA, with a 1.0 mm Cu filter. The laminography images have a resolution of 213 pixels per centimeter. Each image was processed specifically using Adobe Photoshop CS6© software to improve the visibility of biogenic structures, i.e., via adjustment of levels, brightness, contrast, gamma, etc. (see Dorador and Rodríguez-Tovar, 2018 and references therein). Note that for logistic reasons one subcore from station JC231–019 was not include in this study. Additionally, at these two stations gravity cores were collected (Hartman, 2022). X-Ray Fluorescence (XRF) data has been obtained from the gravity cores to track geochemical composition variations (Miguez Salas, 2024).

2.3. Ichnological characterization

An initial qualitative ichnological assessment was carried out to distinguish between biodeformational structures and trace fossils. Since no open burrows have been observed, we prefer to avoid the term *lebensspuren* because we cannot ensure that the traces identified are produced by the current benthic community. Biodeformational structures were characterized by undifferentiated outlines and the absence of a defined geometry, impeding any ichnotaxonomical classification, and revealing a more-or-less mottled ichnofabric. Trace fossils showed sharp outlines and a characteristic recurrent geometry enabling their ichno-taxonomical classification to be established (see González-Lanchas et al., 2022; Rodríguez-Tovar et al., 2015; Rodríguez-Tovar and Dorador, 2014; Uchman and Wetzel, 2011). Biodeformational structures can be related to high bioturbation within the relatively unconsolidated sediments of the mixed layer (ML in Figs. 2 and 3), producing a mottled background (Rodríguez-Tovar and Dorador, 2014). This mixed layer corresponds to a fully bioturbated / homogenized sediment horizon, having a typical thickness in modern open oceans of 3.8–8.0 cm (Zhang et al., 2024). Below the mixed layer, extending to c. 20–35 cm, is a transition layer of heterogeneous mixing resulting from the activity of deeper-burrowing organisms (Berger et al., 1979). Accordingly, the upper part of the study subcores (from here on sections) was classified into the following categories: a) ML-a: absence of discrete traces, presence of mottled background, clear differentiation from the sediment below, b) ML-b: first centimetres showing few discrete traces superimposed on mottled background, and c) TL: absence of mottled background and presence of discrete traces from the transition layer in the
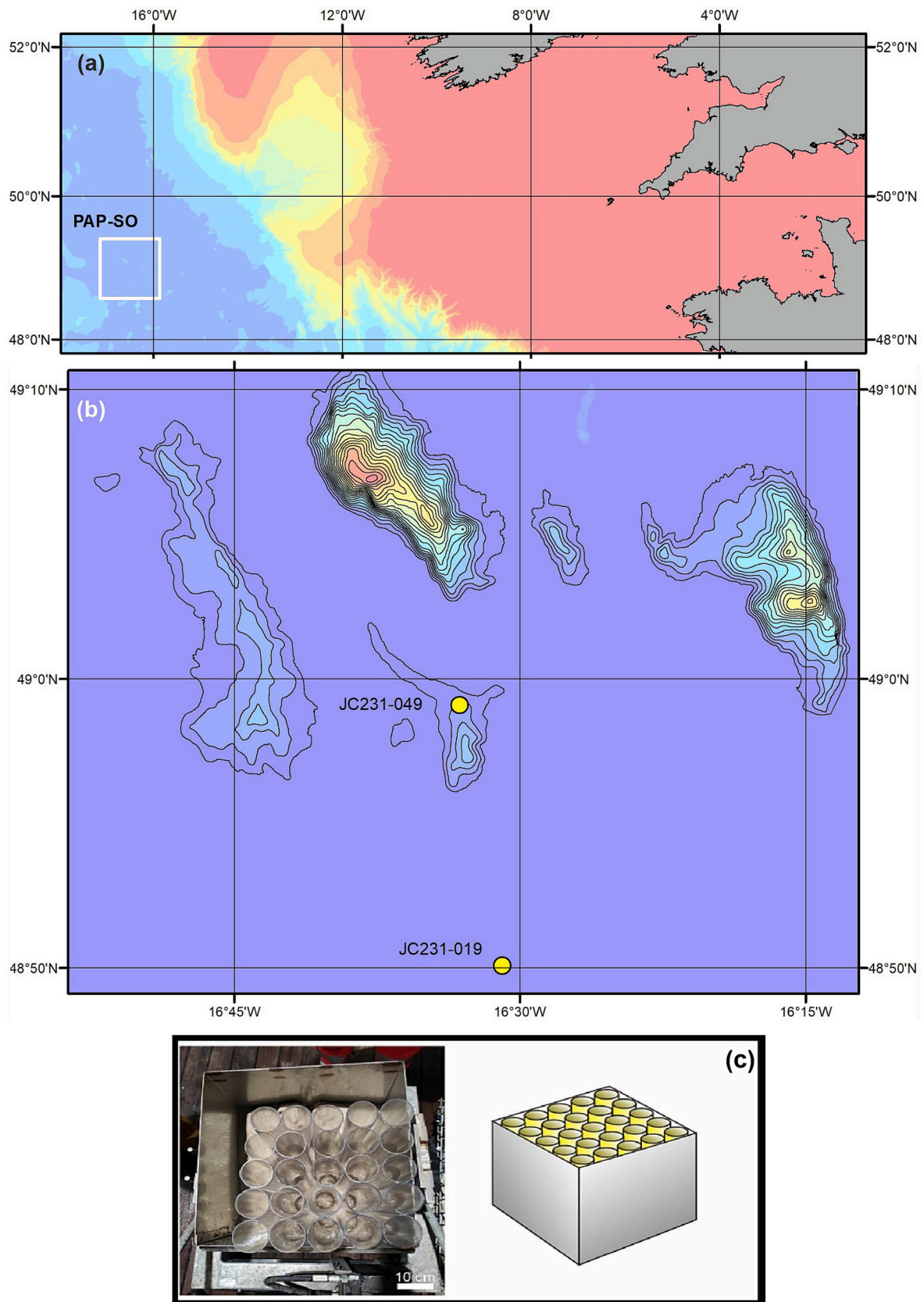
Fig. 1. (a) General location of the Porcupine Abyssal Plain Sustained Observatory (PAP-SO) in the NE Atlantic (http://marineregions.org/mrgid/63025). (b) PAP-SO bathymetry (50 m contours) with core sampling sites, JC231–019 on the abyssal plain and JC231–049 on a small abyssal hill. (c) picture and diagram of the 5 × 5 grid core liner in one of the boxcores (from Dorador et al., 2024).

Table 1
Main trace fossils, ichnological features, and biodeformational structures identified in section images (n = number of sections). Only ichnogenera that are clearly identified were uses for area calculations and size comparison.

Observation	Occurrence		Total area (cm²)	
	JC231–019	JC231–049	JC231–019	JC231–049
	Abyssal plain	Abyssal hill	Abyssal plain	Abyssal hill
	(n = 24)	(n = 25)	(*n* = 24)	(*n* = 25)
Horizontal burrows	137	127	4380.6	3848.5
Vertical burrows	36	21	880.0	467.4
Scolicia	19	12	977.7	1175.1
Planolites	7	20	120.3	434.9
Asterosoma	12	13	904.8	1177.6
Nereites	1	24	10.0	591.9
Chondrites (Intervals)	N/A	N/A		
"Mycellia"/ *Trichichnus* (Intervals)	N/A	N/A		
Helicodromites	9	1	44.5	4.8
Palaeophycus	?1	12	–	88.9
Thalassinoides	7	4	490.6	105.0
?Zoophycos	0	6	–	161.5
Parahaentzschelinia	0	4	–	289.1
Schaubcylindrichnus	1	?1	28.2	–
Graphoglyptid	?1	2	–	–
Bioturbated upwards	6	16	–	–
Completely bioturbated	12	4	–	–
Interval bioturbation	2	2	–	–
Scarcely bioturbated	4	6	–	–
Mixed layer type: ML-a	21	11	–	–
Mixed layer type: ML-b	3	8	–	–
TL	1	6	–	–

uppermost centimetres. Additionally, all sections were qualitatively characterized as: i) completely bioturbated, ii) scarcely bioturbated, iii) increasing bioturbation upwards, and iv) bioturbated in intervals.

Subsequently, identified traces were classified at the ichnogenus level based on the recognition of ichnotaxabases, i.e., standard morphological features, wall, filling, spreiten (see recent review by Bertling et al., 2022). Some discrete traces were not ichnotaxonomically classified because of the absence of diagnostic features. Instead they were grouped based on their predominant orientation, into: i) horizontal burrows, and ii) vertical burrows. Particular attention was given to the recognition of graphoglyptids (i.e., shallow and complex burrow systems; see Uchman and Wetzel, 2011). For quantification, the total area occupied by each ichnogenus was manually annotated in BIIGLE 2.0 (Langenkämper et al., 2017). A between-site comparison was carried out for those ichnogenera in which at least 5 specimens were recorded. These comparisons, and those of mixed layer depths (ML-a and ML-b), were undertaken using the Wilcoxon-Mann-Whitney (WMW) test as implemented in R (Team, 2020).

3. Results

The ichnological assessment revealed that both cores were highly bioturbated but that notable differences could be observed in their respective biodeformational structures and trace fossil assemblages (Figs. 2–5) (Supplementary material 1 and 2). No primary sedimentary structures such as planar lamination or cross-lamination were observed. The cores from both sites were dominated by muddy pelagic and hemipelagic facies and showed no evidence of sedimentation hiatuses.

3.1. Biodeformational structures and transition layer

Sections from the abyssal plain sample (JC231–019) showed dominance of mixed layer type ML-a, with only occasional occurrences of ML-b and TL. The thickness of ML-a was variable with an average depth of 2.8 cm. The majority of these sections were completely bioturbated by discrete trace fossils (Table 1). The abyssal hill sample (JC231–049) had fewer ML-a sections than on the abyssal plain but they were of a similar thickness (Table 2). The mixed layer types ML-b and TL were more frequently registered on the abyssal hill (Table 1). No statistically significant differences in mixed layer depths were detected between the samples ($p > 0.05$; Table 2).

