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Progress in Oceanography

journal homepage: www.elsevier.com/locate/pocean

Subtle variation in abyssal terrain induces significant change in benthic megafaunal abundance, diversity, and community structure

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ARTICLE INFO

Keywords:

Deep sea
Ecology
Seabed environment
Abyssal plain
Porcupine Abyssal Plain Sustained Observatory
Marine photography

ABSTRACT

Bathymetric gradients in the deep sea are known to affect key benthic community characteristics such as diversity. However, most studies investigate large-scale bathymetric variation, while habitat heterogeneity related to modest bathymetric variation has generally been overlooked because of limitations to sampling technology. We investigate the role of modest bathymetric variation (~10 m water depth intervals) on an abyssal hill, and horizontal variation at the 0.1–10 km scale, in the structuring of abyssal megafaunal assemblages. We assess numerical density, biomass density, diversity, and assemblage composition using seabed photographs captured with an autonomous underwater vehicle and sediment characteristics determined from cores. We detect significant differences in sediment particle size and organic carbon content, in relation to modest topographic elevation, with a greater fraction of fine particles and organic carbon on the abyssal plain than the hill. Total megafaunal numerical and biomass density, diversity, and the numerical densities of feeding groups were significantly different with modest topographic elevation; similarly, megafaunal composition varied significantly between ~10 m depth intervals. In relation to mesoscale horizontal variation, we also record significant differences between megabenthic communities in two abyssal plain areas with no significant differences in measured sedimentary characteristics and only a 2 m difference in water depth. Differences in these communities were detected in terms of dominance, assemblage composition by density and biomass, and numerical densities of feeding groups. These observations strongly indicate that previous general concepts of the abyssal environment greatly underestimate this mesoscale heterogeneity, such that beta- and gamma-diversity in the abyss may be higher than estimated. Importantly, these results also have clear implications for the design and interpretation of environmental survey and monitoring programmes in the abyss.

1. Introduction

Bathymetric gradients in the deep sea are known to affect key benthic community characteristics such as diversity (Flach et al., 1998), zonation (Carney, 2005; Carney et al., 1983; Olabarria, 2005), body size (Rex & Etter, 1998; Rex et al., 2006), and standing stocks (Lampitt et al., 1986). However, most studies investigate large-scale bathymetric variation at intervals of hundreds to thousands of metres. Similarly, major bathymetric features in the deep ocean are known to affect the structure and function of benthic communities at large scales, such as noted in seamount studies (e.g. Clark et al., 2009; Mendonca et al., 2012; Rogers, 1994; Rowden et al., 2010). More recently, corresponding variations in community characteristics have also been detected at more modest elevations in studies of abyssal hills (rising < 1000 m above the abyssal plain) and ridges (e.g. Durden et al., 2015a;

Simon-Lledo et al., 2019; Stefanoudis et al., 2016b). While many of the ecological variations noted with water depth may not be causally related to variations in depth or pressure per se, change in water depth appears to serve as a proxy of potential environmental change and heterogeneity. Determining at what scale that heterogeneity becomes important (i.e. ecologically significant) is key to designing and executing an effective environmental survey that has sufficient power to detect any spatial and/or temporal change.

Studying the impact of subtle bathymetric variation at scale has been challenging or impossible because of limitations to positional precision in sampling technology, such as that often used with towed cameras and epibenthic sledges. The development of remotely-operated and autonomous underwater vehicles (ROVs and AUVs) and improvements to underwater navigation systems (e.g. inertial navigation and acoustic systems) combined with high resolution seabed photography

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Received 24 October 2019; Received in revised form 8 June 2020; Accepted 17 June 2020

Available online 24 June 2020

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(Durden et al., 2016c) has revolutionized abyssal benthic ecology by increasing the seabed area and number of organisms studied (e.g. Morris et al., 2014). It has also facilitated detailed ecological surveys and mapping of seabed features at finer scales (e.g. Milligan et al., 2016; Morris et al., 2016; Robert, Jones, Tyler, Van Rooij & Huvenne, 2015) and studies of inter-species spatial distribution relationships (Mitchell et al., accepted for publication).

We investigate the role of modest bathymetric variation (~10 m water depth intervals), and horizontal variation at the 0.1–10 km scale, in the structuring of abyssal megafaunal assemblages in the well-studied seafloor environment of the Porcupine Abyssal Plain Sustained Observatory site (PAP-SO; Hartman et al., 2012). In common with the overwhelming majority of abyssal plain areas worldwide (Harris et al., 2014), the PAP-SO area is punctuated with numerous abyssal hills. Durden et al. (2015a) established the scope for substantial variations in the seabed environment and megabenthic community between hill summits and the surrounding abyssal plain. Subsequent detailed studies of a small hill in the central PAP-SO area indicated no significant variations in the broad scale distribution of the demersal fish fauna (Milligan et al., 2016); however, particulate organic matter and invertebrate megabenthos biomass was significantly greater on that hill (Morris et al., 2016). We extend those latter studies with a detailed examination of variations in the megabenthic community in terms of numerical and biomass density, diversity, and assemblage composition as it varies in relation to modest vertical and greater horizontal scales using seabed photographs captured with an AUV. We revisit the long overturned paradigm of a 'uniform abyss' to establish at what scale the abyssal seabed environment might be considered practically homogeneous in the context of contemporary environmental survey and monitoring programmes – not least the on-going 35+ year time-series observations at the Porcupine Abyssal Plain Sustained Observatory.

2. Methods

2.1. Study location and design

The benthic environment and epifaunal megabenthic assemblages on a single abyssal hill at the Porcupine Abyssal Plain Sustained Observatory (northeast Atlantic), and the adjacent abyssal plain were the focus of this study (Fig. 1). Previous work examined the habitats and communities on the summits (and one flank) of three abyssal hills (summits between 4633 and 4339 m water depth; Durden et al., 2015a); the lowest of these three abyssal hills (H3) and the 'PAP Central' site (P1) of benthic time-series observations on the abyssal plain (4850 m water depth) were examined in the present study (Fig. 2). The habitats of the hill and plain were examined in two ways: (1) in water depth bands (12.5 m intervals); and (2) in spatially discrete areas (see grids, below). Samples and data on the benthic environment and megabenthic assemblages were collected during RRS *Discovery* research cruise 377 (Ruhl & scientists, 2013) using the autonomous underwater vehicle Autosub6000 (Morris et al., 2014), and a Bowers & Connelly Megacorer (Gage & Bett, 2005). The AUV photographic transects formed grids at two scales: (i) three fine-scale grids with transects at 100 m line spacing, 'North Plain' and 'PAP Central' on the abyssal plain, and 'Hill' on the flank of abyssal hill H3, and (ii) a coarse-scale grid with transects at 1 km line spacing (Fig. 2).

2.2. Assessment of the benthic environment

Seabed bathymetry was derived from a composite of data acquired from RRS *Charles Darwin* cruise 158 using a shipborne Kongsberg EM12 multibeam echosounder (Lampitt, 2010) and RRS *James Cook* 062 using an EM120 multibeam echosounder (Ruhl, 2012); both MBES systems were operated at 12 kHz. These data were processed using Caris HIPS and SIPS to a 50 m grid (Fig. 2).

