Comparison of rosette-shape traces in abyssal terrains: Environmental and faunal implications

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A B S T R A C T

Biogenic traces (lebensspuren) result from the activity of benthic organisms on and within the seafloor and are a common feature of deep-sea environments. Rosette-shape traces (RSTs), also referred to as spoke burrows, are a commonly observed and distinctive trace, likely created by echiuran worms during feeding and burrowing. We conduct a quantitative morphometric assessment of RSTs from two contrasting sites at the Porcupine Abyssal Plain Sustained Observatory (PAP-SO; Northeast Atlantic) with similar physico-chemical conditions except for relative sediment compaction, but substantive differences in their megabenthic communities. We quantified RST abundance (numerical density and seafloor cover) and morphological characteristics (spoke number and overlap, spoke length and width, trace area and relative completeness) for 148 individual RSTs observed in some 6800 seafloor photograph (8788 m^{-2} seafloor area) captured with an autonomous underwater vehicle. We derived two primary results between study sites: (a) individual spoke morphology exhibited no statistically significant differences, while (b) individual trace completeness was significantly different. The consistency in spoke morphometrics reflects our identification of a single RST morphotype, potentially representing a single functional group of echiurans. The difference in trace completeness between sites may have resulted from differences in competition for resource with other megabenthic surface deposit feeders, and not to be directly related to relative sediment compaction. By reference to literature data and observations of similar traces in other deep-sea settings, we further suggest that this connection between trace completeness and resource availability may be more generally applicable in both contemporary ecology and paleoichnology.

1. Introduction

Much of the deep-sea floor comprises sedimentary environments, where the feeding, burrowing, and locomotory activities of various benthic organisms can be recorded in the form of traces on the sediment surface (Gage and Tyler, 1991). These traces, referred to as lebensspuren (Seilacher 1954, 1960), are defined as sedimentary structures produced by living organisms (Ewing and Davis, 1967), and can also be preserved in the geological record as trace fossils (e.g., Buatois and Mángano, 2011). Thus, lebensspuren reflect various bioturbation-related processes, such as the modification of geochemical gradients and the redistribution of seafloor food resources (Meysman et al., 2006).

Lebensspuren include a variety of trace types and shapes: simple burrows, trails, faecal casts, depressions, and mounds, as well as more complex forms such as spirals, star-shapes, rosettes, etc. (e.g., Hollister et al., 1975; Dundas and Przeslawski, 2009). Although lebensspuren are abundant in the deep-sea, very few organisms (i.e., trace makers) are observed in the process of forming these features (Miguez-Salas et al., 2022; Brandt et al., 2023), remaining the trace maker a mystery in most cases (e.g., Vecchione and Bergstad, 2022; Przeslawski, 2022). Thus, our understanding of their relationships with environmental variables that may be potential drivers of the numerical density, diversity, and ecosystem functions of the benthic communities that produce them, is still limited.

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In a study of the bathyal (c. 2500 m water depth) Mid-Atlantic Ridge around 50° N, Bell et al. (2013) observed that lebensspuren assemblage composition and areal coverage appeared to have been primarily influenced by local-scale environmental variation independent of organic matter inputs. Przeslawski et al. (2012), assessing lebensspuren from the eastern and western Australian margin in water depths between 1300 and 4400 m, noted that trace richness showed no strong relationship with water depth, sediment total organic carbon, or mud content, although they did detect a relationship with organic matter lability among sites in the eastern study area. Earlier studies suggested that hydrodynamic conditions and the availability of organic material were the primary driving variables for the lebensspuren-forming fauna at the deep-sea (Levin et al., 2001). Other potentially important environmental parameters such as sediment consolidation or porosity and nutrient heterogeneity, in the form of seafloor organic matter spatial patchiness, have not been addressed in detail. Similarly, the potential role of some trace makers in significantly modifying their local environmental conditions, for example through bioturbation and nutrient redistribution, should not be overlooked (Thomson et al., 2000).

One of the frequently encountered deep-sea traces is a multi-rayed surficial feature often referred to as a 'spoke burrow' or 'Rosette-Shape Trace' (RST; Table 1). These RSTs have observed diameters ranging from decimetres to metres (Ewing and Davis, 1967; Ohta, 1984; Young et al., 1985; de Vaugelas, 1989; Bett et al., 1995), may have an associated central burrow opening or depression, may comprise a 'full' or 'partial' set of spokes, and may have an apparently associated adjacent mound (Ohta, 1984; Dundas and Przeslawski, 2009). These types of lebenspurren have been comparatively well-described, with up to ten morphotypes discriminated (Ohta, 1984; Bett et al., 1995).

Rosette-shape traces have variously been attributed to the feeding activities of bivalve molluscs, sipunculan worms, and non-echiuran polychaete worms. Based on in situ observations in shallow water and on deep-sea photographs that serendipitously capture an organism in the act of making the trace, most RSTs are believed to be the work of echiuran worms (Bett and Rice, 1993; Hughes et al., 1994). It is most likely that echiurans relocate by burrowing subsurface based on time-lapse photographic observations and presumed burrow structure (Bett and Rice, 1993; Rice et al., 1994; Bett et al., 1995, Fig. 5 in Bett, 2003). However, how often echiurans relocate is unknown. Recently, the formation of spoke burrows, through echiuran feeding activity, was linked with the seasonal deposition of organic matter to the seafloor in the area of the Porcupine Abyssal Plain Sustained Observatory (PAP-SO; Durden et al., 2020a). However, the relationship of RSTs to environmental variables (e.g., nutrient fluxes, water depth, organic matter quality) and co-occurring faunal composition has not been addressed in detail.

The PAP-SO site has been the subject of extensive time series observations (Hartman et al., 2021), including the use of time-lapse photography that has captured the formation of RSTs by the actions of echiuran proboscides. These photographs recorded both non-bifid, non-green proboscis activity (Bett and Rice, 1993) and bifid, green proboscis activity (Lampitt, 2014). In otter trawl catches, the combined numerical density of echiurans and sipunculans was determined at 4.02

Table 2

Porcupine Abyssal Plain Sustained Observatory (PAP-SO) echiuran and rosette-shaped trace (RST) numerical density and seabed cover.