3.2. Trace fossil assemblage

We recognized the following ichnotaxa during this study (Figs. 2–5):

Asterosoma - was frequently recorded in both samples and appeared as disturbed sediment areas exhibiting a concentric fill surrounding a central tube, representing the cross-section of the branches of a radial structure. When analyzing adjacent laminographs with a different orientation an overall bulb shape can be recognized. In some cases, the central axis and the radiating burrows were observed, with diameters of 0.5–1.5 cm (Fig. 2 sections 10, 11). Occasionally, intervals >10 cm thick (Fig. 3 section 21) were dominated by *Asterosoma*. This ichnotaxon is interpreted as the feeding structure of a vermiform organism (Chamberlain, 1971; Vossler and Pemberton, 1988a) and has been commonly encountered in fully marine environments, ranging from coastal to offshore (Vossler and Pemberton, 1988a).

Chondrites - refers to a regularly branching tunnel system consisting of a small number of master shafts, open to the surface, that ramify at depth to form a dendritic network (Baucon et al., 2020; Bromley and Ekdale, 1984; Kotake, 1991; Vossler and Pemberton, 1988b). In the present study, *Chondrites* was infrequently observed, in rare cases showing branching (Fig. 3 section 15), but usually appeared as small (1–2 mm wide), isolated elliptical spots and short tubes, and occasionally as dense clusters. *Chondrites* is interpreted as a feeding structure associated with deep tiers, showing activity down tens of centimetres within the sediment column, and is likely produced by various organisms (Baucon et al., 2020 for a recent review). Its presence has often been associated with low oxygen levels in bottom and/or pore waters (e. g., Bromley and Ekdale, 1984).

Graphoglyptids – observed as systematic burrow systems, observed in the upper part of some sections (Fig. 5 section 22), in reference to highly organized, often closely spaced circular burrows (Rodríguez-Tovar, 2022). These structures are similar to those identified as graphoglyptid-like forms by Baldwin and McCave (1999).

Helicodromites - observed as spiral, helical, forms in the horizontal plane similar to those identified as *Helicodromites* by Baldwin and McCave (1999). This trace was infrequently observed in both samples (e. g., Fig. 2 section 8). *Helicodromites* is interpreted as a feeding structure, usually linked to low energy environments, sometimes after turbidite deposition (Rodríguez-Tovar et al., 2010).

"Mycellia"/*Trichichnus* - is not a formally named trace fossil, consisting of small, randomly orientated branching filaments up to several centimetres in length and several millimetres thick (Löwemark et al., 2004). In this study, thin filaments around 1 mm thick and up to several centimetres long, were observed as isolated tubes or forming a complex network (Fig. 2). It was most frequent and obvious in the abyssal plain sample (JC231–019). "Mycellia" has been interpreted as mineral-replaced filaments produced by large sulphur-oxiding bacteria or mycelial fungi; they concentrate in monosulphide bands in deeper sediment layers but may be associated with organic patches in nearer-surface layers (Virtasalo et al., 2010). Presence of isolated tubes of a wide range of length and width make difficult the differentiation between "Mycellia" and *Trichichnus*; thus to be conservative, we prefer to group both ichnotaxa as "Mycellia"/*Trichichnus* henceforth.

Nereites - consisted of tunnels (3–5 mm diameter) showing a clear differentiation between the infilling material (lighter) and the surrounded sediment (darker). In some cases, subcircular sections were
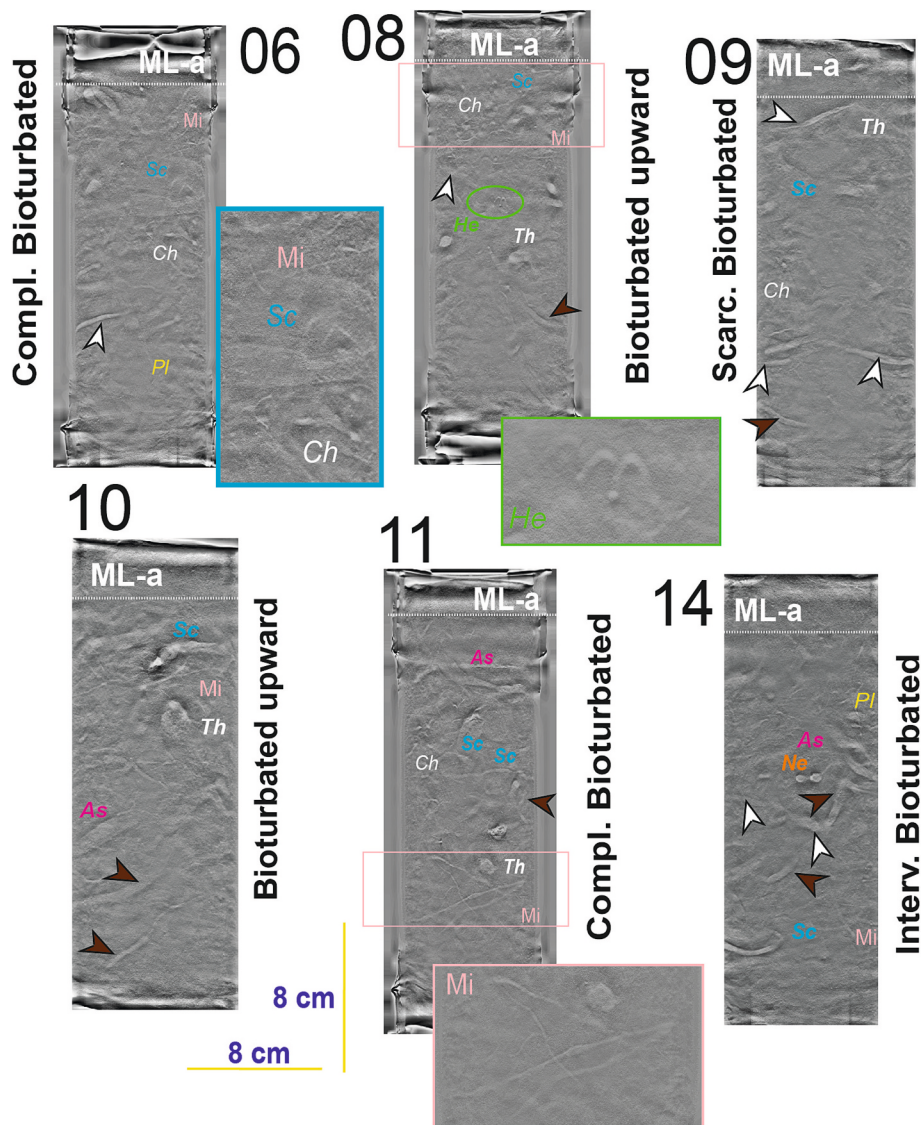
Fig. 2. Selected laminography sections (06, 08, 09, 10, 11, 14) from the abyssal plain box core (JC231–019) showing primary interpretations. *Asterosoma* (*As*), *Chondrites* (*Ch*), *Helicodromites* (*He*), "Mycellia"/*Trichichnus* (*Mi*), *Nereites* (*Ne*), *Planolites* (*Pl*), *Scolicia* (*Sc*), *Thalassinoides* (*Th*). Undifferentiated horizontal and vertical burrows are indicated with white and brown arrows respectively. Note that not all traces have been indicated, just some significant examples. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

observed, occasionally as paired (Fig. 3 section 14; Fig. 4 Section 2) (Rodríguez-Tovar et al., 2015). Tubes were sinuous, in some cases showing as a dense ichnofabric, including features laterally continuous between sections (Fig. 4 sections 11 and 12). The trace was recorded in both samples but was more frequent in the abyssal hill sample (JC231–049, Fig. 4). In modern deep-sea environments, *Nereites* has been observed in and related to redox boundary conditions in the sediment (Wetzel, 2002, 2008). The *Nereites* trace makers sort the sediment leading to a tube filled with fine material surrounded by a coarser grained halo, and appear to be guided chemotactically, presumably maintaining a consistent distance relative to the redox boundary.

Palaeophycus - was represented by unbranched forms, mainly as circular to subcircular cylindrical burrows, smooth and lined. It was only occasionally observed, appearing as lined traces with structureless fill, having the same lithology as the surrounding medium. Some circular sections (5–7 mm in diameter) could be assigned to *Palaeophycus* (Fig. 5 section 19, 20). *Palaeophycus* is a facies crossing form, interpreted as a shallow–mid tier feeding/dwelling structure (pascichnia or domichnia), produced by carnivorous or omnivorous invertebrates, predominantly

polychaetes (Dorador et al., 2021; Keighley and Pickerill, 1995; Pemberton and Frey, 1982; Rodríguez-Tovar and Dorador, 2014).

Parahaentzschelinia - was observed as vertical/oblique grouped tubes (0.4–1.5 cm in diameter) radiating upwards from a vertical master shaft. It was a rare trace, exclusively observed in the abyssal hill sample (JC231–049, Fig. 5 sections 14, 22 and Supplementary material 2). *Parahaentzschelinia* is interpreted as a feeding trace; originally attributed to a worm-like animal, now suggested to be a trace produced by a tellinid bivalve (Knaust, 2017). This trace is observed in past and modern deep-marine deposits (Knaust, 2017; Wetzel, 2008).