Sediment characteristics were assessed from core samples.

Following inspection of the sediment profile and the surficial sediment for glacial dropstones (Durden et al., 2015a), mean sediment particle size was determined in the 0–50 mm depth horizon from triplicate analyses by laser diffraction using a Malvern Mastersizer after homogenization and suspension in a 0.05% (NaPO₃)₆ solution. As particle size distributions were bimodal, results were reported as coarse sediment fraction (> 22.9 μm). Total organic carbon (TOC) content (as percentage dry mass) was determined in the 0–10 mm depth horizon (details in Durden, Ruhl, Pebody, Blackbird & van Oevelen, 2017).

Turbidity in near-bottom water (≤10 m above the seafloor) over the hill and the surrounding plain was measured at 2-second intervals by detecting 880 nm light scattered by suspended particles near the Seapoint Turbidity Meter (Seapoint Sensors, Inc.) mounted on Autosub6000, calibrated to Formazin Turbidity Units (Morris et al., 2016).

2.3. Assessment of the megafaunal community

The megafaunal community was assessed in downward seabed photographs captured with a Point Gray Research Inc. Grasshopper 2 camera (2448 × 2048 pixels; 12 mm lens, 2/3" sensor) mounted on Autosub6000. Images were captured at an interval of 0.9 s, with Autosub6000 operating at a target altitude of 3.2 m. Methods for the processing of photos were detailed by Morris et al. (2014), including the removal of overlap between consecutive images, and their grouping into mosaicked 'tiles', with the resultant tiles comprising approximately 10 images and encompassing a seabed area of ~14 m².

Discernible megafaunal specimens (> 10 mm in size, Bett, 2019; Grassle et al., 1975) were enumerated and classified to the most detailed taxonomic level possible in 6472 tiles (~9 ha seafloor area) using a custom macro in ImagePro Plus (Media Cybernetics) by one of three assessors. To avoid potential unintended spatial bias in the image annotation process, tiles were randomised prior to assessment (see Durden et al., 2016b). Fresh wet weight biomass was estimated for each specimen using the method described in Durden, Bett, Billett, Horton, Morris et al. (2016a). Where only a portion of a specimen was visible, the specimen was enumerated, and the biomass was estimated as half of the individual mean for that morphotype. Quality assurance/quality control of the annotations was conducted by comparing annotations from a subset of 67 tiles from the PAP Central area given to all three assessors, as reported in Durden et al. (2016b); those tiles were removed prior to the analyses reported here. Each morphotype was assigned to a feeding group (suspension feeders, deposit feeders, predators/scavengers) based on existing literature (see summary in Durden et al., 2015a). Note that *Iosactis vagabunda* was excluded from the feeding group analysis, as this anemone is known to switch feeding modes (though the portion of time spent in each feeding mode is unknown) and is the most numerically abundant megafaunal morphotype on the abyssal plain (Durden et al., 2015b). Faunal abundance and fresh wet weight biomass per tile were converted to areal densities (individuals ha⁻¹ and g m⁻²).

2.4. Statistical analysis

To assess changes in the benthic habitat and communities at fine-scale depth increments, environmental and faunal data were divided into depth groups at 12.5 m intervals (Tables 1, S1, S2; Fig. 2), matching those previously employed by Morris et al. (2016). Tiles in each depth group were aggregated by random selection without replacement into sampling units of 60 tiles, to give a known seabed area of approximately 850 m², equivalent to the mean area of the photographic transects reported by Durden et al. (2015a). Note that no photographs were collected from the top of the abyssal hill (H3; depth group 0; Fig. 2B), and that no sediment cores were collected from depth group 3, and only one core was collected from each of depth groups 2 and 4 (Fig. 2A).

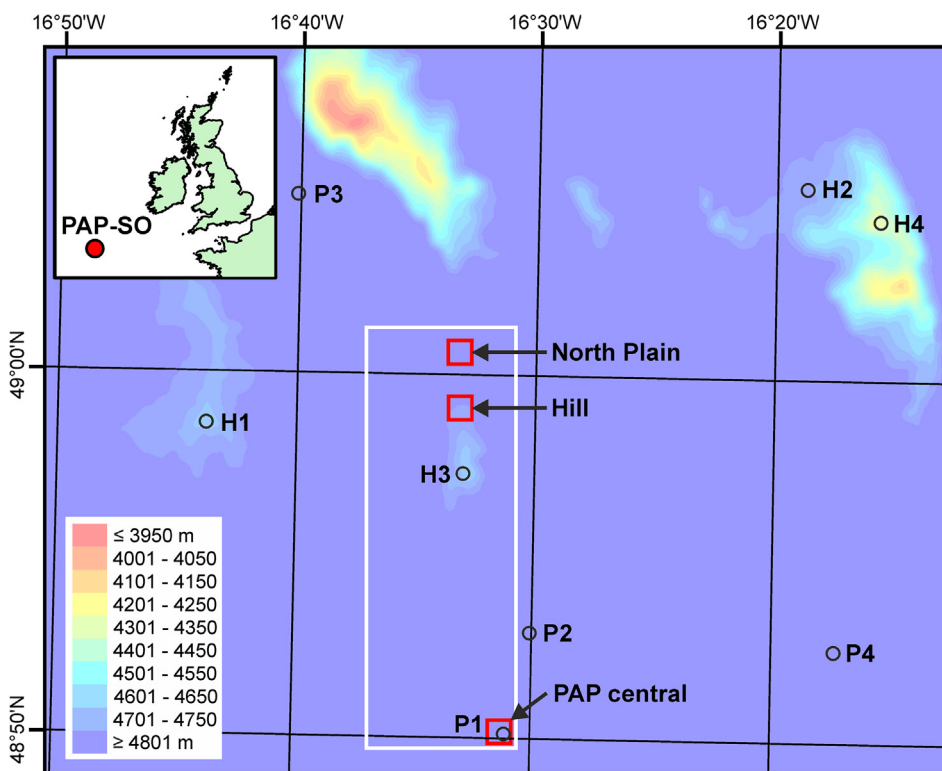


Fig. 1. The local context of the Porcupine Abyssal Plain study area. The current study area included the abyssal plain and one abyssal hill (white box; detailed in Fig. 2); fine-scale grids indicated with red boxes: North Plain, Hill and PAP Central. Also illustrated are locations of a prior photographic study (black diamonds; sites from Durden et al., 2015), encompassing four abyssal plain (P) and four abyssal hill (H) sites. (Map datum WGS 1984; projection UTM Zone 28N; WKID: 102578). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

To assess potential spatial differences in the benthic habitat and communities in the greater area surveyed, the total tile set was separately divided into sets comprising the coarse grid and the three fine-scale grids (Fig. 2). Tiles in each grid were aggregated into sample units of 60 tiles, again based on random selection without replacement.

Numerical and biomass density were computed for all sampling units in both the bathymetric and spatial studies. These data were square root-transformed, while proportional data were arcsine-transformed prior to parametric statistical analyses. Comparisons between depth groups and grids were made using ANOVA, and potential correlations between continuous environmental data (e.g. TOC and coarse sediment fraction) were examined with Spearman's rank method, both with significance reported at $\alpha = 0.05$. To examine spatial variation, numerical density was also computed for tiles aggregated into $200\text{ m} \times 200\text{ m}$ cells.

