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RESEARCH ARTICLE

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Key Points:

- Detailed ichnological analysis through the Heinrich Event 4 (H4)
- The effect of H4 on benthic habitats varies greatly at a local spatial scale (<20 km)
- Seafloor heterogeneity (hill vs. abyssal plains) controlled tracemaker extinction

Supporting Information:

Supporting Information may be found in the online version of this article.

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The Variable Impact of Heinrich Events on the Benthic Environment of the Porcupine Abyssal Plain

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Abstract Heinrich events (HEs) are Pleistocene climate disturbances caused by massive freshwater discharges from the Laurentide Ice Sheet via the Hudson Strait. They appear in marine sediments as layers of ice-rafted detritus (IRD) and significantly impact the benthic environment. While many studies focus on microorganisms, macrobenthic data from ichnological analysis are limited. HEs affect macrobenthic tracemaker communities in various ways, though a general pattern of gradual recovery is observed. However, regional factors strongly influence the environmental effects of HEs on tracemaker communities. In this study, we aim to go one step further and address the influence of these factors on the benthic realm at a short spatial scale. To this end, we investigate the ichnological characteristics of Heinrich Event 4 (H4) together with its geochemical data from three gravity cores taken less than 20 km apart in the Porcupine Abyssal Plain (NE Atlantic). One core is from a small abyssal hill (60 m high), and two from nearby abyssal plains. In the abyssal plains, H4 and subsequent IRD deposition led to the disappearance of trace fossils, with no gradual recovery—unlike previous findings. In contrast, the hill shows rapid recovery after IRD deposition. Geochemical data shows that productivity increased due to H4, which led to low oxygen conditions. We hypothesize that bottom currents along the hill flank improved seafloor oxygenation, enabling quicker recovery, while the plains remained poorly oxygenated. This study underscores how even minor seafloor topography can enhance the resilience of macrobenthic tracemaker communities during paleoclimatic events.

Plain Language Summary Heinrich events were episodes during glacial periods when massive iceberg discharges were released from the Laurentide Ice Sheet (North America) into the North Atlantic Ocean. These events altered the conditions of the deep seafloor and impacted the benthic fauna, including tracemaker communities (i.e., those that produce trace fossils). This study examined Heinrich Event 4 using three gravity cores, taken from slightly different seafloor settings less than 20 km apart in the Porcupine Abyssal Plain (NE Atlantic): two abyssal plains and a 60 m high hill. On the abyssal plains, the climate event caused the tracemaker communities to disappear and they did not recover gradually as expected. However, on the hill, the tracemaker communities returned quickly after the event. We hypothesize that stronger currents around the hill brought in more oxygen, facilitating faster recovery of life. This study highlights how even small differences in deep-sea topography can strongly influence the ability of benthic fauna to cope with major climate changes.

1. Introduction

Heinrich events (HEs) were climatic phenomena during the Pleistocene, driven by massive freshwater discharges from the Laurentide Ice Sheet through the Hudson Strait into the North Atlantic Ocean (e.g., Heinrich, 1988; Hemming, 2004; Hodell et al., 2017). HEs are believed to have significantly disrupted the Atlantic Meridional Overturning Circulation (AMOC) and the formation of North Atlantic Deep Water (NADW) (Max et al., 2022). The freshwater influx is thought to have repeatedly weakened AMOC (Zhou et al., 2021). Alternatively, subsurface warming has been suggested as a potential trigger for destabilizing the Laurentide Ice Sheet, leading to major calving episodes (Max et al., 2022). HEs are recorded in sedimentary deposits as distinct layers of ice-rafted detritus (IRD), known as Heinrich layers (HLs). These IRD layers are usually interbedded with fine-grained deep-sea sediments between 40° and 55°N, in an area of the North Atlantic known as the Ruddiman IRD Belt (Andrews & Voelker, 2018). The thickness of these IRD layers generally decreases from west to east, indicating a North American source (Andrews & Voelker, 2018). HLs deposition is reflected by significant geochemical variations

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that have served as markers for HEs. In particular, increased fluxes of terrigenous material resulted not only in increased concentration of detrital elements but also in enhanced preservation of organic carbon leading to oxygen-depleted conditions (Hinrichs et al., 2001) and a distinct composition of redox-sensitive elements. In summary, HEs are undoubtedly one of the most studied events in marine geology in recent decades, but some aspects are still poorly understood; the interpretation of palaeoenvironmental conditions and changes associated with these events pose a challenge, especially at the time of understanding how spatial heterogeneity may control the global effect of these events on benthic communities, where the dominant organisms feed on and burrow in the sediment (Jumars & Wheatcroft, 1989).

Ichnology serves as a tool in palaeoenvironmental studies, including paleoceanography and paleoclimatology, by providing data essential for interpreting depositional and ecological parameters such as hydrodynamic energy, oxygen levels, sedimentation rates, and nutrient availability (Buatois & Mángano, 2011). Its usefulness in studying the impact of HEs on tracemaker macrobenthic communities has been demonstrated in previous studies (Baas et al., 1997, 1998; Löwemark et al., 2004; Rodríguez-Tovar et al., 2019, 2020). Baas et al. (1998) observed that burrowing organisms react sensitively to variations in the depth of the redox boundary in near-surface sediments, which are associated with a significant decrease in bottom-water oxygenation during Heinrich events. Löwemark et al. (2004) observed no significant changes in ichnocoenosis in connection with H2 and 3 while the ichnofabric of H1 consisted almost entirely of *Chondrites*. Rodríguez-Tovar et al. (2020) observed that during the H1, regional variations (within a 100 km length transect) in the Galicia Interior Basin exerted an impact on the benthic habitat. These authors identified different patterns of extinction and recovery depending on the location in the basin (i.e., Continental slope vs. Galicia Interior Basin vs. East flank Galician bank). These results suggest that HEs can have a wide range of effects on the tracemaker community. This highlights the need for more studies to understand extinction and recovery patterns, or the absence thereof. Moreover, understanding the scale at which seafloor heterogeneity becomes significant is crucial for assessing spatial and temporal changes in both past and future tracemaker communities facing palaeo-climatic events.