Metric	Region	n	Median	95% CI	Unit
'Vermes'[a] numerical density from Billett et al. (2001, 2010)	PAP-SO otter trawl catch data	42 trawls	4.02	3.48–4.59	ha^{-1}
Echiura numerical density[b]	PAP-SO otter trawl data	61 trawls	2.72	2.14–3.54	ha^{-1}
Echiura numerical density from Durden et al. (2020b) [c]	PAP-Central (camera)	33 photographic sample units	42.3	34.9–49.6	ha^{-1}
	North Plain (camera)	5 photographic sample units	37.0	14.1–59.9	ha^{-1}
RST numerical density (present study)	PAP-Central and North Plain combined	680 tiles (8788 m^2)	168	142–195	ha^{-1}
	PAP-Central	400 tiles (5018 m^2)	175	139–212	ha^{-1}
	North Plain	280 tiles (3770 m^2)	159	121–195	ha^{-1}
RST seabed cover (present study)	PAP-Central and North Plain combined	680 tiles (8798 m^b)	1.27	1.02–1.54	%
	PAP-Central	400 tiles (5018 m^2)	1.49	1.11–1.88	%
	North Plain	280 tiles (3770 m^2)	0.97	0.68–1.27	%

[a] 'Vermes', combined category for Echiura and Sipuncula.
[b] Pers. com. Tammy Horton and Amanda Serpell-Stevens, National Oceanography Centre, UK.
[c] n = refers to photographic sample units (one sample unit = 60 tiles, approx. 800 m^2).

Table 1

Examples of rosette-shaped trace (RST) observations in deep-sea studies.

Citation	Location	Depth (m)	Numerical density (ha^{-1})	Notes
Ewing and Davis (1967)	Various Pacific and Atlantic locations	51–5698	No data	First to describe RSTs with nearby gashed mounds (code IIA 2)
Heezen and Hollister (1971)	Adjacent Peru-Chile Trench	3626	No data	
Hollister et al. (1975)	SE Indian Ocean	4225	No data	Spoke-like impressions in Fig. 21.15
Kitchell et al. (1978)	Bellingshausen Basin	4008–5018	No data	RSTs appear in 5% of photographs
Mauviel (1982)	Cape Verde Abyssal Plain	c. 4900	1940	RST (S32 rosette grande) sometimes with nearby gashed mound
Ohta (1984)	Bay of Bengal	2635–5025	No data	10 morphotypes
Mauviel and Sibuet (1985)	Gulf of Biscay	4000	No data	Similar to "Grande rosette"
Young et al. (1985)	Venezuela Basin	3450–5050	210–1690	
de Vaugelas (1989)	Porcupine Seabight,	1676	<10	
Bett et al. (1995)	Cape Verde Abyssal Plain	4600	872	6 morphotypes. Numerical density of 68 ha^{-1} for RST type 2 with nearby gashed mounds
Dundas and Przeslawski (2009); Przeslawski et al. (2012)	Australian continental margin	1500–4000	<1000	
Bell et al. (2013)	Mid-Atlantic Ridge	2500	710–33,000	Class 53
Bett and Rice (1993); Durden et al. (2019, 2020a)	Porcupine Abyssal Plain	4850	No data	RST appearance related with seasonal phytodetritus inputs

ind. Ha^{-1}, with the maximum value recorded in a single trawl being 7.90 ind. Ha^{-1} (Billett et al., 2001, 2010, Table 2). The trawl-caught numerical density of echiurans alone has been estimated at 2.72 ind. Ha^{-1}, with the maximum value recorded in a single trawl being 14.3 ind. Ha^{-1} (pers. com. Tammy Horton and Amanda Serpell-Stevens, National Oceanography Centre, UK). More recently, image-based studies have allowed echiuran density to be estimated at different PAP-SO sites (Table 2; Durden et al., 2020b), and confirmed the presence of both bifid green and non-bifid non-green morphotypes. Biseswar (2005, 2006) identified 15 species-level echiuran taxa from the PAP-SO, 14 from beam trawl (*le chalut à perche*) catches and one from a box core sample. All of these taxa were from the family Bonelliidae, with up to four taxa recovered in a single beam trawl catch, and *Achaetobonellia ricei* Biseswar (2005), *Bengalus longiductus* Biseswar (2006), *Eubonellia longistomum* DattaGupta (1981), *Jakobia densopapillata* Biseswar (2006) the most frequently identified. Three of these taxa, *A. ricei*, *B. longiductus*, and *J. densopapillata* represented new species, and *Bengalus* a new genus.

Given their relatively abundant and diverse occurrence, and their likely significance in bioturbation and particularly the potential subduction of labile organic carbon (Smith et al., 1986; Thomson et al., 2000) we determined to further investigate echiuran ecology at the PAP-SO by reference to their lebensspuren. The aim of the present study was to compare the numerical density and morphological characteristics of RSTs, with an associated gashed mound, from two locations within the PAP-SO. Those locations having both distinct sedimentary characteristics, and benthic megafaunal communities (Durden et al., 2020a). To understand the potential influence of these factors on the prevalence and morphology of the traces, we carried out a quantitative, morphometric study of RSTs in a large set of seabed photographs. We discuss our findings in the context of (a) contemporary echiuran and megabenthos community ecology, and (b) the potential use of RST trace fossil analogues in paleo-environmental reconstructions.

2. Materials and methods

2.1. Study location

The study assessed RSTs at two abyssal plain sites within the Porcupine Abyssal Plain Sustained Observatory area (northeast Atlantic, 4850 m water depth; Hartman et al., 2021): a central location (PAP-Central) and a more northern location (North Plain) (Fig. 1). The two sites are at near-identical water depths, with the North Plain very marginally deeper (2 m). PAP-Central was located >8 km from any elevated topography, while North Plain was closely adjacent to (<2 km) a small abyssal hill and in relative proximity to (c. 4 km) a very large abyssal hill/small seamount. The flanks of the small abyssal hill, with a maximum topographic elevation of c. 200 m, are extensively scalloped by slope failure scarps and the fringing seafloor topography suggestive of slope failure run out deposits (Ruhl, 2013). The adjacent seamount has a topographic elevation in excess of 960 m and in parts is very steep sided and is consequently the likely origin of more numerous and more extensive slope failures and run out deposits (i.e., turbidites).