Planolites – observed as unlined, rarely branched, straight to tortuous, smooth or annulated actively filled burrow, circular to elliptical in cross-section, of variable dimensions and configurations (Dorador et al., 2021; Pemberton and Frey, 1982; Rodríguez-Tovar and Dorador, 2014). The active fill is essentially massive and differs in lithology from the host sediments. In the present samples, *Planolites* was observed as unlined, unbranched, and mainly horizontal to oblique cylindrical forms (0.2–1 cm in diameter, and up to several centimetres in length), filled by lighter material than the surroundings sediment (Figs. 2–5). *Planolites* occurred only occasionally, and could have been
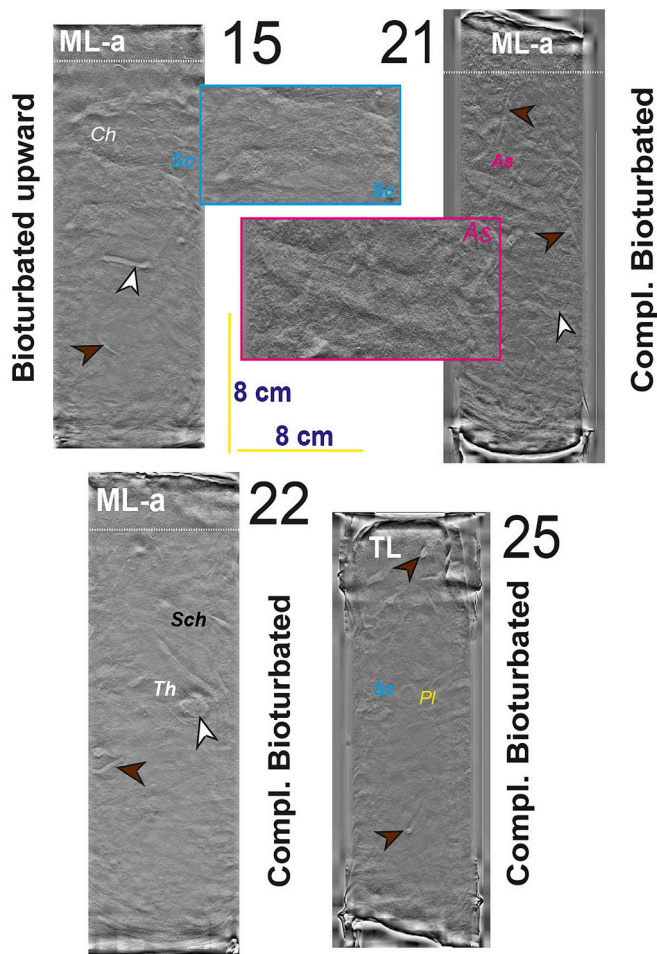
Fig. 3. Selected laminography sections (15, 21, 22, 25) from the abyssal plain box core (JC231–019) showing primary interpretations. *Asterosoma* (*As*), *Chondrites* (*Ch*), *Planolites* (*Pl*), *Schaubcylindrichnus* (*Sch*), *Scolicia* (*Sc*), *Thalassinoides* (*Th*). Undifferentiated horizontal and vertical burrows are indicated with white and brown arrows respectively. Note that not all traces have been indicated, just some significant examples. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Fig. 4. Selected laminography sections (02, 06, 07, 11, 12) from the abyssal hill box core (JC231–049) showing primary interpretations. *Asterosoma* (*As*), *Helicodromites* (*He*), *Nereites* (*Ne*), *Planolites* (*Pl*), *Scolicia* (*Sc*), *Thalassinoides* (*Th*). Undifferentiated horizontal burrows are indicated with white arrows.

misidentified as *Nereites*; however, the isolated occurrences suggested classification as *Planolites*. It is interpreted as a shallow-tier feeding structure produced by soft bodied invertebrates (e.g., Rodríguez-Tovar et al., 2019).

Schaubcylindrichnus - was a U-shape structure observed as lined curved tubes in a sub-horizontal to inclined orientation. In the present samples, some of the observed tubes assigned to *Parahaentzschelinia* could tentatively be identified as *Schaubcylindrichnus*, however a lining was not clearly observed (Fig. 3 section 22). Moreover, *Schaubcylindrichnus* is usually recorded as clustered tubes, instead of isolated pipes. This trace is interpreted as a feeding structure produced by worm-like organisms (e.g., Dorador et al., 2021; Frey and Howard, 1981; Löwemark and Nara, 2010).

Scolicia - is defined as a backfilled burrow with two parallel strings in the bottom part and an oval cross section. In the present samples, it was identified as sub-circular sections around 20 mm in diameter, in some cases showing a tube core, or as longitudinal sections determining a completely bioturbated ichnofabric (Figs. 2–5). In some cases, a meniscate lamination and concentric structure was observed (Fig. 3 section 15), interpreted as part of the active backfill produced during locomotion and feeding of irregular echinoids (e.g., Buatois et al., 2023; Fu and Werner, 2000; Miguez-Salas et al., 2021; Uchman, 1995). This
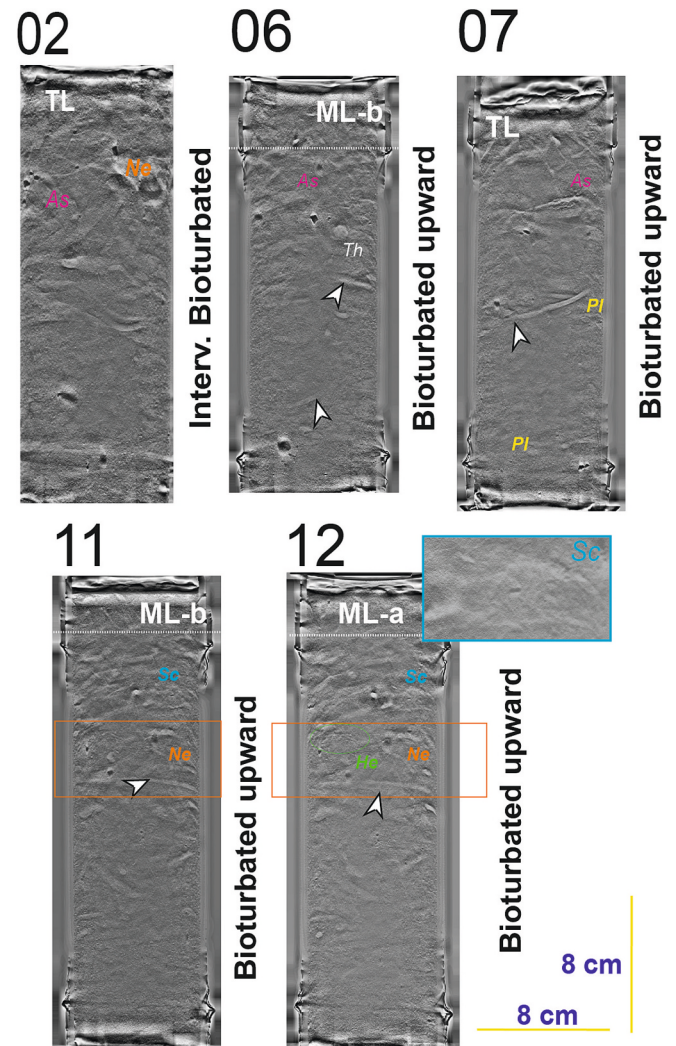
was more frequently and clearly observed in the abyssal plain sample (JC231–019).

Thalassinoides – consisted of a three-dimensional system of cylindrical burrows of variable size. Branches are of Y to T-shaped form, commonly enlarged at the bifurcation points. In the present samples, burrow of relatively large size (1–3 cm in diameter) of circular and elliptical cross sections and straight horizontal cylinders were assigned to *Thalassinoides* (Figs. 2–5). It is interpreted as a dwelling structure produced by callianassid shrimps among other potential tracemakers (e. g., Bromley and Frey, 1974; Myrow, 1995; Rodríguez-Tovar et al., 2017).

?*Zoophycos* - was tentatively identified in the present study as sub-horizontal lamination structures crossing the width of the section images. However, the internal meniscate structure, typical of *Zoophycos* was not observed (Supplementary material 2 Section 3). *Zoophycos* is usually interpreted as a caching behavior structure whose producer is unknown (e.g., Löwemark, 2015; Löwemark and Schäfer, 2003), in some cases associated with high and seasonal primary productivity (Dorador et al., 2016, 2019).
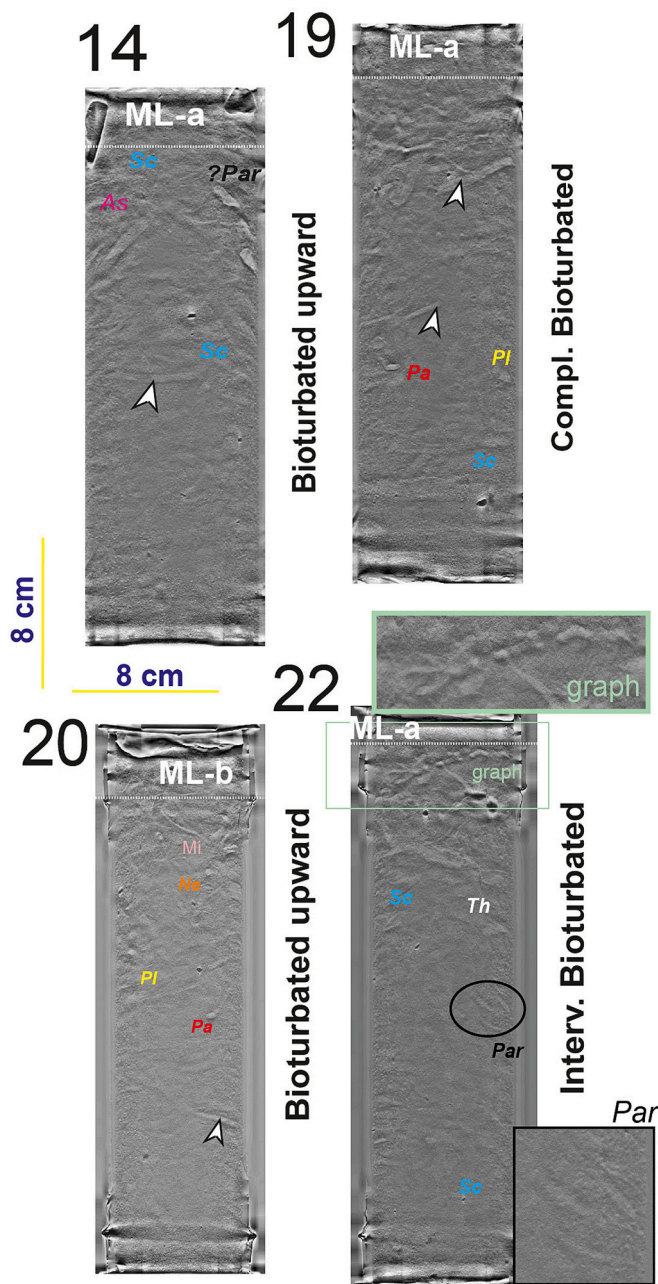
Fig. 5. Selected laminography sections (14, 19, 20, 22) from the abyssal hill box core (JC231–049) showing primary interpretations. *Asterosoma* (*As*), graphoglyptid (graph), "Mycellia"/*Trichichnus* (Mi), *Nereites* (*Ne*), *Parahaentzschelinia* (*Par*), *Planolites* (*Pl*), *Scolicia* (*Sc*), *Thalassinoides* (*Th*). Undifferentiated horizontal burrows are indicated with white arrows.