Univariate Hill's diversity indices (N_q , $q = 0, 1, 2$) were calculated, as was the expected (i.e. rarefied) number of morphotypes (Hurlbert, 1971) at the minimum number of individuals in any sampling unit (across both bathymetric and spatial studies). The 'Abundance Biomass Comparison' (ABC) method provides a means of assessing a key structural component of communities (Warwick, 1986), that provides insight into potential relative level of disturbance or successional state. It can be formally assessed using the W-statistic, a comparison statistic of the difference between density and biomass k-dominance curves (Clarke, 1990; Durden et al., 2015a; Warwick & Clarke, 1994). Community composition was assessed through multivariate analyses of square root-transformed faunal density and biomass data from the sampling units using Bray-Curtis similarity matrices, and the results presented as non-metric multidimensional scaling ordinations. Comparisons between the depth groups and between the grids were made using ANOSIM, with any apparent differences examined using SIMPER. Statistical analyses were performed using R (R Core Team, 2019) and the vegan package (Oksanen et al., 2012).

The potential impact of selected sample unit size on density, number of morphotypes, and biomass was assessed for depth groups and in the grids by constructing accumulation curves of median values computed

by aggregating tiles randomly 1000 times.

3. Results

3.1. Assessment of the depth groups

3.1.1. Benthic habitat

The summit of abyssal hill H3 was estimated at 462 m above the abyssal plain, itself at 4854 m water depth (Figs. 1 and 2). Depth groups 1–5 above the abyssal plain (depth group 6) extended 63 m above the abyssal plain, to 4775 m water depth. The highest elevation sampled in depth group 0, where no photography took place, was at a water depth of 4633 m, less than half the altitude of the summit.

The near-seabed suspended particle load, measured as turbidity, differed significantly with depth group (ANOVA $F[6,85659] = 1168$, $p < 0.001$). It was significantly increased over elevated terrain relative to the abyssal plain (depth group 6; Tables 1, S1), with the magnitude of the increase being in the range 5–10%.

Sediment characteristics varied with elevation. The coarse particle fraction and total organic carbon (TOC) content were significantly different with depth group (ANOVA $F[5,20] = 5.5$, $p < 0.01$ and $F[1,24] = 17.9$, $p < 0.01$, respectively). TOC was significantly negatively correlated with the coarse sediment fraction ($r_s = -0.9$, $p < 0.05$). That is, deeper depth groups generally had a greater proportion of fine sediments, with which more organic carbon was associated.

3.1.2. Megafaunal community

3.1.2.1. Standing stocks. Total megafaunal numerical density was significantly related to depth group (ANOVA $F[5,99] = 21.2$, $p < 0.001$), and generally higher up the hill, except depth group 1 (Tables 1, S2). Megafaunal biomass density also varied significantly with depth group ($F[5,99] = 3.0$, $p < 0.05$), and was higher in depth groups on the hill (1–5) than on the plain (6), peaking in depth group 4, with maximum biomass per sample unit elevated in depth groups 2, 4 and 5 (Table S2).

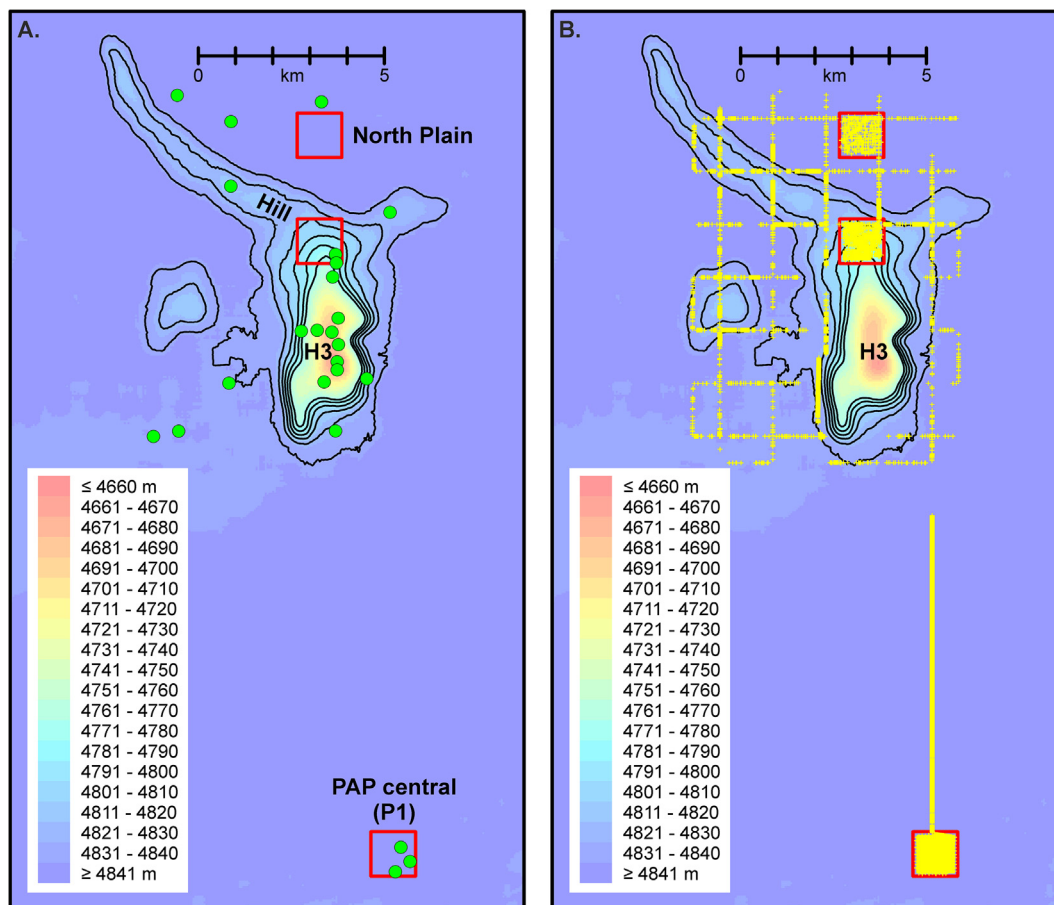


Fig. 2. Details of the current study area, including abyssal hill and plain habitats, with boundaries between depth groups shown in black contours (4775.0, 4787.5, 4800.0, 4812.5, 4825.0, and 4837.5 m water depth) and locations fine-scale grids indicated by red boxes. (A) locations of sediment coring sites and (B) locations of photographic tiles, showing the coarse grid. (Map datum WGS 1984; projection UTM Zone 28N; WKID: 102578). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.1.2.2. Diversity. Overall, 75 morphotypes were observed. All morphotypes found in each of the abyssal hill depth groups (1–5) were also recorded in other depth groups (1–6), while nine morphotypes were only recorded on the abyssal plain (depth group 6). The expected number of morphotypes (EM_{401} ; Table 1) was higher in the shallowest two depth groups (1 and 2). Hill numbers (N_q , $q = 0, 1, 2$) varied significantly with depth group (ANOVA N_0 : $F[5,99] = 3.2$, $p < 0.01$, N_1 : $F[5,99] = 43.2$, $p < 0.001$, N_2 : $F[5,99] = 80.5$, $p < 0.001$), generally increasing with elevation above the abyssal plain.