This study aims to examine the effects of seafloor heterogeneity on macrobenthic tracemaker communities during HEs at a much smaller spatial scale in the deep sea (<20 km). To this end, we selected the Porcupine Abyssal Plain Sustained Observatory (PAP-SO) where hydrodynamic conditions are responsible for benthic megafaunal composition (e.g., density, biomass) (Durden et al., 2020). The reason for selecting PAP-SO is threefold. (a) PAP-SO is a long-running time series site in the Northeast Atlantic that has been collecting benthic environmental data since 1985 (Hartman et al., 2021). (b) The PAP-SO has several abyssal hills that creates notable environmental variability at the targeted spatial scale (see Section 2) (Durden et al., 2015; Morris et al., 2016). (c) In the PAP-SO, Hinrich et al. (2001) identified a pronounced ice-rafted detritus layer related to H4, as well as two less pronounced layers, H1 and H2. They found no clear evidence of H3 or H5. Thus, to investigate the effects of seafloor heterogeneity on macrobenthic tracemaker communities during HEs, we compare gravity cores from three different topographic areas less than 20 km apart: (a) a flank of a small abyssal hill (around 60 m elevation above the surrounding plain), (b) an abyssal plain surrounded by hills and seamounts (2 km apart from the hill gravity core), and (c) an open abyssal plain (10 km apart from the hill) (Figure 1). Similar to Hinrich et al. (2001), the results of our gravity cores indicate that H4 is the only HE with a clearly identifiable ice-rafted detritus layer and geochemical signal across the three study areas. Thus, our objectives regarding H4 are to: (a) compare trace fossil assemblages between hill and plain environments during pre-, syn- and post-ice detrital phases associated with H4; (b) correlate ichnological characteristics with environmental factors reconstructed by using geochemical proxies; and (c) infer past environmental changes associated with H4 based on the distribution of specific trace fossils. Lastly, we examine how spatial heterogeneity may influence future tracemaker communities during freshwater discharges in view of future ice-free oceans.

2. Material and Methods

2.1. Study Area and Core Materials

This study was conducted at three locations within the PAP-SO (Figure 1): (a) the flank of a small abyssal hill, specifically within an area referred to as “Area B” by Morris et al. (2016) and “Hill” by Durden et al. (2020b); (b) an open abyssal plain site known as “PAP-Central” (4,850 m water depth), and (c) a more northern abyssal plain location known as “North Plain” (Durden et al., 2020b). PAP-Central was located >8 km from any elevated

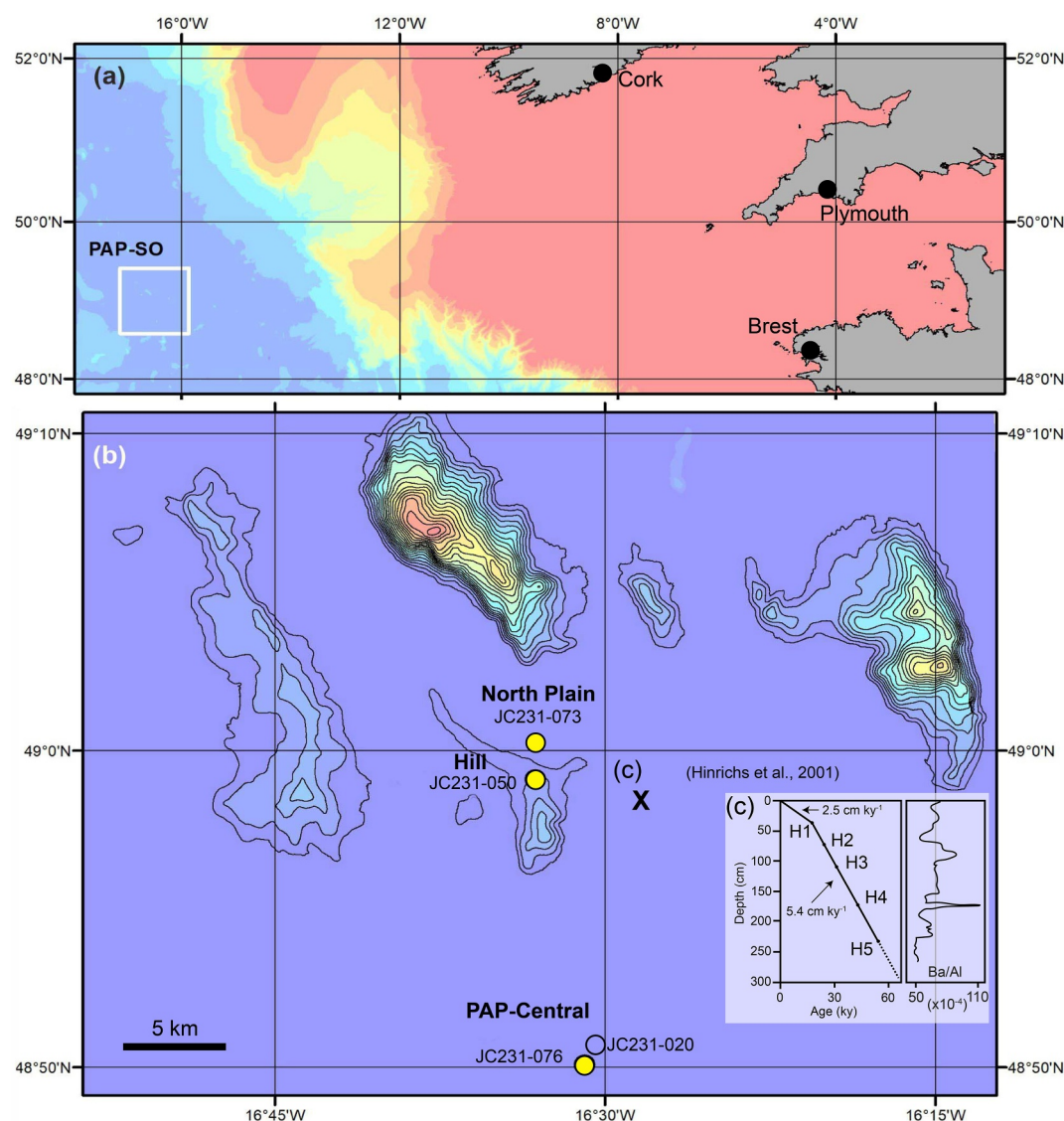


Figure 1. (a) The regional context of the Porcupine Abyssal Plain in the NE Atlantic Ocean. (b) The current study area and location of the cores (yellow dots; empty dot refers to JC231-020 backup core) taken at the Porcupine Abyssal Plain Sustained Observatory, with differentiation of the three sites. (c) Location of the Hinrich et al. (2001) piston core used for temporal correlations. Note the peak in Ba/Al that correlates with H4.

topography, while North Plain was closely adjacent to (<2 km) our study Hill and in relative proximity (c. 4 km) to a very large abyssal hill/small seamount.

The sedimentary environment and megabenthic communities at the three sites have been previously studied, including assessments of total organic carbon, total nitrogen, and mud content at the near surface (Durden et al., 2015, 2020; Morris et al., 2016). Based on multi-corer material, the benthic environment of the study areas showed a greater fraction of fine particles, total organic carbon, and nitrogen on the abyssal plain than on the hill (Durden et al., 2020; Morris et al., 2016). Additionally, the near-seabed suspended particle load (i.e., turbidity) increases significantly over the hill compared to the abyssal plain (data obtained via Seapoint Turbidity Meter) (Durden et al., 2020). This finding is consistent with the near-seafloor current speeds reported by Turnewitsch et al. (2015) in the study area, where the hill experiences speeds of up to 6–8 cm/s, while the plain experiences speeds of 0–3 cm/s. Assuming both areas are subject to the same particle rain rate, the differences in sedimentology allow us to hypothesize the winnowing events of the fine fraction from the hills and, consequently, variations on sediment accumulation rate. Finally, these hydrodynamic conditions are suggested to be responsible for

the fact that megafaunal biomass was significantly greater on the hills than on the plain (Durden et al., 2020; Morris et al., 2016).