3.3. Comparison of assemblages

Both core samples had moderately diverse trace fossil assemblages, mainly consisting of *Asterosoma*, *Chondrites*, graphoglyptids, *Helicodromites*, "Mycellia"/*Trichichnus*, *Nereites*, *Planolites*, *Scolicia*, and *Thalassinoides* (Supplementary material 1 and 2). Other ichnogenera such as *Palaeophycus*, *Parahaentzschelinia*, and?*Zoophycos* were only recorded in the abyssal hill core sample (JC231–049; Table 1) while *Schaubcylindrichnus* was only noted in the abyssal plain sample. According to this, ichnodiversity is slightly higher on the abyssal hill. However, significant differences can be distinguished in the abundance of specific traces (e.g., *Chondrites*, "Mycellia"/*Trichichnus*, *Nereites*) (see Table 1).

The abyssal hill sections are characterized by numerous bioturbation

Table 2
Mixed layer depths and trace fossil extent determined in section images from abyssal plain (JC231–019) and abyssal hill (JC231–049) samples (n = number of observations; WMW, Wilcoxon-Mann-Whitney).

Observation	Sample	n	Median	95 % CI	WMW test (*p*-value)
Mixed layer type: ML-a (cm)	JC231–019 abyssal plain	21	2.8	2.4–3.1	0.96
	JC231–049 abyssal hill	11	2.9	2.5–3.3	
Mixed layer type: ML-b (cm)	JC231–019 abyssal plain	3	2.7	2.0–3.5	0.27
	JC231–049 abyssal hill	8	3.4	3.0–3.8	
Horizontal burrows (cm^2)	JC231–019 abyssal plain	137	31.9	28.3–35.4	0.80
	JC231–049 abyssal hill	127	30.3	27.0–33.4	
Vertical burrows (cm^2)	JC231–019 abyssal plain	36	24.4	19.4–29.0	0.68
	JC231–049 abyssal hill	21	22.2	17.5–26.6	
Asterosoma (cm^2)	JC231–019 abyssal plain	12	75.4	54.7–93.3	0.20
	JC231–049 abyssal hill	13	90.5	76.5–103.1	
Scolicia (cm^2)	JC231–019 abyssal plain	19	51.4	36.8–63.5	**<0.01**
	JC231–049 abyssal hill	12	97.9	73.7–121.1	
Planolites (cm^2)	JC231–019 abyssal plain	7	17.1	11.0–23.0	0.39
	JC231–049 abyssal hill	20	21.7	16.4–26.6	
Chondrites (cm^2)	JC231–019 abyssal plain	5	1.5	0.9–2.1	0.86
	JC231–049 abyssal hill	15	1.9	1.1–2.6	

increasing upwards sequences (*n* = 16) and some graphoglyptid intervals (*n* = 2). Regarding ichnotaxa, vertical stratigraphic distribution was variable; in some cases, it was apparently random but in others showed a precise position through the samples, and even concentration in localized intervals. That was the case for horizons showing dense occurrences of *Nereites* and graphoglyptids in the abyssal hill core sample, and *Scolicia* and "Mycellia"/*Trichichnus* in the abyssal plain core sample. However, these horizons do not have a great lateral continuity, disappearing in most cases in the adjacent sections. Only some *Nereites* horizons can be followed into adjoining sections (Fig. 4). More than 100 horizontal burrows were identified in each sample, while vertical burrows were less common (Table 1). No statistically significant differences were detected in the size of the most common traces (*Asterosoma*, *Chondrites*, *Planolites*, vertical, and horizontal burrows) between the samples. The only trace fossil that shows a significant difference between samples was *Scolicia* (*p* < 0.01), being larger on the hill (Table 2).

4. Discussion

Previous studies have analysed the impact of modest topographic elevations on the benthic communities in the Porcupine Abyssal Plain Sustained Observatory area (Durden et al., 2020b). Variations in some environmental factors such as hydrodynamic energy, total nitrogen, total organic carbon, mud content among others have been noted on elevated terrain in the region (Durden et al., 2015; Morris et al., 2016). On the small abyssal hill studied, topographically enhanced current speeds have been proposed as the main mechanism by which these environmental variations were produced (Morris et al., 2016). Increased near-bottom current speeds over the elevated terrain were thought to

produce significant changes in sediment grain size distributions and the total biomass of megabenthos on the hill (Durden et al., 2020b). Our results showed variations in ichnological (neo- and palaeo-) features between and through the different sections from the two studied settings. Considering that bioturbational sedimentary structures and trace fossil assemblage stratigraphic evolution were different at both sites, a number of questions arise in relation to which of the previously recorded environmental parameters may have influenced the observed ichnological variations.

4.1. The neoichnological record: diving into the mixed layer

In the present study, the neoichnological record was limited to those biogenic structures observable within the sediment column and presumed to be produced by the present endobenthic trace maker community. Thus, our neoichnological information refers to the first centimetres below the sediment surface and are mainly associated with the sediment mixed layer (ML). The thickness of ML-a was not significantly different between the two sites, however, cores showing ML-a type were more frequently observed on the plain than on the hill (Table 2). In the study sites, the benthic biomass is considerably higher on the hill due to topographical enhanced current, especially for suspension feeders (0.625 g m^{-2} on the plain vs. 2.506 g m^{-2} on the hill; see Durden et al., 2020b). Thus, the amount of organic matter incorporated into the sediment column may be higher on the plain (Durden et al., 2020b; Morris et al., 2016). A larger abyssal hill / seamount immediately to the north of our hill study site (see Fig. 1) was studied by Turnewitsch et al. (2015) who demonstrated that bottom water flow-hill interactions resulted in an overall reduction of organic matter deposition. Although the sediments on elevated topography may have a lower total organic matter content, there is evidence that the organic matter present is more labile due to coarser grain fractions which reduce the

particle surface area (Turnewitsch et al., 2015). In the present study, there is also an increase in grain size on the hill (Morris et al., 2016). Therefore, even if there is less organic matter on the hill than on the plain, it may be less refractory.

Increased sediment organic matter content is often positively related to higher endobenthic bioturbation intensity (Boudreau, 1998; Smith and Rabouille, 2002; Yang et al., 2020). However, organic matter freshness has rarely been considered in the case of infaunal bioturbation, being most frequently studied in relation to epibenthic bioturbation (Miguez-Salas et al., 2024b; Przeslawski et al., 2012). The relative lability of sediment-associated organic matter may influence local community composition and feeding behavior (see Durden et al., 2020a) and consequently bioturbation (Fig. 6). The greater frequency of ML-a on studied abyssal plain site might indicate a more active subsurface deposit feeder community that acts to erase discrete trace fossils. This might suggest that subsurface trace maker community abundance / activity is driven by sedimentary total organic carbon variation (organic matter quantity) while the relative lability of the organic matter exerts a second order factor.

The thickness of ML-b was broadly similar at both sites (Table 2). However, its occurrence, as well as that of the transition layer (TL) type profile, was more frequent at the hill site than at the plain site. ML-b layers were characterized by a record of discrete traces superimposed to a mottled background, while TL type profiles showed the absence of ML and the occurrence of discrete traces even in the uppermost centimetres of the section. The development of these discrete traces may not necessarily reflect the presence of distinct trace maker communities at the two study sites. At the hill site, surficial sediments have a reduced mud content (<75 %) compared to the abyssal plain site (>85 %; Morris et al., 2016). This difference likely reflects the greater winnowing of surficial sediments on the hill, this may favour open burrows receiving an infill of coarser material, favouring recognition of discrete trace
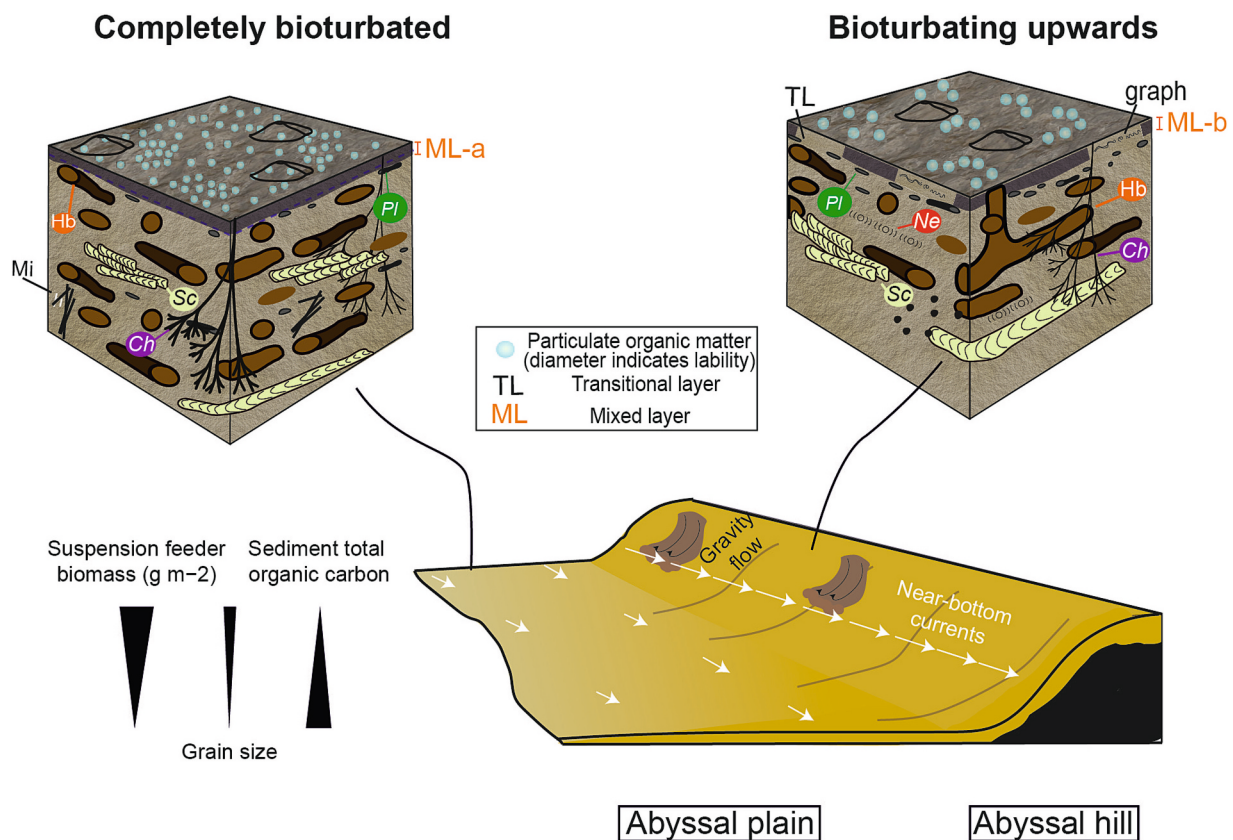