The most common morphotype on the abyssal hill (depth groups 1–5) was Ophiuroidea, with Elpidiidae spp. (comprising *Amperima* sp., *Ellipinion* sp., *Kolga* sp. but excluding *Peniagone* sp.) the second most common, while *Iosactis vagabunda* was the most common on the abyssal plain (depth group 6), followed by Ophiuroidea and Elpidiidae spp. *I. vagabunda* was recorded in all depth groups, but at substantially higher densities in the bottom two depth groups (Table 1). On the abyssal plain (depth group 6), the relative abundance of *I. vagabunda* was double that of depth group 5, which was in turn double that of the shallower depth groups (1–4). The abyssal plain assemblage (depth group 6) was dominated by a few morphotypes (Fig. 3): six morphotypes had numerical densities > 100 ind ha^{-1} , while 41 morphotypes had densities < 10 ind ha^{-1} . The numerical density of *I. vagabunda* was more than double that of the second-ranked Ophiuroidea, while the density of third-ranked Elpidiidae spp. was half that of Ophiuroidea. The assemblages in depth groups 1–3 were characterised by lower dominance: 10 morphotypes had numerical densities > 100 ind ha^{-1} , while 18–22 morphotypes had densities < 10 ind ha^{-1} . The numerical density of

Ophiuroidea was about double than on the abyssal plain (depth group 6), and almost double the density of the second-ranked Elpidiidae spp. The assemblages in depth groups 4 and 5 were of an intermediate state of dominance.

On the abyssal hill (depth groups 1–5), biomass was dominated by Elpidiidae spp. On the abyssal plain (depth group 6), biomass was characterised by high evenness, with the biomass of the first-ranked *Psychropotes longicauda* (1.7 g m^{-2}) $\sim 50\%$ greater than that of third ranked *Molpadiodemas villosus*, with Elpidiidae spp. ranked second. These three holothurian morphotypes were major contributors to megafaunal biomass in all depth groups. In depth group 5, the dominance of Elpidiidae spp. remained apparent: the biomass of Elpidiidae spp. was more than five times that of the third-ranked *M. villosus*. In the most elevated depth groups (1 to 3), assemblage evenness was somewhat higher, with the biomass of Elpidiidae spp. (2.8 – 2.9 g m^{-2}) dominating and contributing double the biomass of Cnidaria sp.16 (ranked either second or third). The W-statistic varied significantly with depth group ($F[5,99] = 5.7$, $p < 0.001$), and was significantly lower on the abyssal plain (depth group 6) than on the abyssal hill (depth groups 1–5). That difference remained statistically significant when the comparison was limited to the abyssal plain (depth group 6) and minimal elevation on the abyssal hill (depth group 5; $F[1,85] = 7.1$, $p < 0.01$).

3.1.2.3. Assemblage composition. Megafaunal composition by numerical density varied significantly between depth groups (ANOSIM $R = 0.88$, $p < 0.001$; Fig. 4a), with the abyssal plain (depth group 6) markedly distinct from all abyssal hill depth groups (1–5). The morphotypes that

Table 1
 Summary of environmental data, near-seabed turbidity, sediment coarse particle content and total organic carbon (TOC) content, and megafaunal community metrics from seabed photographs by depth group and spatial grids expressed as means: density-based diversity metrics (Hill numbers), and density and biomass of *Iosactis vagabunda* and feeding groups; Fine-scale grids: Hill, PAP Central, North Plain; * Assigned depth range for depth groups (group 0 range from cores); depth range from tiles for grids.

| Depth Group or Grid | Depth range (m) * | Turbidity (NTU) | Coarse content (%) | TOC (%) | Density (ind ha ⁻¹) | Biomass (g _{wet} m ⁻²) | Hill numbers | | | EM ₄₀₁ | W | <i>Iosactis vagabunda</i> | | Suspension Feeders | | Deposit Feeders | |
|---------------------|-------------------|-----------------|--------------------|---------|---------------------------------|---|----------------|----------------|----------------|-------------------|-------|---------------------------------|------------------|---------------------------------|------------------------------|---------------------------------|------------------------------|
| | | | | | | | N ₀ | N ₁ | N ₂ | | | Density (ind ha ⁻¹) | Relative density | Density (ind ha ⁻¹) | Biomass (g m ⁻²) | Density (ind ha ⁻¹) | Biomass (g m ⁻²) |
| 0 | 4633-4718 | 0.0599 | 42 | 0.300 | 6638 | 8.168 | 39.00 | 10.68 | 5.67 | 34.7 | 0.060 | 483 | 0.07 | 1793 | 2.468 | 3982 | 5.573 |
| 1 | 4775 - 4787.5 | 0.0601 | 27 | 0.328 | 6948 | 9.403 | 38.20 | 9.79 | 5.21 | 33.8 | 0.043 | 634 | 0.09 | 1736 | 2.747 | 4300 | 6.516 |
| 2 | 4787.5-4800 | 0.0603 | 10 | 0.380 | 6825 | 8.026 | 35.17 | 9.04 | 4.94 | 31.5 | 0.043 | 675 | 0.10 | 1658 | 2.350 | 4213 | 5.537 |
| 3 | 4800 - 4812.5 | 0.0608 | - | - | 6230 | 12.863 | 33.25 | 8.91 | 5.09 | 32.4 | 0.067 | 843 | 0.13 | 1255 | 2.144 | 3953 | 10.504 |
| 4 | 4812.5-4825 | 0.0634 | 32 | 0.350 | 5832 | 8.101 | 33.88 | 7.87 | 4.79 | 31.6 | 0.047 | 1155 | 0.20 | 863 | 1.191 | 3575 | 6.717 |
| 5 | 4825 - 4837.5 | 0.0628 | 22 | 0.354 | 6008 | 7.213 | 33.87 | 6.98 | 3.62 | 32.1 | 0.010 | 2871 | 0.48 | 849 | 0.727 | 2004 | 6.076 |
| 6 | > 4837.5 | 0.0583 | 21 | 0.361 | 6875 | 9.000 | 36.65 | 9.66 | 5.20 | 32.5 | 0.053 | 636 | 0.09 | 1731 | 2.506 | 4202 | 6.470 |
| Hill | 4773-4821 | - | 27 | 0.328 | 6303 | 6.345 | 32.15 | 6.36 | 3.05 | 30.3 | 0.008 | 3460 | 0.50 | 919 | 0.625 | 1632 | 5.622 |
| PAP Central | 4848-4850 | - | 18 | 0.382 | 6110 | 5.723 | 31.80 | 6.64 | 3.87 | 29.5 | 0.007 | 2281 | 0.37 | 771 | 0.633 | 2768 | 4.839 |
| North Plain | 4849-4853 | - | 19 | 0.369 | 5773 | 7.949 | 35.08 | 7.79 | 4.44 | 33.4 | 0.023 | 2168 | 0.38 | 823 | 0.919 | 2508 | 6.923 |
| Coarse grid | 4814-4853 | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - | - |

contributed most to the dissimilarity between the abyssal plain (depth group 6) and minimal elevation on the abyssal hill (depth groups 1-5) were *I. vagabunda* (12%), Elpidiidae spp. (8%) and Ophiuroidea (5%). The composition of the megafaunal assemblage by biomass density also varied significantly with depth group (R = 0.53, p < 0.001; Fig. 4b). Again, the assemblage on the abyssal plain (depth group 6) was distinct from that on the abyssal hill (depth groups 1-5), with dissimilarity between the abyssal plain (depth group 6) and minimal elevation on the abyssal hill (depth group 5) driven by *P. longicauda* (12%), Elpidiidae spp. (10%) and *M. villosus* (8%).