Four gravity cores were collected during the RRS James Cook cruise 231 (Hartman, 2022) using 3 m steel cores (Figure 1). In PAP-Central, two gravity cores (station JC231–020 and station JC231–076) were collected at 48° 50.40'N, 16° 31.30'W, and 48° 50.09'N, 16° 31.33'W respectively, at a depth of 4,848 m. The core of the JC231–020 station was not analyzed for this study and kept as a backup core. A gravity core (station JC231–050) was collected from the Hill at 48° 59.106'N, 16° 33.166'W, at a depth of 4,786 m, approximately 60 m above the abyssal plain. In this case, the gravity core only penetrated less than 2 m. One gravity core (station JC231–073) was collected from the North Plain at 49° 0.657'N, 16° 33.21'W, at a depth of 4,846 m. The cores were stored upright at approximately 6°C for transport to the onshore laboratory.

In the PAP-SO, the anatomy of HEs was studied by Hinrichs et al. (2001) in a piston core located in close proximity (<5 km) to our study Hill and North Plain area (Figure 1). No further studies are known in the area about HEs. These authors obtained a mean sedimentation rates of 2.1 cm ky⁻¹ for the last 18 ka, and 5.4 cm ky⁻¹ prior. Moreover, they identified a prominent H4 at a depth of 1.7 m, based on high concentrations of ice-rafted detritus, significant variations in downcore geochemical profiles of diverse elemental ratios such as Ba/Al, Mg/Al, Si/Al, and Zr/Al, and downcore porosity profiles. Additionally, two less distinct layers, H1 and H2, were detected (0.4 and 0.7 m respectively). In contrast, H3 and H5 were less developed, making some identification criteria inapplicable. We use their results and geochemical profiles for temporal correlation with our study sites. We are aware that using geochemical data for correlations only can generate uncertainty. However, we have confidence in using this type of correlation for several reasons: (a) The spacing between our gravity cores and those of Hinrichs et al. (2001) is less than 10 km. (b) The Armorican Seamount (46°23.8'N, 12°32.8'W; 3,849 m water depth) is located about 100 km southeast of our study area and on the flank of the seamount. It shows H4 at a similar depth of 1.75 m, with a sediment accumulation rate of 2.2 cm ky⁻¹ during the Holocene and 5.6 cm ky⁻¹ thereafter (Thomson et al., 1995), similar to the one of Hinrichs et al. (2001). (c) A deep, low-energy, low-flux site (52°55.10'N, 168°54.80'W; 3,570 m depth) is located between Feni Drift and Porcupine Bank (150 km up north of our study area), had also a similar sedimentation rate of 2.1 cm ky⁻¹ during the Holocene (Thomson et al., 2000). The results obtained here (see Result section) are in good agreement with previous studies regarding the position of H4, and we believe that the geochemical correlation is sufficient.

2.2. Core Analyses

Cores were scanned at the British Ocean Sediment Core Research Facility (BOSCORF) using a Geotek Ltd. ScoutXcan multi-angle digital 2D X-ray system, following the Computed Laminography methodology outlined by Dorador et al. (2024). The system utilizes a 65 W Thermo Kevex 130 kV Microfocus X-ray source, which was operated at 115 kV and 425 μA with a 1.0 mm Cu filter for this study. The resulting laminography images have a resolution of 213 pixels per centimeter. Image processing was performed using Adobe Photoshop CS6©, with adjustments to levels, brightness, contrast, and gamma to enhance the visibility of biogenic structures (see Dorador & Rodríguez-Tovar, 2018, and references therein). From these study sites, X-ray fluorescence (XRF) core scanning data were obtained at the Scientific Instrumentation Center of the University of Granada to determine downcore variations in geochemical composition (raw XRF data and specific acquisition features can be found in Miguez Salas, 2024). Following the XRF results and based on the identification of HEs intervals, the three cores were subsampled for geochemical analyses (ICP-OES and ICP-MS), with a total of 216 samples, focusing on detrital, palaeo-oxygenation and palaeoproductivity proxies (Miguez Salas, 2025). With the aim of correlating our results as far as possible with those of Hinrichs et al. (2001), we used the Ba/Al ratio as a proxy for palaeoproductivity; Zr/Al, Rb/Al and Si/Al ratios as detrital proxies; and Zn/Al, Ni/Al and Mo/Al ratios for palaeo-oxygenation. These elemental ratios are powerful tools for paleoceanographic reconstructions. Variations in the concentration of Ba is commonly used as a palaeoproductivity proxy (e.g., Martínez-Ruiz et al., 2019; Paytan & Griffith, 2007) if the Ba enrichment is due to biogenic barite formed in the water column and not to detrital input or diagenetic precipitation. To verify this origin, samples from the intervals of interest (i.e., H4) were analyzed by scanning electron microscopy (SEM) at the Center for Scientific Instrumentation, University of Granada. The biogenic versus detrital origin of the barite has been checked in each gravity core and determined by this visual analysis (Figure S1 in Supporting Information S1). The concentration of detrital elements such as Zr, Rb and Si is often used to reconstruct terrigenous input and unravel sources and provenance (Calvert &

Pedersen, 2007). Similarly, redox sensitive element concentrations (e.g., Zn, Mo, Ni) offer valuable information to characterize deep-water redox conditions.

2.3. Ichnological Analysis

An initial qualitative ichnological assessment was carried out on the laminography images to distinguish trace fossil intervals where ichnotaxonomic assignment was possible. Subsequently, identified traces were classified at the ichnogenus level based on the recognition of ichnotaxabases, that is, standard morphological features, wall, filling, spreiten (see recent review by Bertling et al., 2022). As is common in core analysis, ichnotaxonomic identification was in most cases limited to the ichnogenus level. A quantitative estimate (i.e., bioturbation percentage) of the bioturbation associated with a given ichnotaxon, or for the total bioturbated area, was then obtained. Quantitative estimation was carried out at intervals of environmental significance identified on the basis of XRF data. Bioturbation Intensity (BI) is the percentage of bioturbation obtained from discrete trace fossils with differentiated contours and characteristic shapes, without quantitative assessment of the mottled background. These quantifications were done in Fiji (Miguez-Salas et al., 2019; Schindelin et al., 2012). In parallel, sedimentological features such as erosion surfaces, detrital intervals and laminations were characterized.