Fig. 6. Schematic diagrams of ichnological features that characterize the studied abyssal plain and hill. *Chondrites* (*Ch*), graphoglyptid (graph), "Mycellia"/*Trichichnus* (*Mi*), *Nereites* (*Ne*), *Planolites* (*Pl*), *Scolicia* (*Sc*), and Horizontal burrows (*Hb*).

fossils by providing contrast between the host and infilling sediment. Thus, development of ML-b types or the absence of ML on the hill may primarily reflect the environmental characteristics (e.g., grain size, hydrodynamics) rather than the trace maker community specifically.

The applicability of these observations to the fossil record is limited. However, the development of ML-a on the plain demonstrates that typical mottled background ichnofabrics actually reflect stable favorable conditions while appearance of discrete traces on the mixed layer may reflect a more dynamic environments in the deep-sea. Other important factors that may help the enhanced development of discrete traces include differential fluid precipitation processes induced by the contrasting material between host and infilling sediment (e.g., porosity contrast, burrow induced differential flow). However, addressing ichnological-induced "diagenetic" processes goes beyond the scope of the current study. Finally, it is important to emphasize that within the same site (i.e., the same box core), there is lateral variability in the appearance of the different types of ML (e.g., Fig. 4 sections 6 and 7). Therefore, we cannot assume that ML attributes are laterally continuous even at a small scale (e.g., metric scale).

Graphoglyptids are a common component of the *Nereites* ichnofacies, that are typically recorded from oligotrophic deep-sea environments and associated with deep-sea flysch areas, preserved almost exclusively as casts on the soles of turbidite beds (Heard and Pickering, 2008; Rodríguez-Tovar, 2022; Rodríguez-Tovar et al., 2020; Seilacher, 1977; Uchman, 2003). The observation of graphoglyptids in some hill site samples, in the upper part of the transition layer below a very thin or absent mixed layer, suggests 1) the presence of gravity flows on the flank of the hill that favour the scouring and casting of these shallow burrow systems and 2) the existence of sediment areas with sporadic decrease in organic matter availability at the hill seafloor (Fig. 6).

4.2. The palaeoichnological record

Our samples record a moderately diverse trace fossil assemblage, mainly consisting of *Asterosoma*, *Chondrites*, *Helicodromites*, "Mycellia"/*Trichichnus*, *Nereites*, *Planolites*, *Scolicia*, and *Thalassinoides*, with density variations between-site in "Mycellia"/*Trichichnus*, *Nereites* and in some of the least frequent ichnotaxa such as *Palaeophycus*, *Parahaentzschelinia*, *Schaubcylindrichnus*, and?*Zoophycos*. However, two features highlight potential palaeoenvironmental differences between the study sites: 1) dominance of completely bioturbated sections in the abyssal plain profiles, suggesting long-term maintenance of favorable conditions during deposition; and 2) dominance of increasing bioturbation upward sequences in the abyssal hill profiles which may be related to more favorable conditions in recent times, as represented by the uppermost centimetres of these profiles. Aside from these general qualitative considerations, some trace fossil features can potentially be related with specific palaeoenvironmental conditions, such as organic matter quality and patchiness (Fig. 6).

Scolicia was the only ichnogenus to show significant differences in size between sites, being larger on the abyssal hill (Table 2). Fluctuations in organic matter supply in muddy pelagic deposits have previously been related to ichnological features of *Scolicia* (Wetzel, 2008; Wetzel and Uchman, 2018). The abundance and size of *Scolicia* traces have been noted to increase with greater inputs of fresh nutrients emplaced by bottom currents (Miguez-Salas et al., 2021). The larger *Scolicia* traces on the hill may be related to the potentially greater amount of relatively labile organic matter supplied by enhanced near-bottom currents (Turnewitsch et al., 2015) (Fig. 6).

The record of "Mycellia"/*Trichichnus* intervals seemed to support the higher occurrence of food patches on the abyssal plain. "Mycellia"/*Trichichnus* has been interpreted to be produced by large sulphur-oxiding bacteria or mycelial fungi concentrated in monosulphide bands in the lower substratum levels, associated with organic patches upward (Löwemark et al., 2004; Virtasalo et al., 2010). Thus, its occurrence at different sediment depths (Fig. 2 section 11), mainly in the abyssal plain

setting, could reveal heterogeneous concentration of organic matter through the studied interval. The record of *Scolicia*-bearing horizons (Supplementary material 1 and 2) may also be related to localized organic matter patches, as no lateral continuity of these intervals was observed in nearby sections.

The occurrence of *Nereites* ichnofabrics is one of the few examples in ichnology where the relationship between oxygenation and food supply is thought to be relatively well understood (Wetzel, 2002, 2008). *Nereites* trace makers maintain a consistent distance relative to the redox boundary within the sediment column. The transition from oxic to anoxic conditions is usually characterized by high concentrations of microbial biomass on which the *Nereites* trace makers are inferred to feed. Thus, the *Nereites* tier in fossil ichnofabrics may reflect the position of the redox boundary (Wetzel, 2002, 2008). The coarse-grained sediments (reducing particle surface area) in abyssal hill surficial sediments has been suggested to be bigger than that of surrounding abyssal plains as a result of flow/hill interactions (Turnewitsch et al., 2015). This coarser sediment favour organic matter preservation within the sediment (i.e., more labile organic matter). On one hand, local dense ichnofabrics of *Nereites*, primarily observed on the hill (Fig. 4 sections 11 and 12), could indicate oxic/anoxic boundaries associated with past fluctuations of microbial biomass potentially related to winnowing and depositional events since near-bottom currents are rather discontinuous in time (Aller, 1989) (Fig. 6). On the other hand, the nearly absence of the ichnofabric of *Nereites* in the plain may be related with continuous favorable conditions (see discussion below) where the gradual upward migration of the burrowing community overprinted the ichnofabric of *Nereites*. However, both hypotheses remain speculative based on the obtained results.

In Cenozoic hemipelagic sediments, *Zoophycos* has mainly been related to quiescent conditions, and used to interpret energy variations, sedimentation rates, and food availability (Dorador et al., 2016; Löwemark, 2015; Löwemark and Schäfer, 2003; Löwemark and Werner, 2001). The bathymetric distribution of *Zoophycos* in modern deep-sea sediments suggests that the trace fossil is restricted to water depths greater than 1000 m, extending to at least 5000 m water depth (Löwemark and Werner, 2001; Rodríguez-Tovar et al., 2011). *Zoophycos* identification is usually straightforward because these structures appear as roughly parallel, sub-horizontal to inclined spreiten, which commonly traverse a whole core. The ethological interpretation of the *Zoophycos* trace maker is of the collection of food materials on the sediment surface and its storage at depth in the sediment to prevent oxidation and its use by other organisms (Löwemark and Schäfer, 2003). *Zoophycos* is typically present in intervals deposited at sedimentation rates of 5–20 cm kyr^{-1} (Dorador et al., 2016). When sedimentation rates are lower than 5 cm kyr^{-1} the exposure time of organic matter to oxygen becomes so long that essentially no organic matter is preserved within the sediment. It is therefore possible that the near absence of *Zoophycos* in the studied abyssal settings reflects both the rapid consumption of fresh organic matter by epibenthic megafauna (Bett et al., 2001) and its relatively complete oxidation as a result of low sediment accumulation rates at the Porcupine Abyssal Plain (Hinrichs et al., 2001).

4.3. From palaeo- to recent trace maker community

Our results indicate varying palaeoenvironmental histories for the abyssal hill and abyssal plain sites studied. The dominance of completely bioturbated sections together with no substantive changes in the trace fossil assemblage through the studied time interval suggest long-term maintenance of favorable conditions on the abyssal plain. It is likely that the abyssal plain trace maker community has not undergone a significant change in the last thousands of years (Fig. 6). The abyssal hill profiles appear to record a more dynamic evolution. The bioturbation increasing upward sequences may be related to more favorable conditions in recent times on the abyssal hill (Fig. 6). This bioturbation upward sequences in the abyssal hill and the more favorable conditions

hypothesis is consistent with the evolution of the Ba/Al (i.e., a common paleoproductivity proxy) in the first 40 cm of the gravity cores (Miguez Salas, 2024). Ba/Al profiles show an increasing trend in the hill while having a flat evolution in the plain (see Miguez Salas, 2024). The trace fossil assemblage observed in the upper half of the sections was not substantially different from that characterized on the abyssal plain. Specific trace fossil features (e.g., graphoglyptids, bigger *Scolicia*) can potentially be related with variations in grain size and organic matter degradation that result from bottom current interactions with the hill topography. Overall, it seems likely that the bioturbation increasing upward sequences in the hill represent a trace maker community that has undergone a significant change in the last thousands of years.