The surficial sediment columns at the two sites were highly contrasting, at PAP-Central, sediments become substantially consolidated within c. 10 cm of the sediment surface, while at North Plain sediments are homogeneous and unconsolidated to >40 cm below the sediment surface (Ruhl, 2013). More recent sampling, during RRS *James Cook* cruise 231 in May 2022, with a gravity corer at the North Plain suggested that the unconsolidated surface sediment layer extends to >100 cm thickness (Hartman, 2022). Similarly, sub-bottom profiling (Kongsberg SBP120) during the same cruise suggested the presence of a thickened surface sediment unit in the North Plain area (Hartman, 2022). Taken together these observations suggest that the North Plain area has been subject to one or more substantial, locally sourced, turbidite emplacements, the most recent of which remains in a substantially unconsolidated state.

In more general terms, sedimentary total organic carbon content, and sedimentary coarse fraction (particles >22.9 μm), were not
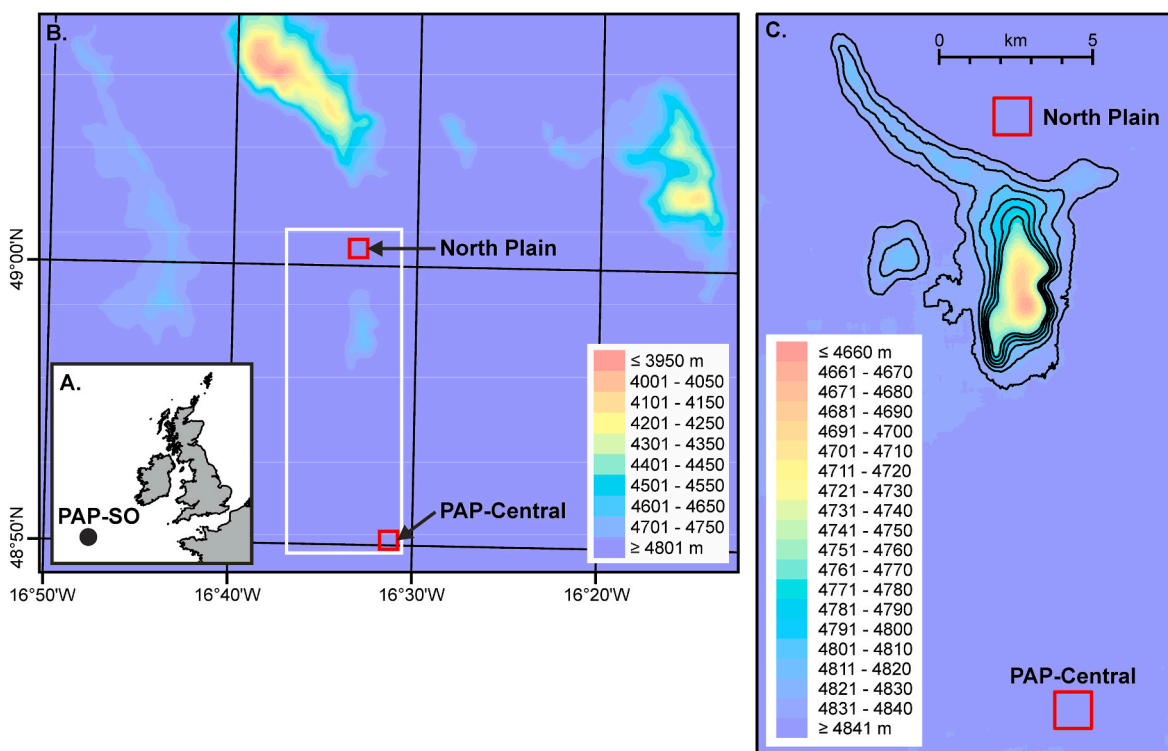

Fig. 1A-B). Location of the Porcupine Abyssal Plain Sustained Observatory (PAP-SO) and the current study area (white box). C) Additional detail of the current study area, showing the two study sites (PAP-Central and North Plain) and the topography of the adjacent small abyssal hill.

significantly different between the two sites (Durden et al., 2020b). Photographically-assessed echiuran numerical density was similar for both sites, 42.3 and 37.0 ind. Ha⁻¹ for PAP-Central and North Plain respectively (Durden et al., 2020b). However, the associated mega-benthos communities differed; importantly, statistically significant differences were detected between sites in the total numerical density of deposit feeders, which was lower at PAP-Central, and in deposit feeder biomass, which was higher at PAP-Central (Durden et al., 2020b).

2.2. Identification and assessment of RST morphology

The RSTs were assessed in seabed photographs, as described in Durden et al. (2020b). In brief, photographs were captured using the autonomous underwater vehicle *Autosub6000* during RRS *Discovery* cruise 377 in July 2012 (Ruhl, 2013). At the two study sites, downward-facing photographs were captured along transect lines in a grid pattern with 100 m spacing, from a target altitude of 3.2 m, at a frame interval of 0.9 s. Photographs were processed to remove the

overlap between successive images and were mosaicked into 'tiles' of approximately 10 images (Morris et al., 2014). A random selection of tiles from each site was made using the random sorting filter of BIIGLE 2.0 software (Langenkämper et al., 2017). The resultant set of tiles from PAP-Central comprised 400 tiles (5018 m² total seafloor area), and the North Plain dataset 280 tiles (3770 m²).