3. Results

The XRF data set (e.g., Ba/Al, Si/Al, Ni/Al ratios) shows H4 in PAP-Central at almost the same depth (about 1.6 m) as in the Hinrichs et al. (2001) piston core (Figures 1 and 2). No signal of H1, H2, H3 or H5 is observed (Figure 2). In the North Plain it is observed at 1.4 m and its signal is very similar (Figure 3). Furthermore, the XRF data set (palaeoproductivity and palaeo-oxygenation) exhibits two peaks at nearly the same depth (0.3 and 0.55 m, respectively) as the H1 and H2 in the Hinrichs et al. (2001) piston core. However, these peaks show an absence of IRD layers and variations on detrital proxies (Figure 3). In the Hill, H4 Ba/Al ratio peak is found at 1.6 m (Figure 4). Moreover, the XRF data set reveals two peaks at 0.4 and 0.6 m, respectively, which are similar to those identified for H1 and H2 in the Hinrichs et al. (2001) piston core (Figure 4).

In general terms, the ICP-OES and ICP-MS results revealed similar patterns as the XRF (Figures 2–4) (see the full data set in Miguez Salas, 2025). The H4 IRD layers are easily identified in all sites and are followed by a sharp contact with more or less pronounced lamination at the top (Figure 5). The SEM analysis of barite crystal samples from all three locations show a dominance of biogenic barite over detrital grains (see Figure S1 in Supporting Information S1). Bioturbation Intensity (BI) varies throughout the cores, but remains relatively low (<25%) in most parts (Figures 2–4). Higher BI intervals are associated with dense *Nereites*, *Pilichnus*, *Planolites*, or *Thalassinoides* ichnoassemblages, but values always remain below 50% (Figure 5). These comparatively high BI intervals are not associated with H4. Ichnological data from the H4 impact show a similar general pattern in the abyssal plains during pre-, syn-, and post-IRD layer deposition, with a disappearance of bioturbation in the post-IRD layers. However, the Hill core shows a different pattern; unlike the PAP-Central and North Plain sites, the complete disappearance of bioturbation is not observed in the post-IRD layers.

3.1. PAP-Central

The PAP-Central gravity core records relatively high BI within the first meter below the seafloor (Figure 2). A peak in the Ba/Al ratio and in the element ratios of detrital proxies is observed around 20 cm, but no significant changes in BI are recorded. Within the uppermost meter of the core, the highest BI values (around 50%) are associated with dense *Nereites* and *Pilichnus* ichnoassemblages (Figures 2 and 5). The *Pilichnus* ichnoassemblages also contains small, straight, vertical structures that resemble “*Mycellia*”/*Trichichnus* (Figure 5). Both ichnoassemblages are correlated with low Ba/Al ratio, stable detrital inputs and oxygenation (Figure 2). From 1 to 1.5 m, there is a pervasive laminated interval associated with relatively high Ba/Al ratio values and detrital input together with low oxygenation, especially when the lamination is more pronounced (as indicated at about 1.4 m in Figure 2). The BI is almost 0% in this interval, only some *Chondrites* are recorded.

The ichnological analysis of the H4 reveals that sediments underlying the IRD layer of H4 exhibit a high BI (45%) with discrete trace fossils such as *Planolites*, *Thalassinoides*, and *Chondrites* as well as a developed mottled background (Figures 2 and 5). Sediments corresponding to the IRD layer show a progressive decrease in BI (<15%) with few discrete trace fossils, predominantly *Planolites*. Above the IRD layer, a sharp contact is