In terms of feeding types, the numerical densities of deposit feeders, suspension feeders and predators/scavengers were significantly different between depth groups (ANOVA F[5,99] = 374, p < 0.001, F [5,99] = 103, p < 0.001, and F[5,99] = 2.3, p < 0.05, respectively), with suspension feeder density decreasing down the hill. Dissimilarity in trophic composition between depth groups increased down the hill, and was driven by deposit feeders in depth groups 1-2 (37%) and 2-3 (36%), then by suspension feeders in depth groups 3-4 (51%) and 4-5 (53%), and then by deposit feeders between depth groups 5 and 6 (77%). The biomass densities of deposit and suspension feeders varied significantly between depth groups (F[5,99] = 3.0, p < 0.05; F[5,99] = 69.1, p < 0.001, respectively), the latter being ~300+% of the value on the abyssal plain in depth groups 1-4, and 160% of the value on the abyssal plain in depth band 5. The relative biomass of deposit feeders contributed most to dissimilarity in trophic composition between all depth groups (58-73%; Fig. 5).

3.2. Assessment of fine and coarse-scale grids

3.2.1. Benthic environment

The abyssal hill fine grid (Hill) was located on the flank of abyssal hill H3 (Fig. 1). The North Plain fine grid was located on the abyssal plain to the north of abyssal hill H3, and approximately 3 km from a seamount further to the north. The PAP Central fine grid was located in the primary area of the PAP-SO time series. The Coarse grid surrounded abyssal hill H3 and encompassed predominantly abyssal plain, but also included a low ridge-like extension of abyssal hill H3 to the northwest (~25 m above the seabed), and a low knoll-like area about 2 km west of abyssal hill H3 (Fig. 2).

The mean water depth of the Hill fine grid was 50 m above the abyssal plain, but ranged over 48 m, on the flank of the abyssal hill H3 at depths equivalent to depth groups 1-4. Median seabed slope was 2.5°. The two fine grids on the abyssal plain were at slightly different depths within depth group 6. Mean water depth of the North Plain fine grid was significantly, but minimally, deeper (< 2 m) than that of the PAP Central fine grid (F[1,36] = 1999.8, p < 0.001). The median slope in the North Plain grid was 0.4°, slightly higher than at PAP Central fine grid (0.3°). The mean water depth of the Coarse grid was shallower than the two fine grids on the plain, and ranged 39 m, at water depths within depth groups 4-6.

3.2.2. Megafaunal community

3.2.2.1. Standing stocks.

Megafaunal community numerical density was significantly different between the grids (F[3,102] = 62.6, p < 0.001; Tables 1 and S2), though these differences were not particularly marked. Total density was also significantly different between fine grids (F[2,52] = 21.2, p < 0.001), with the highest density found in the Hill grid and lowest density in the grids on the abyssal plain. The biomass density of the megafaunal community also significantly differed between grids (F[3,102] = 7.7, p < 0.001), and between fine grids (F[2,52] = 8.5, p < 0.001). The highest biomass density was found in the Hill grid, and the lowest in the grids on the abyssal plain. Note that the North Plain and PAP Central fine grids were not statistically significantly different in terms of either numerical or biomass density.

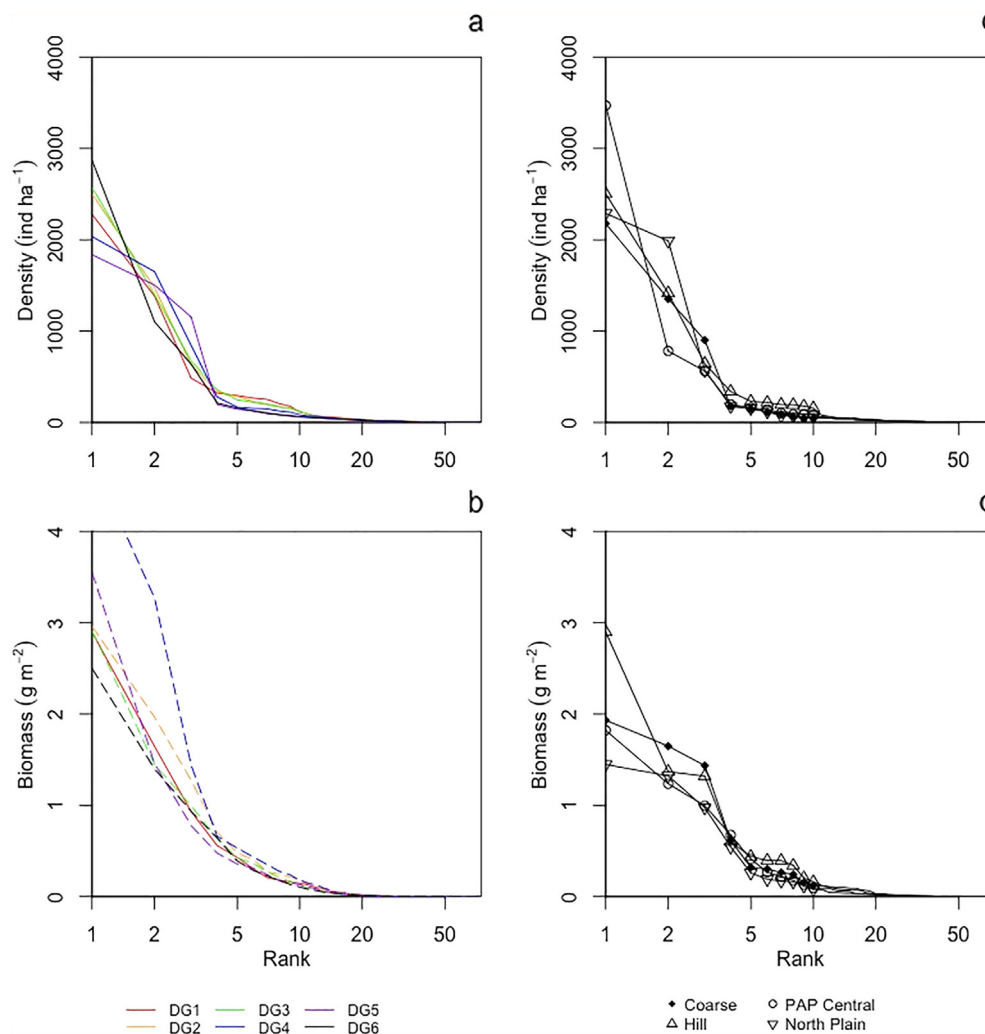


Fig. 3. Ranked numerical density and fresh wet weight biomass in the megafaunal assemblages on an abyssal hill by 12.5 m depth group (a, b), and by grid (c, d).