RSTs observed in the tiles comprised a range of morphologies, including types that resembled those of prior studies (e.g., Ohta, 1984; Bett et al., 1995). We considered only those RSTs consisting of relatively broad grooves radiating from a common point, with an adjacent gashed mound (Fig. 2). This restricted morphological selection was imposed to ensure data comparability within this study and was based on the assumption that the appearance of a nearby gashed mound is likely related to specific lifestyle and/or feeding behaviour, limiting the potential identity of the trace maker(s) to a particular functional type. We note here that, echiurans with green bifid proboscides were observed producing RSTs but were not included in this assessment as they were not associated with adjacent gashed mounds.
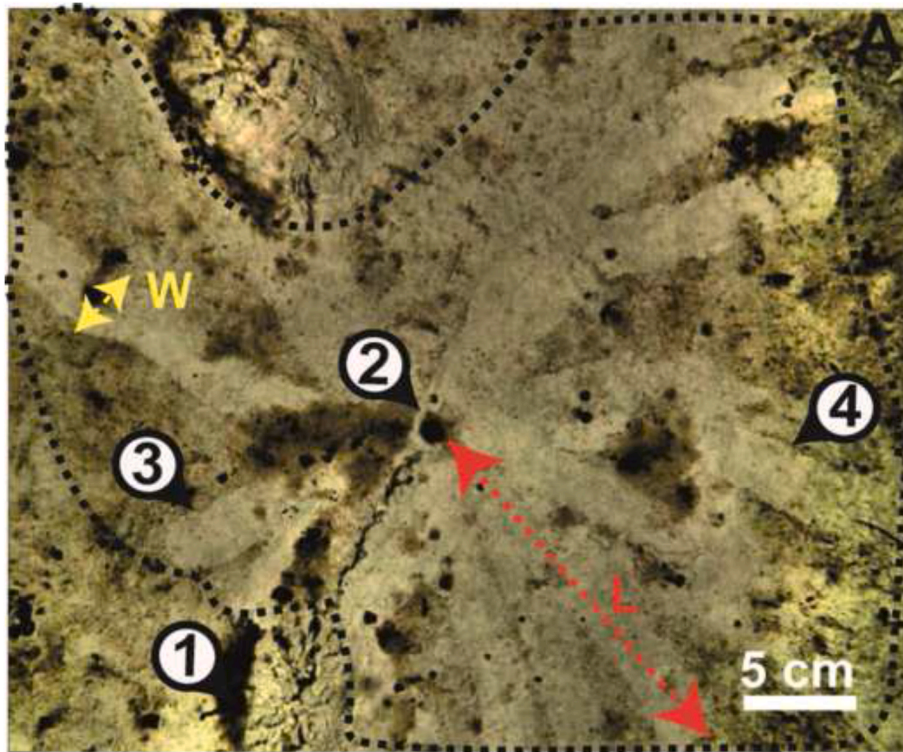