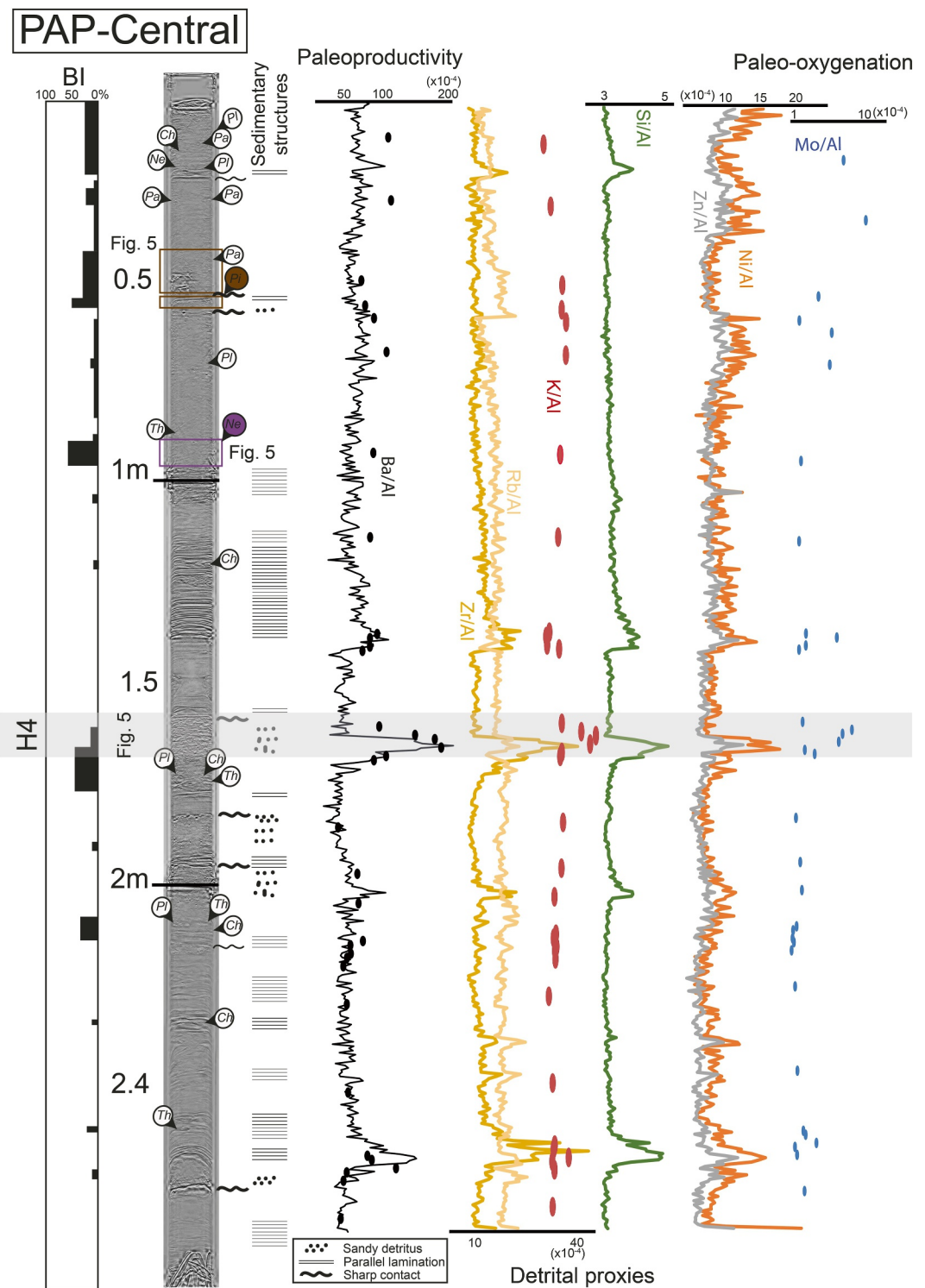


Figure 2. PAP-Central core laminography images after treatment. On the left Bioturbation Intensity (BI) evolution. On the right sedimentological features and geochemical proxies used for this study: Ba/Al for palaeoproductivity; Zr/Al, Rb/Al, K/Al and Si/Al as detrital proxies; Zn/Al, Cr/Al, Ni/Al and Mo/Al for palaeo-oxygenation. The dots represent the results obtained through ICP-OES and ICP-MS analyses. Note: *Ch*, Chondrites; *Ne*, Nereites; *Pa*, Paleophycus; *Pi*, Pillichnus; *Pl*, Planolites; *Th*, Thalassinoides.

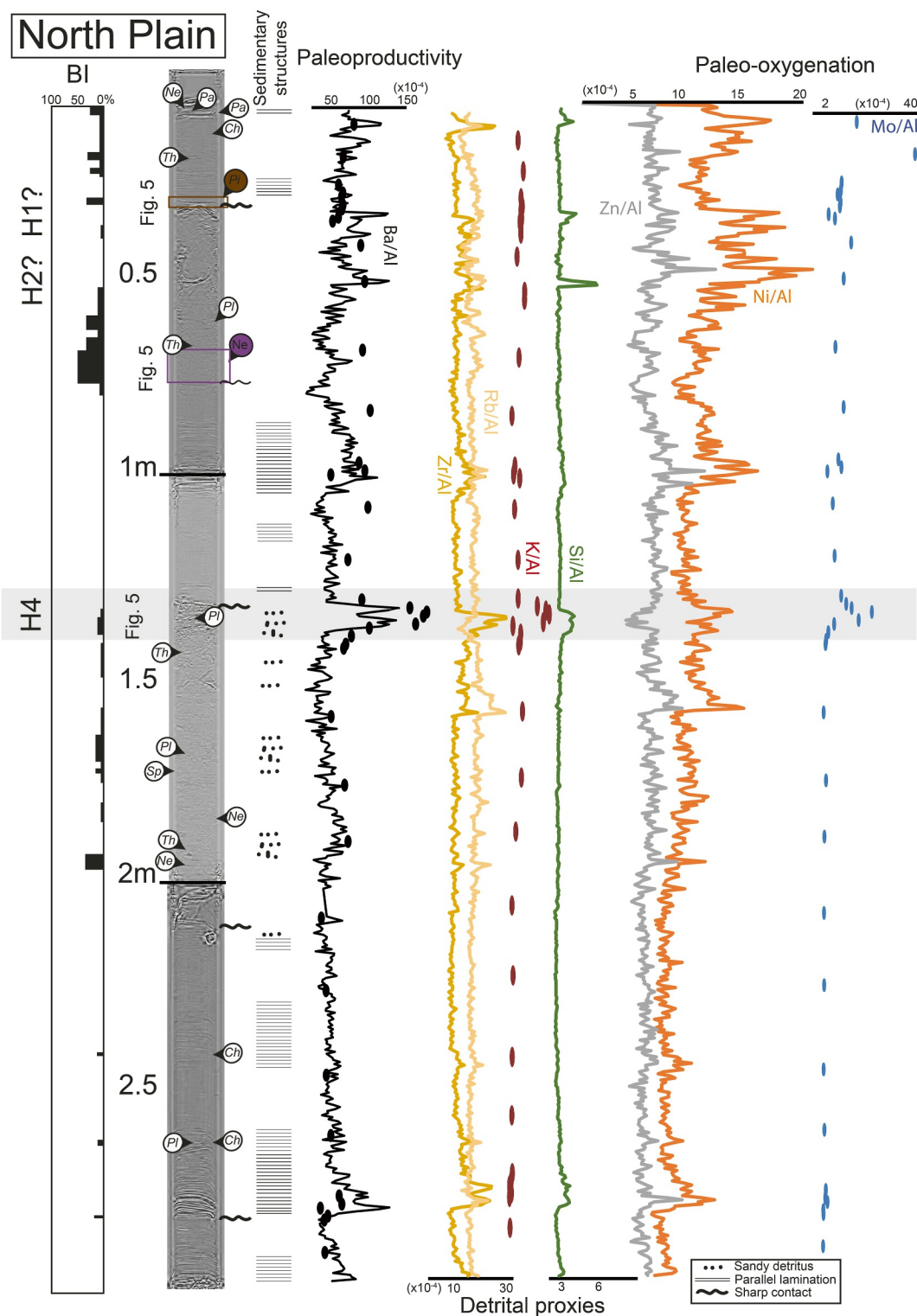


Figure 3. North Plain core laminography images after treatment. On the left Bioturbation Intensity (BI) evolution. On the right sedimentological features and geochemical proxies used for this study: Ba/Al for palaeoproductivity; Zr/Al, Rb/Al, K/Al and Si/Al as detrital proxies; Zn/Al, Cr/Al, Ni/Al and Mo/Al for palaeo-oxygenation. The dots represent the results obtained through ICP-OES and ICP-MS analyses. Note: *Ch*, Chondrites; *Ne*, Nereites; *Pa*, Paleophycus; *Pi*, Pilichnus; *Pl*, Planolites; *Sp*, Spirophyton; *Th*, Thalassinoides.