3.2.2.2. Diversity. All diversity metrics tested varied significantly between the grids (EM₄₁₀: $F[3,102] = 11.6$, $p < 0.001$; N_0 : $F[3,102] = 11.4$, $p < 0.001$; N_1 : $F[3,102] = 100.4$, $p < 0.001$; N_2 : $F[3,102] = 227.0$, $p < 0.001$). Across the diversity metrics, the highest values were associated with elevated terrain (on the abyssal hill) or mixed terrain (in the Coarse grid), and the lowest values were associated with the abyssal plain fine grids. In a direct comparison of the North Plain and PAP Central fine grids, N_2 was significantly different ($F[1,36] = 38.8$, $p < 0.001$), with reduced dominance in the North Plain relative to the PAP Central fine grid assemblage.

The identities and rank order of the six most common morphotypes in the PAP Central fine grid, North Plain fine grid, and the Coarse grid were the same (Fig. 3), but their numerical densities differed (Fig. 6). At the PAP Central fine grid, there was high numerical dominance by the first-ranked *I. vagabunda*, which comprised 55% of the total numerical density. By contrast, the assemblage was more even in terms of density at the North Plain fine grid, and the density of first-ranked *I. vagabunda* was 75% of that at PAP Central, and comprised only 37% of the total (Table 1), with Elpidiidae spp. and Ophiuroidea in higher densities there than at PAP Central (Fig. 6). The density of first-ranked *I. vagabunda* in the Coarse grid was most similar to that of the North Plain in absolute terms and in relation to the total (38%). Numerical densities of *I. vagabunda*, Elpidiidae spp. and Ophiuroidea were higher in the regions of the coarse grid that crossed the hill extension than in the areas of the coarse grid on the open abyssal plain (Fig. 6).

Megafaunal biomass density in all grids was largely dominated by

holothurian morphotypes. The top ranked morphotypes by biomass density in all grids included Elpidiidae spp., *M. villosus*, *P. longicauda* and *Oneirophanta mutabilis*. The assemblage by biomass in the abyssal plain fine grids and coarse grid were similar in terms of evenness, with Elpidiidae spp. being top-ranked in the North Plain and coarse grids, contributing ~25% to community biomass at each. However, in the PAP Central fine grid, Elpidiidae spp. contributed only 15% to assemblage biomass. By contrast, in the Hill fine grid, the biomass density of first-ranked Elpidiidae spp. contributed 32% to assemblage biomass and the third-ranked morphotype was an anemone, *Cnidaria* sp.16.

The difference between abundance and biomass k-dominance plots, the W-statistic, varied significantly between grids (ANOVA $F[3,102] = 5.4$, $p < 0.01$). It was very low in the North Plain and PAP Central fine grids, similar to that of depth group 6 (i.e. abyssal plain). In contrast, it was high in the Hill fine grid, and similar to the values for depth groups 1–5. The W-statistic for the Coarse grid, which represented a mixture of abyssal plain and moderately elevated terrain, had an intermediate value between those of the abyssal plain fine grids and the Hill fine grid.

3.2.2.3. Assemblage composition. Megafaunal assemblage composition by numerical density was significantly different between grids (ANOSIM $R = 0.87$, $p < 0.001$; Fig. 4c). The difference between the two abyssal plain fine grids (North Plain and PAP Central) was substantial and significant ($R = 0.87$, $p < 0.001$), with that dissimilarity driven by variations in the numerical density of

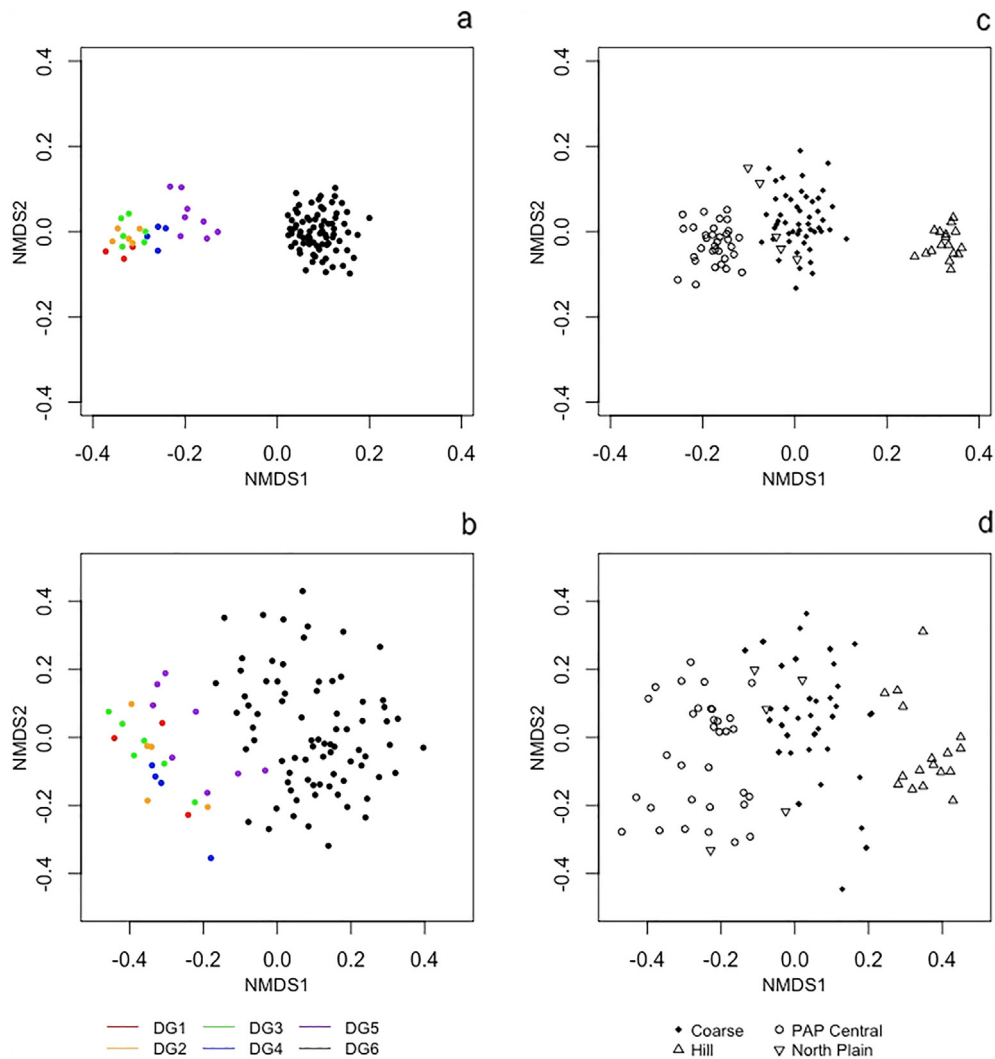


Fig. 4. 2-Dimensional non-metric dimensional scaling ordination plots of square-root transformed numerical density (ind ha^{-1}) and biomass density (g m^{-2}), replicate sample units in the 12.5 m depth groups (a, b), and by grid (c, d).