The subsampling of each box core in a 5 × 5 grid was designed with the idea of approaching the lateral distribution/continuity of trace fossils. The observed intervals associated with specific ichnotaxa (e.g., "Mycellia"/*Trichichnus* or *Scolicia*) may be related to temporal and/or local conditions, e.g., occurrence of organic matter patches. The occurrence of organic matter patches on the seafloor, and the foraging motions of the benthic fauna to consume these patches, have been previously approached based on their traces (Durden et al., 2020a; Kaufmann and Smith, 1997). Here we have an absence of lateral continuity in these intervals across adjacent sections, suggesting that these trace fossil features are not associated with large-scale spatial changes. This is not unexpected, heterogeneous nutrient distribution is widely observed in modern seafloors (see Iken et al. (2001) as a representative case in the study area). For example, small-scale distribution of organic matter patches control echinoid (i.e., *Scolicia* trace makers) feeding movement patterns rather than the bulk amount of nutrients (Miguez-Salas et al., 2022). In short, this spatio-temporal patchwork emerges from the seasonal sedimentation patterns, the interplay between bottom currents and topography leading to local resuspension (Lampitt, 1985), and the spatial variability in the activity of micro- and meiofauna among other factor (Patching and Eardly, 1997).

Considering the palaeoichnological analysis of deep-sea sediments generally, in well-oxygenated environments influenced by bottom currents (>5 cm s^{-1}), organic matter availability / supply may be a major limiting environmental factor for specific trace makers. In particular, there is a need to consider three aspects related to organic matter availability: quantity (deposition/erosion/burial), quality (freshness/ decomposition), and spatial distribution (homogeneous/patchy). The close relationship between depositional processes and the local physical/chemical conditions affecting the trace maker community must also be considered (e.g., hydrodynamics driving variations in grain size distributions). These general considerations are consistent with recent studies evidencing the influence of hydrodynamic energy and seafloor heterogeneity in food supply in the control of both past and present trace maker communities (Dorador et al., 2021, Dorador et al., 2019; Miguez-Salas et al., 2021, Miguez-Salas et al., 2020). Therefore, occasional changes on trace fossil assemblages associated with significant spatial-temporal environmental variations (e.g., sea level changes, basin scale de-oxygenation events), must be interpreted with caution considering the deep-sea environmental and topographical heterogeneity.

Our results highlight the complexity of the deep-sea environment, demonstrating that small lateral variation in bioturbated sedimentary assemblages appear even within the same box core (i.e., at a metrical scale). Above all, our study has shown that even small-scale local topographic variations in the deep sea can produce substantial changes in the trace maker communities. During the last decades, the improvement and increase in mapping surveys of the seafloor have revealed the heterogeneity of the deep sea (Riehl et al., 2020). Recent estimates suggest that globally, there are around 25 million hill/mountain-scale seafloor features taller than 100 m (Wessel et al., 2010), that may extend over 41 % of the ocean floor (Harris, 2014). Although there are still uncertainties, it seems reasonable to assume that a very significant part of the global deep-sea floor has a varied topography. Thus, seafloor landscapes and their influence on trace fossil diversity may have been overlooked and requires more attention when conducting palaeoenvironmental reconstructions. To conclude, our results indicate both a need for further study of this complexity and the need for caution in interpreting fossil and modern systems without reference to local environmental conditions, e.g., seafloor topography.

CRediT authorship contribution statement

Olmo Miguez-Salas: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Francisco J. Rodríguez-Tovar:** Writing – review & editing, Writing – original draft, Investigation, Formal analysis. **Javier Dorador:** Writing – review & editing, Methodology, Formal analysis. **Brian J. Bett:** Writing – review & editing, Validation, Resources. **Miros S.J. Charidemou:** Writing – review & editing, Visualization, Formal analysis, Data curation. **Jennifer M. Durden:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition.

Declaration of competing interest

Olmo Miguez Salas reports financial support was provided by Spain Ministry of Science and Innovation. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi. org/10.1016/j.palaeo.2024.112524.

References

Aller, J.Y., 1989. Quantifying sediment disturbance by bottom currents and its effect on benthic communities in a deep-sea western boundary zone. Deep Sea Res. Part A Oceanogr. Res. Pap. 36, 901–934. https://doi.org/10.1016/0198-0149(89)90035-6.

Baldwin, C.T., McCave, I.N., 1999. Bioturbation in an active deep-sea area: implications for models of trace fossil tiering. PALAIOS 14, 375. https://doi.org/10.2307/3515463.

Baucon, A., Bednarz, M., Dufour, S., Felletti, F., Malgesini, G., Neto de Carvalho, C., Niklas, K.J., Wehrmann, A., Batstone, R., Bernardini, F., Briguglio, A., Cabella, R., Cavalazzi, B., Ferretti, A., Zanzerl, H., McIlroy, D., 2020. Ethology of the trace fossil Chondrites: form, function and environment. Earth Sci. Rev. 202, 102989. https://doi.org/10.1016/j.earscirev.2019.102989.

Bell, J.B., Jones, D.O.B, Alt, C.H.S., 2013. Lebensspuren of the Bathyal Mid-Atlantic Ridge. Deep-Sea Res. II Top. Stud. Oceanogr. 98, 341–351. https://doi.org/10.1016/j.dsr2.2012.09.004. ECOMAR: Ecosystems of the Mid-Atlantic Ridge at the Sub-Polar Front and Charlie-Gibbs Fracture Zone.

Berger, W.H., Ekdale, A.A., Bryant, P.P., 1979. Selective preservation of burrows in deep-sea carbonates. Mar. Geol. 32, 205–230. https://doi.org/10.1016/0025-3227(79)90065-3.

Bertling, M., Buatois, L.A., Knaust, D., Laing, B., Mángano, M.G., Meyer, N., Mikuláš, R., Minter, N.J., Neumann, C., Rindsberg, A.K., Uchman, A., Wisshak, M., 2022. Names for trace fossils 2.0: theory and practice in ichnotaxonomy. Lethaia 55, 1–19. https://doi.org/10.18261/let.55.3.3.

Bett, B.J., Malzone, M.G., Narayanaswamy, B.E., Wigham, B.D., 2001. Temporal variability in phytodetritus and megabenthic activity at the seabed in the deep Northeast Atlantic. Prog. Oceanogr. 50, 349–368. https://doi.org/10.1016/S0079-6611(01)00066-0. High resolution temporal and spatial study of the benthic biology and geochemistry of a North-Eastern Atlantic abyssal locality (BENGAL).

Boudreau, B.P., 1998. Mean mixed depth of sediments: the wherefore and the why. Limnol. Oceanogr. 43, 524–526. https://doi.org/10.4319/lo.1998.43.3.0524.

Brandt, A., Chen, C., Tandberg, A.H.S., Miguez-Salas, O., Sigwart, J.D., 2023. Complex sublinear burrows in the deep sea may be constructed by amphipods. Ecol. Evol. 13, e9867. https://doi.org/10.1002/ece3.9867.

Bromley, R.G., Ekdale, A.A., 1984. *Chondrites*: a trace fossil indicator of anoxia in sediments. Science 224, 872–874. https://doi.org/10.1126/science.224.4651.872.

Bromley, R.G., Frey, R.W., 1974. Redescription of the trace fossil *Gyrolithes* and taxonomic evaluation of *Thalassinoides*, *Ophiomorpha* and *Spongeliomorpha*. Bull. Geol. Soc. Den. 23.

Buatois, L.A., Mángano, M.G., Carmona, N.B., 2023. *Scolicia*, ichnotaxonomic practices, and the limits of behavioural convergence. Ichnos 30, 338–361. https://doi.org/10.1080/10420940.2024.2325468.

Chamberlain, C.K., 1971. Morphology and ethology of trace fossils from the Ouachita Mountains, Southeast Oklahoma. J. Paleontol. 45, 212–246.

Dorador, J., Rodríguez-Tovar, F.J., 2018. High-resolution image treatment in ichnological core analysis: initial steps, advances and prospects. Earth Sci. Rev. 177, 226–237. https://doi.org/10.1016/j.earscirev.2017.11.020.

Dorador, J., Wetzel, A., Rodríguez-Tovar, F.J., 2016. *Zoophycos* in deep-sea sediments indicates high and seasonal primary productivity: ichnology as a proxy in palaeoceanography during glacial–interglacial variations. Terra Nova 28, 323–328. https://doi.org/10.1111/ter.12224.

Dorador, J., Rodríguez-Tovar, F.J., Mena, A., Francés, G., 2019. Lateral variability of ichnological content in muddy contourites: weak bottom currents affecting organisms' behavior. Sci. Rep. 9, 17713. https://doi.org/10.1038/s41598-019-54246-3.

Dorador, J., Rodríguez-Tovar, F.J., Mena, A., Francés, G., 2021. Deep-sea bottom currents influencing tracemaker community: an ichnological study from the NW Iberian margin. Mar. Geol. 437, 106503. https://doi.org/10.1016/j.margeo.2021.106503.

Dorador, J., Rodríguez-Tovar, F.J., Charidemou, M.S.J., Miguez-Salas, O., 2024. Computed Laminography for the study of biogenic structures in sediment cores: a step between two- and three-dimensional imaging. Mar. Geol. 470, 107267. https://doi.org/10.1016/j.margeo.2024.107267.

Durden, J.M., Bett, B.J., Jones, D.O.B., Huvenne, V.A.I., Ruhl, H.A., 2015. Abyssal hills – hidden source of increased habitat heterogeneity, benthic megafaunal biomass and diversity in the deep sea. Prog. Oceanogr. 137, 209–218. https://doi.org/10.1016/j.pocean.2015.06.006.

Durden, J.M., Bett, B.J., Huffard, C.L., Pebody, C., Ruhl, H.A., Smith, K.L., 2020a. Response of deep-sea deposit-feeders to detrital inputs: a comparison of two abyssal time-series sites. Deep-Sea Res. II Top. Stud. Oceanogr. 173, 104677. https://doi.org/10.1016/j.dsr2.2019.104677.

Durden, J.M., Bett, B.J., Ruhl, H.A., 2020b. Subtle variation in abyssal terrain induces significant change in benthic megafaunal abundance, diversity, and community structure. Prog. Oceanogr. 186, 102395. https://doi.org/10.1016/j.pocean.2020.102395.