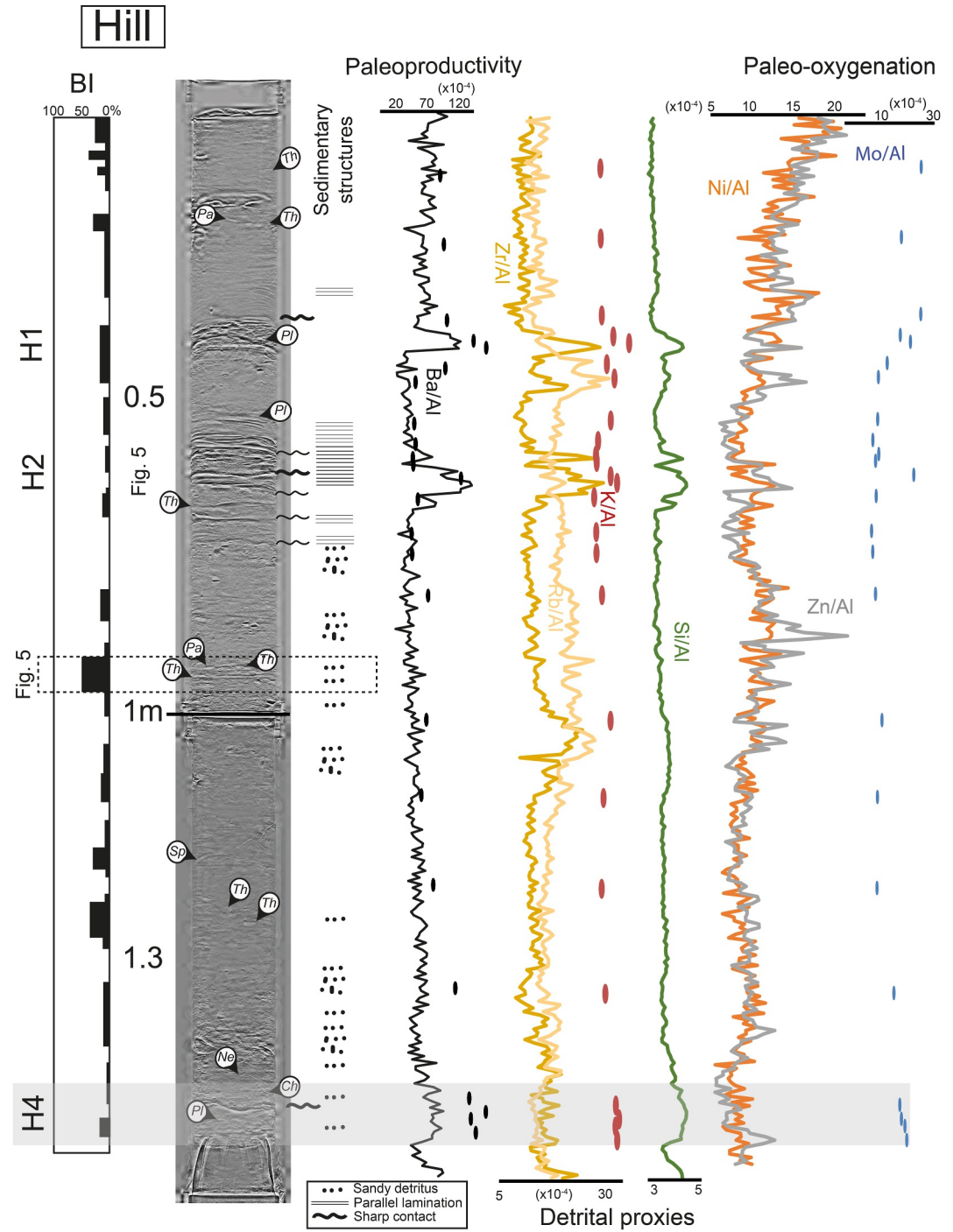


Figure 4. PAP-Central core laminography images after treatment. On the left Bioturbation Intensity (BI) evolution. On the right sedimentological features and geochemical proxies used for this study: Ba/Al for palaeoproductivity; Zr/Al, Rb/Al, K/Al and Si/Al as detrital proxies; Zn/Al, Cr/Al, Ni/Al and Mo/Al for palaeo-oxygenation. The dots represent the results obtained through ICP-OES and ICP-MS analyses. Note: *Ch*, Chondrites; *Ne*, Nereites; *Pa*, Paleophycus; *Pl*, Planolites; *Sp*, Spirophyton; *Th*, Thalassinoides.

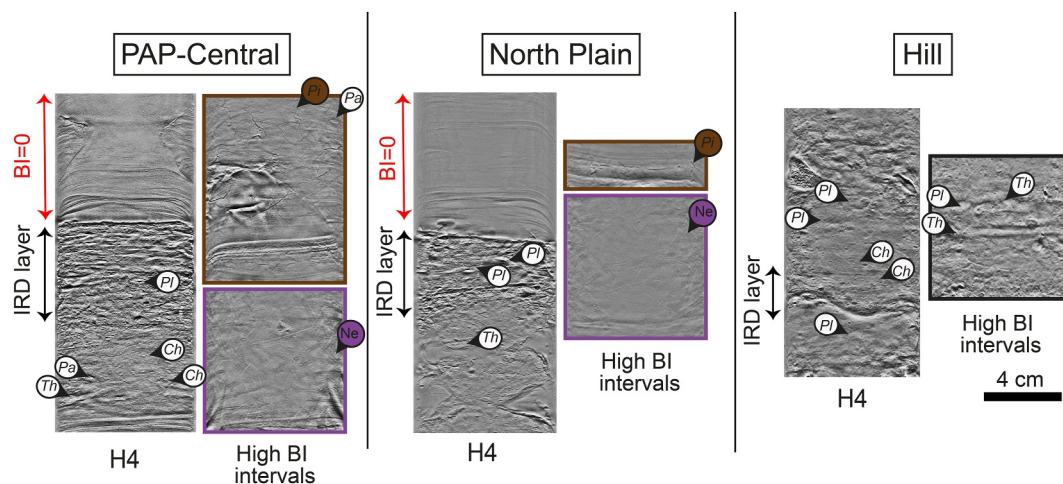


Figure 5. Treated images of the H4 evolution and selected intervals with high BI values in the cores studied (see Figure 1 for location). Note: *Ch*, Chondrites; *Ne*, Nereites; *Pa*, Paleophycus; *Pi*, Pilichnus; *Pl*, Planolites; *Th*, Thalassinoides.

recorded, and sediments display an absence of discrete trace fossils for the overlying 30 cm. The increase in bioturbation occurs only after the following laminated interval (Figure 2).

Below the H4, two peaks of the Ba/Al ratio and detrital proxies are observed at around 2 and 2.5 m, but only the second shows a corresponding significant decrease in oxygenation. The first peak is associated with sandy detritus similar to an IRD layer. The second peak is associated with a pervasive lamination (Figure S2 in Supporting Information S1). The BI is almost constant at 0% during the lower part of the core and no significant changes are associated with these two peaks.