Ophiuroidea (12%), and *I. vagabunda* (8%). Dissimilarity between the Hill grid and the fine grids on the abyssal plain was dominated by variations in the density of *I. vagabunda* (11–14%), Cnidaria sp.16 (6–7%) and Elpidiidae spp. (6–7%). Megafaunal composition by biomass was significantly different between grids (ANOSIM $R = 0.57$, $p < 0.001$; Fig. 4d). The difference between the North Plain and PAP Central fine grids ($R = 0.43$, $p < 0.01$) was driven by variations in the biomass of large sea cucumbers: *P. longicauda* (13%), *M. villosus* (9%), *Oneirophanta mutabilis* (6%), *Benthothuria* sp. (5%). Dissimilarity between the Hill fine grid and the abyssal plain fine grids was driven by biomass variations in Cnidaria sp.16 (12%), *P. longicauda* (10%), *M. villosus* (7–8%), and Elpidiidae spp. (6–7%).

Variations in trophic composition between grids are presented in Table 1 and Fig. 5. The numerical density of suspension and deposit feeders was significantly different between the grids ($F[3,102] = 201.1$, $p < 0.001$ and $F[3,102] = 548.1$, $p < 0.001$, respectively), with both highest in the Hill grid. The densities of these feeding groups were also significantly different between the North Plain and PAP Central fine grids ($F[1,36] = 7.2$, $p < 0.05$ and $F[1,36] = 187.7$, $p < 0.001$, respectively), with the dissimilarity in trophic composition driven by variations in the numerical density of deposit feeders (75%), which was lower at PAP Central. The biomass density of suspension feeders and deposit feeders were significantly different between the grids ($F[3,102] = 67.6$, $p < 0.001$ and F

$[3,102] = 4.1$, $p < 0.01$), with the higher biomass of suspension feeders in the Hill fine grid the driving factor in the dissimilarity between the Hill and the abyssal plain fine grids (59–63%).

3.3. Impact of sample unit size

Estimated numerical density, in both the depth groups and grids analyses, stabilised to an asymptotic value at a sampling unit size of $\sim 300 \text{ m}^2$ seabed (Fig. S3). Biomass density estimates stabilised at a sampling unit size of $\sim 800 \text{ m}^2$ for most depth groups and the grids. In marked contrast, species richness (as number of morphotypes) had not reached an asymptotic value at a sampling unit size of $\sim 5000 \text{ m}^2$ in any case. At the analytical sampling unit size employed in the present study ($\sim 800 \text{ m}^2$), the number of morphotypes in the North Plain and PAP Central fine grids were very similar to one another, but appeared distinct to the Coarse grid and Hill fine grid. However, at larger sampling unit sizes (e.g. $> 2000 \text{ m}^2$; Figure S3) the North Plain fine grid result appears to diverge from that of the PAP Central fine grid to become more similar to the Hill fine grid and Coarse grid.

4. Discussion

We have detected substantive, and statistically significant, differences in abyssal megafaunal assemblages and seabed habitats that

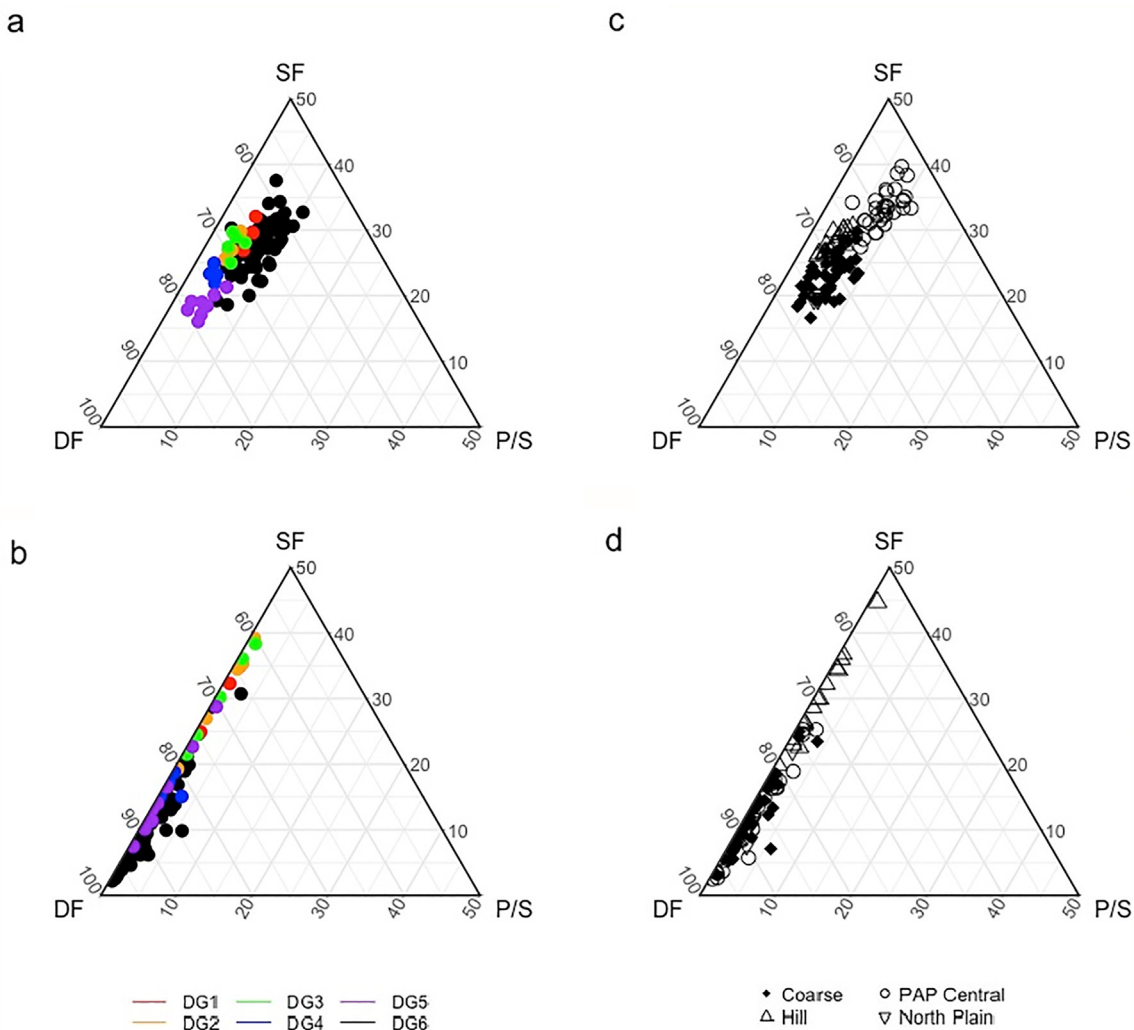


Fig. 5. Ternary plots of density and biomass by feeding groups, with *Iosactis vagabunda* removed, replicate sample units coloured by depth group (a, b), and in the grids (c, d).

appear to be related to both (a) very modest differences in seafloor elevations (order 10 m), and (b) spatial differences within the level-bottom abyssal plain environment (i.e. between the PAP Central and North Plain fine grids). These quantitative results provide important insights into the environmental controls and structuring of abyssal communities, and consequently how best to survey and monitor the ecological characteristics of such environments in the face of potential human-driven impacts, such as climate change and resource exploitation.