Fig. 2A. Example seafloor image from the Porcupine Abyssal Plain Sustained Observatory (PAP-Central) showing a rosette-shape trace and associated gashed mound (1). Also indicating central burrow opening (2), a spoke (3), spoke with overlap (4), measurement of spoke width (W, yellow line), measurement of spoke length (L, red line), and trace area measurement (black dashed line). B. Interpreted sketch of the feature (modified from Izumi and Yoshizawa, 2016). The question marks indicate that the complete burrow morphology of the RST below the seafloor is unknown.
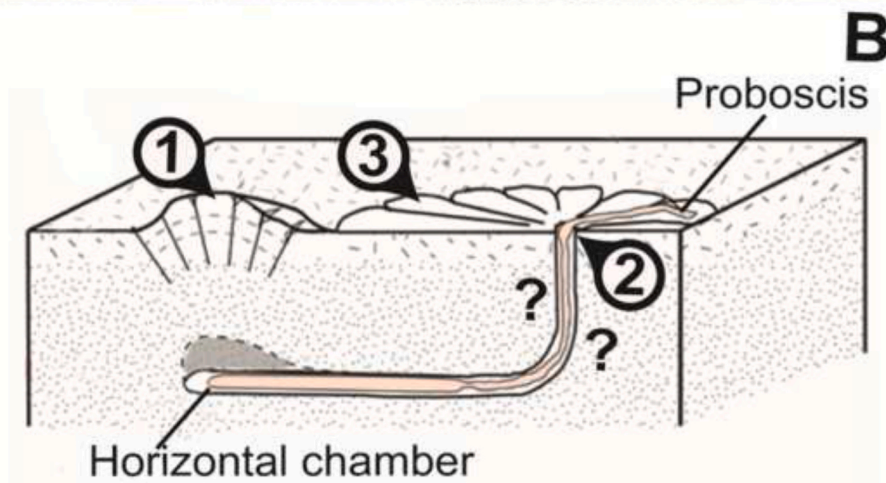
Trace morphometric data were collected from relatively fresh and undisturbed RSTs with gashed mounds that were recognizable within an image. RSTs observed to be highly degraded, such that the limits of the spokes could not be clearly differentiated were discounted from the analyses (see Fig. 3 E and F). Similarly, only complete RSTs with gashed mounds were enumerated and measured, while those only partially captured within the tile were discounted. Morphological features of each complete RST were measured as follows: length and width of each spoke, number of spokes, number of overlapping spokes (i.e., when spokes overlap from the burrow opening to their extremity), and the rosette-shape area (see Fig. 2). Spoke aspect ratio was subsequently calculated as median spoke length/median spoke width for individual RSTs. Rosette-shape area was measured by tracing the limits of the observed spokes (e.g., the green dashed line in Fig. 2). Additionally, an area proxy value was calculated from the median spoke length assuming a complete full circular area. Trace area ratio was calculated as measured area/proxy area to provide an indication of trace completeness. All morphometric measurements were made using BIIGLE 2.0 software (Langenkämper et al., 2017).
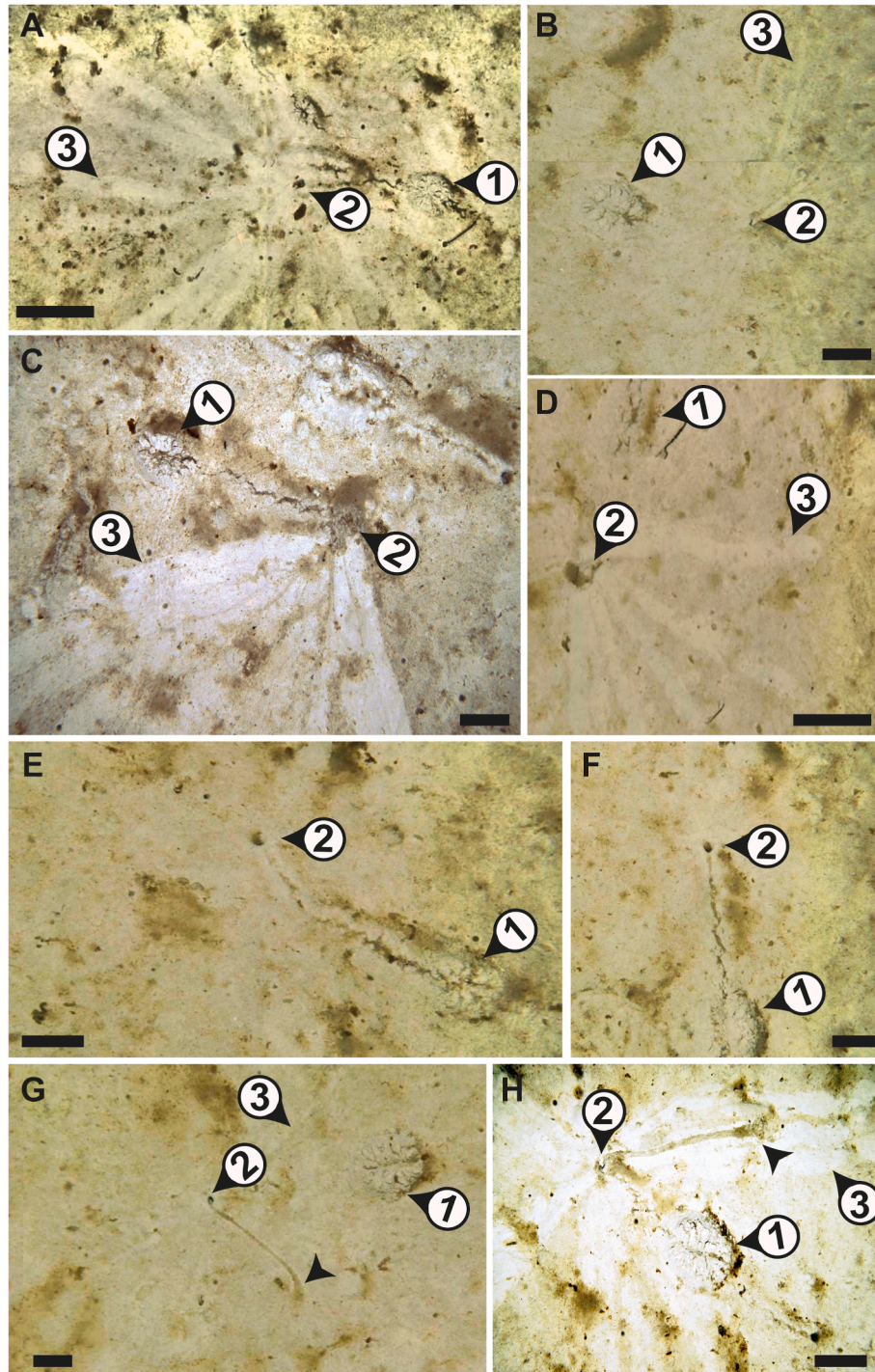
Fig. 3. Further examples of rosette-shape traces from the current study, with features numbered as in Fig. 2 A-D) Traces with nearby gashed mounds. E-F) Examples of traces not included in current analysis on the basis of their degraded condition, with spokes indistinct. G-H) Echiuran proboscis (black triangle), presumed to be in the act of producing spoke trace, note spatulate/truncate form. Scale bars = 10 cm.

2.3. Statistical analysis

Rosette-shape trace abundance (numerical density, seabed cover) and morphometric characteristics (spokes per trace, overlapping spokes per trace, spoke length, spoke length per trace, spoke width, spoke width per trace, spoke aspect ratio, trace measured area, trace proxy area, trace area ratio) were summarised as median values. Parameter precision was determined using 95% confidence intervals estimated by a bootstrapping procedure implemented in R (version 4.0.1, 2020-06-06; R Core Team, 2020) with the 'boot' package, in all cases based on 10,000 randomisations and using the adjusted bootstrap percentile (BCa) method (Davison and Hinkley, 1997; Canty and Ripley, 2021). Comparisons between sites were undertaken using the Wilcoxon-Mann-Whitney test as implemented in R (R Core Team, 2020). This statistical analysis was performed twice in the case of spoke length and width, initially considering all spoke lengths and widths, and secondly only considering the median values for each RST.

3. Results

In total 88 RSTs with a nearby gashed mound were assessed in the images from PAP-Central and 60 in those from North Plain (Fig. 3 and Tables 2 and 3). RST spokes were frequently near square ended to occasionally sub-rounded truncate at their extremity (e.g., lower left of Fig. 2). Generally, the spokes were comparatively broad and radiated linearly from a central burrow opening. The gashed mounds observed were sub-circular to ovoid in outline, with a long axis of 7–20 cm, and an upper surface that was variously fractured (Figs. 2 and 3). These mounds were typically located within one spoke length of the central burrow opening (Fig. 3). In some cases, the gashed mound and the corresponding burrow opening were connected by a sub-linear fracture (Figs. 2 and 3). Note that gashed mounds were present both when RSTs were mostly complete, with near full radial spoke coverage, and when only a few spokes had been completed. The trace maker was apparent in three cases, the presumed echiuran proboscides were translucent/uncoloured and spatulate/truncate (Fig. 3 G, H).