3.2. North Plain

The North Plain gravity core, similar to the PAP-Central core, records relatively high BI during the first meter (Figure 3). The XRF data set reveals two peaks in the Ba/Al ratio and the paleo-oxygenation proxies at around 0.35 and 0.5 m (Figure 3), with the second peak being more pronounced. ICP-OES and ICP-MS only reflects minor variations in detrital proxies, the Ba/Al ratio and the paleo-oxygenation proxies (Figure 3). Following Hinrichs et al. (2001) piston core, these two peaks may correlate with H1 and H2 but here no IRDs are observed (Figure S2 in Supporting Information S1). Above the first peak (H1?), as the paleo-oxygenation proxies and the Ba/Al ratio profiles decrease, a dense but thin interval of *Pilichnus* ichnoassemblages is observed, reaching BI values of 40% (Figure 5 and Figure S2 in Supporting Information S1). Above the second peak (H2?), BI is 0% (Figure S2 in Supporting Information S1). Below the second peak (around 0.7 m) the highest BI values (around 50%) of the core are associated with dense *Nereites* assemblage (Figures 3 and 5). This assemblage is correlated with relatively low Ba/Al ratio, stable detrital inputs and oxygenation. From 0.8 to 1.1 m there is a pervasive lamination associated with relatively high Ba/Al ratio values, a small increase in detrital inputs together with slightly lower oxygenation, especially when the lamination is more pronounced (see around 1 m in Figure 3). The BI is 0% in this laminated interval. This interval can also be correlated stratigraphically with the PAP-Central gravity core (about 1.3 m) (Figure 2).

The ichnological analysis of the H4 reveals that sediments underlying the IRD layer of H4 exhibit a low to moderate BI (15%–30%) with discrete trace fossils such as *Planolites* and *Thalassinoides* (Figure 5). Sediments corresponding to the IRD layer show similar BI with dominant *Planolites*. Above the IRD layer, a sharp contact is recorded, and sediments display an absence of discrete trace fossils for the overlying 60 cm. The increase in bioturbation occurs only after the following laminated interval (Figure 3).

Below H4, the 1.5–2 m interval records stable proxies and moderate to low BI (10%–25%). At 2.7 m, a peak in the Ba/Al ratio and detrital inputs, together with a decrease in oxygenation, is associated with a pervasive lamination (Figure S2 in Supporting Information S1). BI is almost constant at 0% in the lower part of the core and no

significant changes are associated with this peak (Figure 3 and Figure S2 in Supporting Information S1). This interval can also be correlated stratigraphically with the PAP-Central gravity core (about 2.5 m) (Figure 2).

3.3. Hill

The Hill gravity core records moderate but more constant BI during the first 0.5 m (Figure 4). A peak in Ba/Al ratio and detrital proxies, together with low oxygen conditions is observed around 0.4 m (H1) (Figure 4). This peak drops down the BI to 0%, but pre-peak BI values are recovered shortly thereafter (Figure 4 and Figure S2 in Supporting Information S1). Above and during H2 deposition (0.6 m), no significant changes are observed in BI despite variations in all proxies (productivity, detrital inputs and oxygenation) (Figure S2 in Supporting Information S1).

Below H2, the core records largely stable proxies and moderate to low BI (15%–40%) (Figure 4). Even in some intervals (around 0.9 m) BI can reach almost 50% (Figure 5). No thick pervasive laminated intervals are observed as in the PAP-Central and North Plain gravity cores (Figure 4). Only around 1–1.1 m an increase in detrital proxies associated with low oxygen conditions is observed. However, this variation seems to have no effect on the BI values. This lower part of the core has several sandy detrital layers (Figure 4).

The ichnological analysis of the H4 (1.6 m) reveals that sediments underlying the IRD layer of H4 exhibit a low to moderate BI (15%–20%) (Figures 4 and 5). Sediments corresponding to the IRD layer also show low BI (<10%) with few discrete trace fossils such as *Planolites* and *Chondrites*. Above the IRD layer, a sharp contact is recorded followed by 3 cm of lamination with no discrete trace fossils. Then, BI goes back again to similar values recorded below the IRD (Figure 4).

4. Discussion

4.1. Ichnology of the H4 at the Porcupine Abyssal Plain

Several palaeoenvironmental changes are evident on a global scale during the HEs, with variations in water temperature and salinity being the most commonly reported features, primarily due to the build-up of a subsurface heat reservoir in the subpolar Atlantic and subsequent extensive ice melting during the HEs (Max et al., 2022). However, other factors, such as oxygenation and nutrient availability, may have played an important role for the benthic habitat. Large freshwater discharges associated with iceberg surges may have led to the decreases in bottom water oxygenation during HEs in the North Atlantic due to changes in ocean circulation and possibly productivity (Hoogakker et al., 2016). These changes are clearly identified by combining depth profiles of detrital and redox sensitive elements, as well as the Ba/Al ratio which overall reflects productivity. The importance of nutrient availability and oxygen conditions has been shown to be the main limiting factors for macrobenthic tracemaker communities during H1 in the North Atlantic (Rodríguez-Tovar et al., 2019, 2020). Near the Hudson Strait's mouth, Rodríguez-Tovar et al. (2019) found that during the onset of H1, the dominance of *Chondrites* suggests highly dysoxic conditions. In contrast, the subsequent layer, characterized by a more diverse trace fossil assemblage (*Planolites* and *Thalassinoides*) and the disappearance of *Chondrites*, indicates improved oxygen levels and increased benthic food availability for larger tracemakers. Also in the Iberian Margin, the increase in freshwater input associated with the HEs led to a decrease in bottom water oxygenation and thus an increase in *Chondrites* concentrations (Baas et al., 1997, 1998; Löwemark et al., 2004). In contrast to other previous studies, we did not observe concentrations of *Chondrites* associated with H4 or the others HEs, which could give a more detailed indication of the effects of oxygenation on the seafloor tracemaker communities (Bromley & Ekdale, 1984). In all of the studied core material related to H4, *Chondrites* appear as a component of the ichnoassemblage, which is dominated by *Planolites* (Figure 5). The presence of *Thalassinoides* and *Planolites*, even in the presence of *Chondrites*, indicates relatively favorable oxygen and nutrient conditions (see Rodríguez-Tovar et al., 2019). Thus the presence of *Chondrites* per se is not an indication of low oxygen conditions when is part of a diverse assemblage.

The H4 signal in the PAP-SO (NE Atlantic Ocean) shows a consistent ichnological pattern across both abyssal plain cores (Figure 5). The absence of discrete trace fossils just above the IRD layers suggests a prolonged hostile environment for the macrobenthic tracemaker community after the H4 event. Moreover, even when post-event oxygen levels in bottom and pore waters appear to have returned to pre-event levels (e.g., Mo/Al profile in Figures 2 and 3), BI remains at 0. This is also the case for the palaeoproductivity and detrital input proxies. During

the initial phase of H4, freshwater influx led to an increase in palaeoproductivity and enhanced organic carbon fluxes. SEM observations confirm that the IRD layers associated with elevated Ba/Al ratios are characterized by increasing biogenic barium content at all three sites, although some detrital grains were also observed (see Figure S1 in Supporting Information S1). This in turn led to enhanced oxygen consumption and subsequent unfavourable oxygen conditions, eventually shifting to highly dysoxic to anoxic levels (Figures 2 and 3). This in turn led to a gradual decrease in BI during the IRD deposition (Figure 5). We hypothesize that during IRD deposition, the period of low oxygen was rather long, preventing any macrobenthic tracer from surviving (Rodríguez-Tovar et al., 2020).