Ewing, M., Davis, R.A., 1967. Lebensspuren photographed on the ocean floor. In: Deep-Sea Photography. John Hopkins Press, Baltimore.

Frey, R.W., Howard, J.D., 1981. *Conichnus* and *Schaubcylindrichnus*: redefined trace fossils from the upper cretaceous of the Western Interior. J. Paleontol. 55, 800–804.

Frey, R.W., Pemberton, S.G., Saunders, T.D.A., 1990. Ichnofacies and bathymetry: a passive relationship. J. Paleontol. 64, 155–158. https://doi.org/10.1017/S0022336000042372.

Fu, S., Werner, F., 2000. Distribution, ecology and taphonomy of the organism trace, Scolicia, in Northeast Atlantic deep-sea sediments. Palaeogeogr. Palaeoclimatol. Palaeoecol. 156, 289–300. https://doi.org/10.1016/S0031-0182(99)00146-7.

Gage, J.D., Bett, B.J., 2005. Deep-sea benthic sampling. In: Methods for the Study of Marine Benthos. John Wiley & Sons Ltd, pp. 273–325. https://doi.org/10.1002/9780470995129.ch7.

Gage, J., Tyler, P.A., 1991. Deep-Sea Biology: A Natural History of Organisms at the Deep-Sea Floor. Cambridge University Press.

González-Lanchas, A., Dorador, J., Rodríguez-Tovar, F.J., Sierro, F.J., Flores, J.-A., 2022. Trace fossil characterization during termination V and MIS 11 at the western Mediterranean: connection between surface conditions and deep environment. Mar. Geol. 446, 106774. https://doi.org/10.1016/j.margeo.2022.106774.

Harris, P.T., 2014. Shelf and deep-sea sedimentary environments and physical benthic disturbance regimes: a review and synthesis. Mar. Geol. 353, 169–184. https://doi.org/10.1016/j.margeo.2014.03.023.

Hartman, S.E., 2022. RRS James Cook Cruise 231, 01 May-19 May 2022 (Time-series studies at the Porcupine Abyssal Plain Sustained Observatory).

Hartman, S.E., Bett, B.J., Durden, J.M., Henson, S.A., Iversen, M., Jeffreys, R.M., Horton, T., Lampitt, R., Gates, A.R., 2021. Enduring science: three decades of observing the Northeast Atlantic from the Porcupine Abyssal Plain Sustained Observatory (PAP-SO). Prog. Oceanogr. 191, 102508. https://doi.org/10.1016/j.pocean.2020.102508.

Heard, T.G., Pickering, K.T., 2008. Trace fossils as diagnostic indicators of deep-marine environments, Middle Eocene Ainsa-Jaca basin, Spanish Pyrenees. Sedimentology 55, 809–844. https://doi.org/10.1111/j.1365-3091.2007.00922.x.

Hinrichs, J., Schnetger, B., Schale, H., Brumsack, H.-J., 2001. A high resolution study of NE Atlantic sediments at station Bengal: geochemistry and early diagenesis of Heinrich layers. Mar. Geol. 177, 79–92. https://doi.org/10.1016/S0025-3227(01)00125-6.

Iken, K., Brey, T., Wand, U., Voigt, J., Junghans, P., 2001. Food web structure of the benthic community at the Porcupine Abyssal Plain (NE Atlantic): a stable isotope analysis. Prog. Oceanogr. 50, 383–405. https://doi.org/10.1016/S0079-6611(01)00062-3. High resolution temporal and spatial study of the benthic biology and geochemistry of a North-Eastern Atlantic abyssal locality (BENGAL).

Kaufmann, R.S., Smith, K.L., 1997. Activity patterns of mobile epibenthic megafauna at an abyssal site in the eastern North Pacific: results from a 17-month time-lapse photographic study. Deep-Sea Res. I Oceanogr. Res. Pap. 44, 559–579. https://doi.org/10.1016/S0967-0637(97)00005-8.

Keighley, D.G., Pickerill, R.K., 1995. The ichnotaxa *Palaeophycus* and *Planolites*: historical perspectives and recommendations. Ichnos 3, 301–309. https://doi.org/10.1080/10420949509386400.

Knaust, D., 2017. Atlas of Trace Fossils in Well Core: Appearance, Taxonomy and Interpretation. Springer.

Kotake, N., 1991. Packing process for the filling material in *Chondrites*. Ichnos 1, 277–285. https://doi.org/10.1080/10420949109386362.

Kristensen, E., Penha-Lopes, G., Delefosse, M., Valdemarsen, T., Quintana, C., Banta, G., 2012. What is bioturbation? The need for a precise definition for fauna in aquatic sciences. Mar. Ecol. Prog. Ser. 446, 285–302. https://doi.org/10.3354/meps09506.

Lampitt, R.S., 1985. Evidence for the seasonal deposition of detritus to the deep-sea floor and its subsequent resuspension. Deep Sea Res. Part A Oceanogr. Res. Pap. 32, 885–897. https://doi.org/10.1016/0198-0149(85)90034-2.

Langenkämper, D., Zurowietz, M., Schoening, T., Nattkemper, T.W., 2017. BIIGLE 2.0 - browsing and annotating large marine image collections. Front. Mar. Sci. 4.

Löwemark, L., 2015. Testing ethological hypotheses of the trace fossil *Zoophycos* based on Quaternary material from the Greenland and Norwegian Seas. Palaeogeogr. Palaeoclimatol. Palaeoecol. 425, 1–13. https://doi.org/10.1016/j.palaeo.2015.02.025.

Löwemark, L., Nara, M., 2010. Morphology, ethology and taxonomy of the ichnogenus *Schaubcylindrichnus*: notes for clarification. Palaeogeogr. Palaeoclimatol. Palaeoecol. 297, 184–187. https://doi.org/10.1016/j.palaeo.2010.07.028.

Löwemark, L., Schäfer, P., 2003. Ethological implications from a detailed X-ray radiograph and 14C study of the modern deep-sea zoophycos. Palaeogeogr. Palaeoclimatol. Palaeoecol. 192, 101–121. https://doi.org/10.1016/S0031-0182(02)00681-8. New Interpretations of Complex Trace Fossils.

Löwemark, L., Werner, F., 2001. Dating errors in high-resolution stratigraphy: a detailed X-ray radiograph and AMS-14C study of *Zoophycos* burrows. Mar. Geol. 177, 191–198. https://doi.org/10.1016/S0025-3227(01)00167-0.

Löwemark, L., Schönfeld, J., Werner, F., Schäfer, P., 2004. Trace fossils as a paleoceanographic tool: evidence from late quaternary sediments of the southwestern Iberian margin. Mar. Geol. 204, 27–41. https://doi.org/10.1016/S0025-3227(03)00351-7.

Meysman, F., Middelburg, J., Heip, C., 2006. Bioturbation: a fresh look at Darwin's last idea. Trends Ecol. Evol. 21, 688–695. https://doi.org/10.1016/j.tree.2006.08.002.

Miguez-Salas, O., Huffard, C.L., Smith, K.L., McGill, P.R., Rodríguez-Tovar, F.J., 2020. Faunal assemblage changes, bioturbation and benthic storms at an abyssal station in the northeastern Pacific. Deep-Sea Res. I Oceanogr. Res. Pap. 160, 103277. https://doi.org/10.1016/j.dsr.2020.103277.

Miguez-Salas, O., Rodríguez-Tovar, F.J., de Weger, W., 2021. The late Miocene Rifian corridor as a natural laboratory to explore a case of ichnofacies distribution in ancient gateways. Sci. Rep. 11, 4198. https://doi.org/10.1038/s41598-021-83820-x.

Miguez-Salas, O., Vardaro, M.F., Rodríguez-Tovar, F.J., Pérez-Claros, J.A., Huffard, C.L., 2022. Deep-sea echinoid trails and seafloor nutrient distribution: present and past implications. Front. Mar. Sci. 9, 903864. https://doi.org/10.3389/fmars.2022.903864.

Miguez Salas, O., 2024. Three gravity core XRF data from the Porcupine Abyssal Plain [Data set]. Zenodo. https://doi.org/10.5281/zenodo.10879950.

Miguez-Salas, O., Bett, B.J., Torres-Montilla, S., Rodríguez-Tovar, F.J., Durden, J.M., 2023a. Comparison of rosette-shape traces in abyssal terrains: environmental and faunal implications. Deep-Sea Res. I Oceanogr. Res. Pap. 197, 104051. https://doi.org/10.1016/j.dsr.2023.104051.

Miguez-Salas, O., Rodríguez-Tovar, F.J., Ekdale, A.A., Kaiser, S., Brandt, A., Gooday, A.J., 2023b. Northernmost (Subarctic) and deepest record of *Paleodictyon*:

paleoecological and biological implications. Sci. Rep. 13, 7181. https://doi.org/10.1038/s41598-023-34050-w.

Miguez-Salas, O., Brandt, A., Knauber, H., Riehl, T., 2024a. Diversity and density relationships between lebensspuren and tracemaking organisms: a study case from abyssal Northwest Pacific. Biogeosciences 21, 641–655. https://doi.org/10.5194/bg-21-641-2024.

Miguez-Salas, O., Saeedi, H., Brandt, A., Riehl, T., 2024b. Seafloor bioturbation intensity on the deep sea: more complex than organic matter. Limnol. Oceanogr. 69, 1857–1869. https://doi.org/10.1002/lno.12632.

Morris, K.J., Bett, B.J., Durden, J.M., Benoist, N.M.A., Huvenne, V.A.I., Jones, D.O.B., Robert, K., Ichino, M.C., Wolff, G.A., Ruhl, H.A., 2016. Landscape-scale spatial heterogeneity in phytodetrital cover and megafauna biomass in the abyss links to modest topographic variation. Sci. Rep. 6, 34080. https://doi.org/10.1038/srep34080.

Myrow, P.M., 1995. *Thalassinoides* and the enigma of early paleozoic open-framework burrow systems. Palaios 10, 58–74. https://doi.org/10.2307/3515007.