The estimated numerical density of complete RSTs was 175 ha^{-1} at PAP-Central and 159 ha^{-1} at North Plain (Table 2) and similar between both areas (W = 56,357 p = 0.69). The total seabed area covered by RSTs at PAP-Central and North Plain was 1.5 and 1.0% respectively (Table 2) and similar between both areas (W = 55,447, p = 0.90). The

median number of spokes per RST and the median number of overlapping spokes per RST were slightly higher at PAP-Central; the differences were nevertheless statistically significant in both cases (p < 0.01; Table 3). No statistically significant differences were detected in individual spoke length or width values between the study areas. Similarly, spoke median length and median width per RST, and spoke aspect ratio exhibited no statistically significant differences between the locations (Table 3). Individual RST area was statistically significantly different between the North Plain (median 0.53 m^2) and the PAP-Central (0.79 m^2) areas (Table 3; Fig. 4 A), while proxy trace area showed no statistically significantly difference between the sites (Fig. 4 B). However, relative individual trace completeness, as trace area ratio, did exhibit a statistically significant difference between the sites, being highest at PAP-Central, (p < 0.01; Table 3; Fig. 4 C).
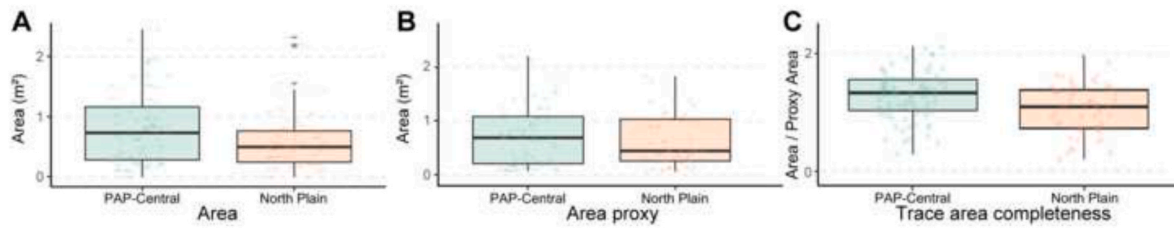
4. Discussion

Our results showed that RST numerical density, RST seabed cover and the individual morphological characteristics of the spokes (e.g., spoke length and width, aspect ratio) were similar at both abyssal plain sites. However, the number of spokes, the number of overlapping spokes, the individual trace area, and the trace completeness varied significantly between study areas (Table 3). This suggests that RST trace makers at the PAP-Central site were feeding from a greater area per trace, making more complete traces, prior to halting feeding and we assume moving to a new feeding location. Considering that the numerical density of echiurans (Durden et al., 2020b), the numerical density of RSTs, and RST seabed cover were similar at both sites, a number of questions arise in relation to what parameters may be behind specific RST morphological variations.

4.1. Echiuran ecology: RST density

Given our inability to identify the specific taxon responsible for any given spoke burrow, we limited our study to a single type of lebensspuren – that with an associated gashed mound – in the hope of obtaining data that would be more consistent between our study sites. That effort appears to have been generally successful in terms of spoke morphometrics; neither the individual spoke lengths or widths, nor the median spoke lengths or widths of individual RSTs, exhibited any statistically significant differences between sites (Table 3). While this does not provide any direct evidence of taxonomic consistency among the trace makers, we do believe that it provides evidence of functional-type consistency among the trace makers.

Quantifying a very similar RST, reported as type 2, Bett et al. (1995) recorded a numerical density of 68 ha^{-1} from photographic studies of sites on the Cape Verde Abyssal Plain (CVAP, c. 21° N, 31° W, 4560 m water depth). Note that value increased to 783 ha^{-1} when only data derived from an epibenthic sledge camera were considered, suggesting a limited ability to discriminate the type 2 trace in photographs taken with an off-bottom towed camera system used in the same study (see Fig. 7 of Bett et al., 1995). Mauviel (1982) also photographically surveyed similar spoke burrows ("*grande rosette*") at sites on the CVAP (c. 19° N, 30° W, 4900 m water depth) reporting a numerical density of 1940 ha^{-1}, though note this value encompasses a broader range of lebensspuren types ("*Cette rosette est parfois associée à un grand tumulus, un volcan ou à un tumulus crevasse*"). Taking these CVAP data together, gashed mound type RST density appears to be of the order 1000 ha^{-1}, substantially higher than our present estimate for the Porcupine Abyssal Plain (PAP) at 168 ha^{-1}. In our study, only complete RSTs were considered, so our density values are lower than those obtained if we had considered any partial appearance of RST. Regardless, we consider that our density estimates at PAP would be considerably lower than those observed at CVAP. We note that this is the reverse of the trend in megabenthos (and echiuran) numerical and biomass density at these two sites, as reported by Thurston et al. (1998), with PAP megabenthos biomass being over

Table 3

Porcupine Abyssal Plain Sustained Observatory rosette-shaped trace (RST) morphological data comparison between PAP-Central (PC) and North Plain (NP). (WMW, Wilcoxon-Mann-Whitney).

Metric	Site	n	Median	95% CI	WMW test (p-value)
Number of spokes per RST	PC	88	10	10–11	**<0.01**
	NP	60	8	7–9	
Number of overlapping spokes per RST	PC	88	4	3–5	**<0.01**
	NP	60	2	1.5–3	
Individual spoke length (mm)	PC	548	386	360–416	0.11
	NP	885	349	332–373	
Median spoke length per RST (mm)	PC	88	459	358–491	0.85
	NP	60	378	333–529	
Individual spoke width (mm)	PC	760	26.3	25.4–27.0	0.12
	NP	449	27.0	26.1–28.0	
Median spoke width per RST (mm)	PC	88	26.3	24.2–27.9	0.35
	NP	60	27.8	24.7–31.0	
Spoke aspect ratio	PC	80	15.1	12.2–17.3	0.32
	NP	60	13.3	12.2–14.9	
Measured area (m^2)	PC	88	0.79	0.62–0.88	**0.018**
	NP	60	0.53	0.42–0.64	
Proxy trace area (m^2)	PC	88	0.66	0.40–0.75	0.85
	NP	60	0.44	0.34–0.87	
Trace area ratio	PC	88	1.34	1.17–1.42	**<0.01**
	NP	60	1.09	0.81–1.21	

Fig. 4. Box plots of rosette-shape trace A) measured area, B) area proxy, and C) trace area completeness (measured/proxy) for PAP-Central (green) and North Plain (orange) study sites.