This evolution contrasts with that of the Hill, where the disappearance of trace fossils is absent, despite having low oxygenation during IRD deposition as well (Figure 4). After H4, conditions began to improve, as indicated by the sparse presence of discrete trace fossils such as *Planolites* and *Chondrites* (Figure 5). Thus, shortly after the deposition of the IRD layer, a significant transition to oxic bottom and pore waters occurred, probably due to the flow of bottom currents carrying aerated water (see next discussion section), which led to the re-establishment of background palaeoclimatic and palaeoceanographic conditions. Overall, oxygen conditions followed a trend from dysoxic to severely dysoxic/anoxic and finally to oxic, leading to a rapid recovery of macrobenthic tracemakers in the Hill. In contrast, in the more “calm” abyssal plains, the palaeoenvironmental changes associated with H4 caused a long-lasting perturbation that the tracemaker community was unable to overcome.

4.2. The Impact of Seafloor Heterogeneity and Heinrich Events on Tracemaker Communities

The Galicia Bank is an elongated basement high with a north–south orientation, acting as a horst on the continental slope. It separates the Galicia Interior Basin from the Iberia Abyssal Plain, rising from a depth of 3,800 m to less than 500 m at its summit (Medialdea et al., 2008). Rodríguez-Tovar et al. (2020) found an absence or scarce discrete trace fossils within the IRD layer of H1, as well as in the overlying sediments on the flank of the Galicia Bank. Density current processes in this area create unfavorable conditions for the macrobenthic tracemaker community, compounding the broader effects of H1. In contrast, the Galician Interior Basin (central and continental slope parts) exhibits conditions conducive to the development of a multitiered tracemaker community characteristic of the *Zoophycos* ichnofacies, typically associated with fine-grained sediments rich in organic matter within low-energy subtidal environments (Rodríguez-Tovar et al., 2020). In other words, their results are the opposite to those reported here, with a disappearance of bioturbation in the flank of the Galicia Bank, while we observe a much smaller effect of H4 in the flank of the Hill.

Many factors may account for this difference. On the one hand, the size of the topographic heterogeneity and the spatial scale of the comparison may be important factors. The study by Rodríguez-Tovar et al. (2020) study covers a lateral variability of about 100 km and the Galicia Bank is a topographic feature with a bathymetric range of more than 2000 m, whereas in our study, the Hill is just 62 m above the seafloor and we compare cores in a radius of 20 km. Density current processes will be of a completely different magnitude, affecting the Galicia Bank flank more strongly, while in the Hill they seem to play a secondary role (Miguez-Salas et al., 2024). On the other hand, bottom currents that flow along the slope of an elevated topography (e.g., continental slopes, seamount flanks) are known to strongly affect deep-sea tracemaker communities (e.g., Miguez-Salas et al., 2020, 2021). The Mediterranean Outflow Water flows northward along the Iberian Margin and passes through the Galicia Interior Basin, controlling the tracemaker community distribution and features (Dorador et al., 2019). These bottom currents, which can carry aerated water masses, may have favored a rapid recovery after H1 in the Galicia Interior Basin compared to the Galicia Bank flank, which is dominated by density current flows (i.e., downslope gravity flows).

In our study area, bottom currents flowing along the Hill slope also play an important role, redistributing the sediment (Turnewitsch et al., 2015), controlling benthic fauna distribution (Durden et al., 2020), and affecting the tracemaker density (Miguez-Salas et al., 2024). Numerous quantitative measurements of bottom currents in the study area have shown that hydrodynamics primarily control the sedimentological and faunal characteristics of these benthic environments (Durden et al., 2020; Morris et al., 2016). This creates a greater fraction of fine particles, total organic carbon, and nitrogen on the abyssal plain than on the elevated terrains of the study area (Morris et al., 2016). Additionally, previous studies of the Hill's coarse-grained sediments, which have a reduced particle surface area compared to the abyssal plain, have revealed lower rates of proteinaceous organic matter degradation than surrounding abyssal plain sediments (Turnewitsch et al., 2015). In other words, the elevated topography and its sediments favor the preservation of organic matter rather than its degradation (Turnewitsch

et al., 2015). Assuming similar pelagic rain and a surplus of organic matter associated with HEs in the study area, low-oxygen conditions due to organic matter degradation would be more dramatic on the abyssal plains, causing a collapse of the food web and creating long-lasting unfavorable conditions for the tracemaker community.

Unfortunately, we have no clear record of any other HEs appearing in all the three cores. To expand the discussion, however, these hypotheses are consistent with the other HEs recorded in the North Plain and Hill gravity cores. For example, H2 in the North Plain led to the disappearance of the tracemaker community (see Figure S2 in Supporting Information S1), whereas H2 and H1 in the Hill had a minor effect or induced gradual recovery of the tracemaker community, respectively (see Figure S2 in Supporting Information S1). Therefore, we suggest that the hydrodynamic regime and sedimentary features of the study area had a significant impact on limiting organic matter degradation during and after H4 (probably also during H1 and H2), as well as during the subsequent period of low seafloor oxygenation. In contrast, the less dynamic abyssal plain would experience a more prolonged period of low oxygenation due to pervasive organic matter degradation (see the temporal evolution of palaeo-oxygenation proxies in Figures 2 and 3), resulting in the disappearance of the entire tracemaker community, as evidenced by the lack of bioturbation in the post-IDR layers. In general, beyond the effect of HEs, the highest BI values are correlated with stable values of detrital, palaeo-oxygenation and palaeoproductivity proxies (Figures 2–4).

In short, the effects of bottom currents seem to have helped the tracemaker community to overcome the adversities of HEs. Above all, we emphasize the importance of seafloor heterogeneity at the time of climate events such as HEs in controlling the effects of disappearance and recovery of tracemaker communities, even at spatial scales of tens of kilometres.

5. Conclusions

The combination of ichnological and geochemical analysis during the Heinrich Event 4 (H4) from three closely spaced and contrasting sites (less than 20 km apart) of the Porcupine Abyssal Plain Sustained Observatory (PAP-Central, North Plain and Hill) provides the following conclusions:

H4 had a different impact on the macrobenthic tracemaker community at the three sites, despite their proximity.

H4 may have resulted in an extinction of the tracemaker community at PAP-Central and North Plain and no gradual recovery is observed, while in the flank of the Hill, a rapid recovery is recorded after H4.

Bottom currents flowing along the flank of the Hill may have aerated the seafloor, leading to a rapid recovery while restricted oxygenation was maintained in the abyssal plains.

Above all, this study highlights that in times of climate change, the seafloor habitat heterogeneity, even at local scales, is an important factor affecting benthic communities.

Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

Availability Statement

The geochemical XRF, ICP-MS and ICP-OES data is archived in Zenodo (Miguez Salas, 2024, 2025).

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