Patching, J.W., Eardly, D., 1997. Bacterial biomass and activity in the deep waters of the eastern Atlantic—evidence of a barophilic community. Deep-Sea Res. I Oceanogr. Res. Pap. 44, 1655–1670. https://doi.org/10.1016/S0967-0637(97)00040-X.

Pemberton, S.G., Frey, R.W., 1982. Trace fossil nomenclature and the *Planolites-Palaeophycus* dilemma. J. Paleontol. 843–881.

Przeslawski, R., Dundas, K., Radke, L., Anderson, T.J., 2012. Deep-sea lebensspuren of the Australian continental margins. Deep-Sea Res. I Oceanogr. Res. Pap. 65, 26–35. https://doi.org/10.1016/j.dsr.2012.03.006.

Rabouille, C., Stahl, H., Bassinot, F., Tengberg, A., Brunnegard, J., Hall, P., Kiriakoulakis, K., Reyss, J.-L., Dezileau, L., Crassous, P., Roos, P., Lampitt, R.S., 2001. Imbalance in the carbonate budget of surficial sediments in the North Atlantic Ocean: variations over the last millenium? Prog. Oceanogr. 50, 201–221. https://doi.org/10.1016/S0079-6611(01)00054-4. High Resolution Temporal and Spatial Study of the Benthic Biology and Geochemistry of a North-Eastern Atlantic Abyssal Locality (BENGAL).

Ramirez-Llodra, E., Brandt, A., Danovaro, R., De Mol, B., Escobar, E., German, C.R., Levin, L.A., Martinez Arbizu, P., Menot, L., Buhl-Mortensen, P., Narayanaswamy, B. E., Smith, C.R., Tittensor, D.P., Tyler, P.A., Vanreusel, A., Vecchione, M., 2010. Deep, diverse and definitely different: unique attributes of the world's largest ecosystem. Biogeosciences 7, 2851–2899. https://doi.org/10.5194/bg-7-2851-2010.

Rex, M.A., Etter, R.J., Morris, J.S., Crouse, J., McClain, C.R., Johnson, N.A., Stuart, C.T., Deming, J.W., Thies, R., Avery, R., 2006. Global bathymetric patterns of standing stock and body size in the deep-sea benthos. Mar. Ecol. Prog. Ser. 317, 1–8. https://doi.org/10.3354/meps317001.

Riehl, T., Wölfl, A.-C., Augustin, N., Devey, C.W., Brandt, A., 2020. Discovery of widely available abyssal rock patches reveals overlooked habitat type and prompts rethinking deep-sea biodiversity. Proc. Natl. Acad. Sci. 117, 15450–15459. https://doi.org/10.1073/pnas.1920706117.

Rodríguez-Tovar, F.J., 2022. Ichnological analysis: a tool to characterize deep-marine processes and sediments. Earth Sci. Rev. 228, 104014. https://doi.org/10.1016/j.earscirev.2022.104014.

Rodríguez-Tovar, F.J., Dorador, J., 2014. Ichnological analysis of pleistocene sediments from the IODP Site U1385 "Shackleton Site" on the Iberian margin: approaching paleoenvironmental conditions. Palaeogeogr. Palaeoclimatol. Palaeoecol. 409, 24–32. https://doi.org/10.1016/j.palaeo.2014.04.027.

Rodríguez-Tovar, F.J., Uchman, A., Payros, A., Orue-Etxebarria, X., Apellaniz, E., Molina, E., 2010. Sea-level dynamics and palaeoecological factors affecting trace fossil distribution in Eocene turbiditic deposits (Gorrondatxe section, N Spain). Palaeogeogr. Palaeoclimatol. Palaeoecol. 285, 50–65. https://doi.org/10.1016/j.palaeo.2009.10.022.

Rodríguez-Tovar, F.J., Löwemark, L., Pardo-Igúzquiza, E., 2011. Zoophycos cyclicity during the last 425ka in the northeastern South China Sea: evidence for monsoon fluctuation at the Milankovitch scale. Palaeogeogr. Palaeoclimatol. Palaeoecol. 305, 256–263. https://doi.org/10.1016/j.palaeo.2011.03.006.

Rodríguez-Tovar, F.J., Dorador, J., Grunert, P., Hodell, D., 2015. Deep-sea trace fossil and benthic foraminiferal assemblages across glacial Terminations 1, 2 and 4 at the "Shackleton Site" (IODP Expedition 339, Site U1385). Glob. Planet. Chang. 133, 359–370. https://doi.org/10.1016/j.gloplacha.2015.05.003.

Rodríguez-Tovar, F.J., Miguez-Salas, O., Duarte, L.V., 2017. Toarcian oceanic anoxic event induced unusual behaviour and palaeobiological changes in *Thalassinoides* tracemakers. Palaeogeogr. Palaeoclimatol. Palaeoecol. 485, 46–56. https://doi.org/10.1016/j.palaeo.2017.06.002.

Rodríguez-Tovar, F.J., Hernández-Molina, F.J., Hüneke, H., Llave, E., Stow, D., 2019. Contourite facies model: improving contourite characterization based on the ichnological analysis. Sediment. Geol. 384, 60–69. https://doi.org/10.1016/j.sedgeo.2019.03.010.

Rodríguez-Tovar, F.J., Miguez-Salas, O., Hernández-Molina, F.J., Hüneke, H., 2020. First record of graphoglyptids in cyprus: indicative presence of turbidite deposits at the Pakhna formation. Ichnos 27, 237–243. https://doi.org/10.1080/10420940.2019.1688801.

Seilacher, A., 1967a. Bathymetry of trace fossils. Mar. Geol. 5, 413–428. https://doi.org/10.1016/0025-3227(67)90051-5. Depth indicators in marine sedimentary environments.

Seilacher, A., 1967b. Fossil behavior. Sci. Am. 217, 72–83.

Seilacher, A., 1977. Pattern analysis of *Paleodictyon* and related trace fossils. Trace fossils, 2. Geol. J. 9, 289–334.

Simon-Lledó, E., Bett, B.J., Huvenne, V.A.I., Schoening, T., Benoist, N.M.A., Jones, D.O.B., 2019. Ecology of a polymetallic nodule occurrence gradient: implications for deep-sea mining. Limnol. Oceanogr. 64, 1883–1894. https://doi.org/10.1002/lno.11157.

Smith, C.R., Rabouille, C., 2002. What controls the mixed-layer depth in deep-sea sediments? The importance of POC flux. Limnol. Oceanogr. 47, 418–426. https://doi.org/10.4319/lo.2002.47.2.0418.

Team, R.C. (2020). RA language and environment for statistical computing, R Foundation for Statistical. Computing.

Trauth, M.H., Sarnthein, M., Arnold, M., 1997. Bioturbational mixing depth and carbon flux at the seafloor. Paleoceanography 12, 517–526. https://doi.org/10.1029/97PA00722.

Turnewitsch, R., Lahajnar, N., Haeckel, M., Christiansen, B., 2015. An abyssal hill fractionates organic and inorganic matter in deep-sea surface sediments. Geophys. Res. Lett. 42, 7663–7672. https://doi.org/10.1002/2015GL065658.

Uchman, A., 1995. Taxonomy and palaeoecology of flysch trace fossils: the Marnoso-arenacea formation and associated facies (Miocene, Northern Apennines, Italy). Beringeria 15, 3.

Uchman, A., 2003. Trends in diversity, frequency and complexity of graphoglyptid trace fossils: evolutionary and palaeoenvironmental aspects. Palaeogeogr. Palaeoclimatol. Palaeoecol. 192, 123–142. https://doi.org/10.1016/S0031-0182(02)00682-X. New Interpretations of Complex Trace Fossils.

Uchman, A., Wetzel, A., 2011. Deep-sea ichnology: the relationships between depositional environment and endobenthic organisms. In: Developments in Sedimentology. Elsevier, pp. 517–556. https://doi.org/10.1016/B978-0-444-53000-4.00008-1.

Virtasalo, J.J., Löwemark, L., Papunen, H., Kotilainen, A.T., Whitehouse, M.J., 2010. Pyritic and baritic burrows and microbial filaments in postglacial lacustrine clays in the Northern Baltic Sea. JGS 167, 1185–1198. https://doi.org/10.1144/0016-76492010-017.

Vossler, S.M., Pemberton, S.G., 1988a. Skolithos in the upper cretaceous cardium formation: an ichnofossil example of opportunistic ecology. Lethaia 21, 351–362. https://doi.org/10.1111/j.1502-3931.1988.tb01763.x.

Vossler, S.M., Pemberton, S.G., 1988b. Superabundant Chondrites: a response to storm buried organic material? Lethaia 21, 94. https://doi.org/10.1111/j.1502-3931.1988.tb01757.x.

Wessel, P., Sandwell, D.T., Kim, S.-S., 2010. The global seamount census. Oceanography 23, 24–33.

Wetzel, A., 2002. Modern *Nereites* in the South China Sea—ecological association with redox conditions in the sediment. PALAIOS 17, 507–515. https://doi.org/10.1669/0883-1351.

Wetzel, A., 2008. Recent bioturbation in the deep South China Sea: a uniformitarian ichnologic approach. PALAIOS 23, 601–615. https://doi.org/10.2110/palo.2007.p07-096r.

Wetzel, A., Uchman, A., 2018. The former presence of organic matter caused its later absence: burn-down of organic matter in oceanic red beds enhanced by bioturbation (Eocene Variegated Shale, Carpathians). Sedimentology 65, 1504–1519. https://doi.org/10.1111/sed.12436.

Yang, Z., Qian, Q., Chen, M., Zhang, R., Yang, W., Zheng, M., Qiu, Y., 2020. Enhanced but highly variable bioturbation around seamounts in the Northwest Pacific. Deep-Sea Res. I Oceanogr. Res. Pap. 156, 103190. https://doi.org/10.1016/j.dsr.2019.103190.

Zhang, S., Solan, M., Tarhan, L., 2024. Global distribution and environmental correlates of marine bioturbation. Curr. Biol. 34, 2580–2593.e4. https://doi.org/10.1016/j.cub.2024.04.065.