30-times higher than that at CVAP, that factor being increasing to over 180-times when only deposit feeder biomass is considered. This apparent discrepancy between lebensspuren numerical density and megabenthos abundance was considered by Bett et al. (1995), who noted that the former represents a dynamic balance between trace production and trace destruction rates, with the destruction rate likely closely linked to megabenthos abundance in quiescent abyssal environments. In the case of the CVAP, Bett et al. (1995) estimated that trace residence time could be on the order of 1–5 years, whereas on the PAP we would speculate that residence time would be considerably shorter, likely on the order of weeks to months.

The potential for an inverse relationship between lebesspuren trace abundance and megabenthos abundance was suggested in the early works by Kitchell et al. (1978; polar deep-sea) and Young et al. (1985; abyssal Venezuela Basin), with the latter authors noting that "The dynamics of biological activities affecting sedimentary structures are such that simple [positive] correlations between densities or diversities of Lebensspuren and similar measures of megafauna should not be expected" [p. 297]. Wheatcroft et al. (1989) developed this notion further in a simple numerical model of trace dynamics that indicates that the inverse relationship particularly relates to the relative abundance of trace "erasers" among the megabenthos; however, they also note the additional significance of sediment mixing by infaunal organisms and the physical reworking of surficial sediments by energetic bottom currents (e.g., Miguez-Salas et al., 2020). This potentially inverse relationship between lebensspuren numerical density or seabed cover and megabenthos abundance, and by inference organic matter supply (e.g., Wei et al., 2010; Bett, 2019), is likely to be potentially significant to any neo- or paleoichnological interpretation of these parameters. However, this consideration is unlikely to have impacted our study as megabenthos abundance varied little between sites and had the same trend as RST numerical density and seabed cover, all factors being higher at the PAP-Central site.

4.2. Echiuran ecology: potential impact of resource competition

As both sites are open, level-bottom, abyssal plain locations having near-identical (4848–4850 m and 4849–4850 m) water depths and sediment particle size distributions (18% and 19% particles >22.9 μm; Durden et al., 2020b), we identified variations in (a) the megabenthic communities, and (b) relative sediment consolidation, as the most likely potential drivers of RST characteristics. We discuss the former here and the latter in the following section (4.3.).

The numerical density and biomass density of deposit feeders varied statistically significantly between sites ($p < 0.01$), with the former lower at PAP-Central (1632 ind. Ha^{-1} PAP-Central, 2768 ind. Ha^{-1} North Plain) but the latter greater at PAP-Central (56.22 kg ha^{-1} PAP-Central, 48.39 kg ha^{-1} North Plain) (Durden et al., 2020b). That suggests that PAP-Central supports fewer but substantially larger megabenthic organisms, for example, apparent average individual biomass was almost twice as high at PAP-Central (34.4 g ind.$^{-1}$) as it was at North Plain (17.5 g ind.$^{-1}$). Despite the overall lower numerical density of deposit feeders at PAP-Central, higher densities of the largest benthic invertebrate known from the PAP-SO, the sea cucumber *Psychropotes longicauda*

(27.8 ind. Ha^{-1} PAP-Central, 12.3 ind. Ha^{-1} North Plain, $p < 0.01$; Durden et al., 2020b) were observed. *Psychropotes longicauda* is known to have the highest sediment surface tracking rate at PAP-SO (see Durden et al., 2019). Thus, the competition for nutrient resources among the benthic community at PAP-Central seafloor may be much greater than in the North Plain.

Given these observed differences in megabenthic communities between locations, we suggest that there may be a substantive difference in the availability of, and/or competition for, surface detritus between our study sites and that this may have influenced the recorded characteristics of the RSTs. When detrital material availability is low and/or competition for that resource is high, echiurans may feed from a greater area around a single burrow, and consequently develop more complete RSTs, in order to satisfy their energy requirements from a particular location. We consider that the significantly greater completeness of traces at the PAP-Central site may have been a response to greater competition for the sediment surface detritus resource.

Spoke morphology, length and width, observed in the present study is similar to prior studies by Ohta (1984, type III trace) and Bett et al. (1995, type 2 trace). However, the number of spokes per RST in our study was considerably lower than the data presented by Ohta (1984), up to 44 spokes, from sites in the Bay of Bengal. Nevertheless, Ohta (1984) did not specify the location where this trace (type III) was observed and his study area covered a broad range of environments (e. g., water depths between 2635 and 5025 m and stations separated by 1300 km approx.). Thus, a wide range in surface primary production (and thus, food supply to the deep seafloor; e.g., Lutz et al., 2007) and seafloor ecological conditions may be expected. Regardless of particular morphotype, the number of spokes per RST has been rarely documented in other studies; however, based on literature photographs, the number of spokes per RST appears to be typically higher than in our observations (see, e.g., Fig. 4 In Bett et al., 1995; type 2 A large rosette in Dundas and Przeslawski, 2009). This also appears to be true for the number of overlapping spokes; for example, Fig. 3 in Ohta (1984) illustrates more than 15 spokes overlapping, whereas as our data records a median value of four or less per RST (Table 2).

The apparently higher values observed in the literature for spoke number and overlap could potentially be related to resource supply, with the Porcupine Abyssal Plain being relatively eutrophic by comparison to the relatively oligotrophic Cape Verde Abyssal Plain (Bett et al., 1995), deep central Bay of Bengal (Ohta, 1984), and the deep Eastern Australian Margin (Dundas and Przeslawski, 2009). We might suggest that fewer spokes per RST, and consequently fewer overlapping spokes, may reflect the greater resource availability in relatively eutrophic settings, consistent with our earlier suggestion that trace completeness is inversely related to resource availability.

4.3. Echiuran ecology: potential impact of sediment consolidation

Seamounts and abyssal hills are very common features of the abyssal environment, with abyssal hill terrain potentially the most widespread landform on Earth (Harris et al., 2014). These isolated topographic elevations in the abyss modify local hydrodynamics and consequently impact the deposition of organic and inorganic particulate material both

on these features and to the immediately surrounding abyssal plain environments (e.g., Morris et al., 2016 and references therein). In addition to these hydrodynamic effects, seamounts and abyssal hills provide the source material for gravity flows that deposit sedimentary material, turbidites, on to adjacent abyssal plains potentially modifying local sediment characteristics, such as particle size distribution, and relative consolidation (Rebesco et al., 2014). Sediment consolidation has rarely been considered in relation to lebensspuren analysis (e.g., Uchman and Perveslar, 2006). In the abyssal northeastern Pacific (Station M, c. 35° N 123° W, 4000 m water depth) Miguez-Salas et al. (2020) observed that the action of benthic storm events resuspended and removed surficial sediments, exhuming a more consolidated surface, and that this process altered lebensspuren formation. In the study of lebensspuren as trace fossils (paleoichnology), sediment consolidation is considered a limiting environmental factor, controlling trace maker behaviour, trace fossil formation, and morphological attributes (Buatois and Mángano, 2011). Morphological changes in trace fossils, resulting from different degrees of substratum firmness, are thought to be common in both shallow-water and deep-sea environments (e.g., Fig. 6.2 in Buatois and Mángano, 2011).

Sediment consolidation varied markedly between our two study sites (Ruhl, 2013; Hartman, 2022), with the upper sediment column in the North Plain area having >100 cm of unconsolidated turbidite deposit while the PAP-Central area sediments were consolidated within c. 10 cm of the sediment surface. We are unaware of any prior research on the impact of substratum consistency on RST morphology. Our results appear to suggest that the relative consolidation of the upper sediment column had no impact on spoke morphometrics, and by implication that it did not influence either echiuran feeding behaviour or RST formation. This seems reasonable given that the volumetric mass density of Porcupine Abyssal Plain soft-bodied invertebrates has been estimated at 1.05–1.06 (Benoist et al., 2019), almost identical to that of the ambient seawater. However, we cannot predict or elucidate if the consolidation can affect RST burrow morphology (e.g., burrow penetration depth, burrow dip angle; see question marks in Fig. 1). Our present observations of course do not cover trace taphonomy, so may be relevant to neoichnology, but may not necessarily hold in a paleoichnological sense.

As detailed above (section 4.2.), we did record statistically significant differences in the number of spokes per trace, trace area, and trace completeness between the two study areas, but consider this most likely to be related to resource competition rather than sediment consolidation. Consequently, it is possible that these parameters were indirectly impacted by relative sediment consolidation via the latter's effect on the broader megabenthos community (Durden et al., 2020b).

4.4. Application to the fossil record

Rosette-shape trace fossil analogues are found in the fossil record and have been documented since the Cambrian and experienced an evolutionary diversification through the Phanerozoic (Muñoz et al., 2019). Rosette-shape trace fossil in general could be produced by diverse clades, including worms (particularly polychaetes), crustaceans (amphipods and decapods), bivalves and even fish (Häntzschel, 1970). Given the morphology of the RSTs considered in the present study (e.g., spoke length and width, trace area) and the most similar ichnogenera related to echiuran trace makers, the analogues of our RSTs may be *Asterichnus*, *Estrellichnus*, and *Cladichnus* (Muñoz et al., 2019; Adserá et al., 2020). The primary differences in traces between our two study sites concern variations in the number of spokes per trace, trace area, and trace completeness, factors which may also be important in paleoichnological assessments. In the literature, variations in these parameters can be appreciated within ichnospecies (e.g., *Cladichnus fischeri*), where specimens exhibit different degrees of trace completeness (see Fig. 1D in Muñoz et al., 2019). However, no morphological measurement of completeness has been conducted. Also, specimens of other rosette-shape ichnospecies (e.g., *Dactyloidites ottoi*) have been

documented to show area variations within the same depositional beds, changes in the number of spokes, and degree of overlapping (Wilmsen and Niebuhr, 2014).

Combining these paleoichnological observations with the neo-ichnological information of the present study suggests that relative RST completeness and trace area may be useful parameters in both the interpretation of the fossil record and the study of contemporary echiuran ecology. As detailed above (section 4.1.), the numerical density of RSTs can be a complex parameter to interpret, it may exhibit an inverse relationship with echiuran density and potentially annual particulate organic carbon flux. In contrast, assessment of individual RST completeness and area might provide a more direct proxy measure of resource availability. It is conceivable that a combined analysis of RST numerical density and individual trace completeness or area could offer a valuable insight into paleo-environmental conditions.

5. Conclusions

The analysis of rosette-shape traces (RSTs) from two contrasting sites at the Porcupine Abyssal Plain Sustained Observatory (PAP-Central and North Plain) provides the following conclusions.

- Comparing our present results with published data on similar RSTs in a relatively oligotrophic abyssal setting, we note a potential inverse relationship between numerical density of RSTs and the abundance of megabenthos, and by inference organic matter supply, at least in those quiescent abyssal environments, where trace destruction is dominated by over-tracking by other members of the megabenthos.
- RST variation between the two PAP-SO study areas was related to individual trace completeness (expressed as number of spokes, number of overlapping spokes, trace area, and trace area ration); we suggest that this difference may have been primarily driven by relative levels of competition for sediment surface detrital resource with other members of the megabenthic community.
- We further suggest, by reference to RST characteristics in other deep-water environments, that RST completeness may be a useful proxy for relative resource availability and more generally for echiuran ecology.
- The marked difference in sediment consolidation between our two study sites did not appear to impact spoke morphology, nor directly trace completeness, though it remains conceivable that sediment consolidation impacted megabenthos community composition and thereby relative levels of resource competition.
- Our observations may be of relevance in paleoichnology, particularly in terms of the potential linkage between RST completeness and resource availability. We would recommend the statistical assessment of RST assemblage completeness as a routine component of studies of contemporary rosette shape lebensspuren and rosette shape trace fossils in paleoenvironmental assessments.

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