4.1. The impact of modest topographic elevation

The significant heterogeneity found here provides new insights into the fine-scale habitat gradients affecting abyssal community structure. Over a 12.5 m change in bathymetry, we found changes of 59% in community biomass, 10% in community density, 60% in the density of the most common morphotype, and 7% in the rarefied number of morphotypes (Table 1). Notably, the topographic elevations we examined were comparatively ‘gentle’ with soft sediment cover throughout; they did not include sharp depth gradients, such as scarps or cliffs, or rocky outcrops, which would provide more habitat heterogeneity and might more obviously host different faunal communities (e.g. fewer deposit feeders). These small variations in topography are not often considered in relation to larger bathymetric features, but are extremely numerous and exist at small spatial scales in the abyss.

Depth is likely a proxy for other environmental factors associated with bathymetric features, such as alterations in bottom water flow. Abyssal hills are known to enhance current speeds and alter the direction of current flow (Turnewitsch et al., 2013). Current speeds up to double those measured on the abyssal plain have been observed on an adjacent hill (~900 m in elevation), with resultant winnowing producing coarser sediments (Turnewitsch et al., 2015). The sedimentary environment examined in this study was significantly different with the small change in topographic elevation; changes of up to 14% in TOC and 170% in coarse sediment content were observed between successive depth groups (Table 1). Topographically enhanced current speeds on abyssal hill H3 have also been linked to a small but statistically significant increase in deposited particulate organic matter (Morris et al., 2016). Similar hydrodynamic processes occur to greater degrees on seamounts, where more extreme alterations of substratum type and current flow regimes are coupled with interactions between water masses and differences in bottom water temperatures, causing alterations to surface ocean processes, primary productivity and organic matter deposition, with consequent effects on the associated benthic communities (Clark et al., 2009; Rogers, 2018). Observations of gradients in the benthic environments with water depth on seamounts have found increased benthic biomass and beta diversity (Rogers, 2018; Victorero et al., 2018), while seamount summit community structure was found to be related to seabed habitat differences associated with seamount depth, nutrient availability and water chemistry (Lundsten

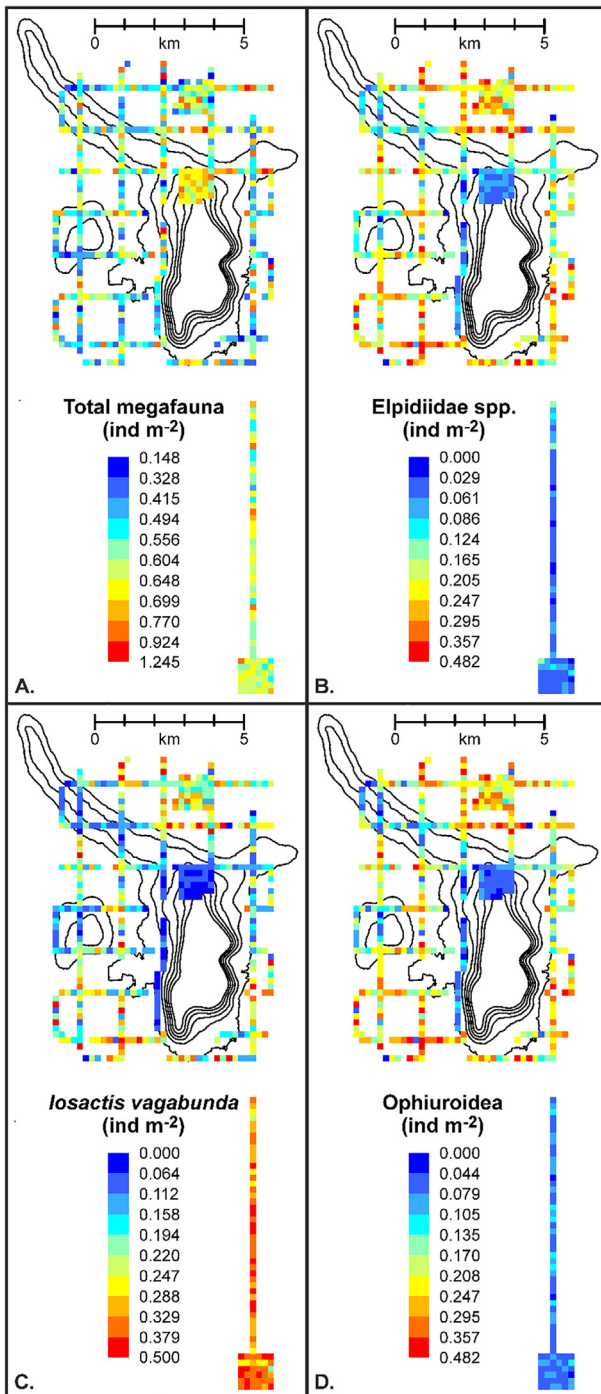


Fig. 6. Numerical density of total megafauna and selected taxa in photographic tiles aggregated in 200×200 m cells. (Map datum WGS 1984; projection UTM Zone 28N; WKID: 102578).

et al., 2009).

This study provides insight into fine-scale variability in abyssal hill assemblages and their diversity, further refining the findings of a previous study that investigated the summit of this hill (H3; Durden et al., 2015a) and two others in the area (elevations 163–462 m above the abyssal plain), along with the flank of the hill (elevation 73 m), in comparison to the abyssal plain. The variations in megafaunal community structure detected in that study cannot be directly compared in detail to the present study because of the different photographic equipment and platforms used, and the greater seabed area covered; details of those differences are given in Morris et al. (2014). An example

from the PAP Central (P1) location, where metre-scale bathymetric heterogeneity is absent, illustrates the discrepancies between community estimates: numerical density was estimated at $2400\text{--}3500$ ind ha^{-1} and biomass at $2.4\text{--}5.2$ g m^{-2} as measured previously, compared to 6303 ind ha^{-1} (95% confidence interval 6185–6423; Table S2) and 6.345 g m^{-2} (95% confidence interval 5.582–7.198) in the present study. However, comparisons between patterns found within each of the studies can be made. The present study found generally similar patterns, but of a lesser magnitude: 10–15% higher numerical density on the hill (depth groups 1 and 2, Hill fine grid) than on the abyssal plain (depth group 6, PAP Central fine grid) rather than the 150% difference found by Durden et al. (2015a), and 13–43% greater biomass on the hill than on the abyssal plain in the present study rather than the 300% found previously. The coarse fraction of sediment was much greater in the previous hill samples (52–69%; Durden et al., 2015a) than in any of the depth groups in this study (10–42%), while ice rafted dropstones were also previously observed on the summit of abyssal hill H3 (Stefanoudis et al., 2016a). The differences between the studies are consistent with the subtle topographic variation addressed in the present case and the hill summit to plain contrasts addressed by Durden et al. (2015a).

Numerical and biomass density peaked along the side of the hill, rather than at the top of the flank or the summit in both the previous and current studies. The depth groups in this study extend up to the top of the northern flank of the hill (depth group 1), but not to its summit (H3 in the previous study; Fig. 1). The flank (H2, at an elevation similar to depth groups 0–2 in this study) and the summit (H4) of another proximate abyssal hill were also studied by Durden et al. (2015a), and both numerical and biomass density on the H2 flank were 2.2 and eight times the values found on the abyssal plain (at PAP Central; 120% and 700% higher, respectively), and 1.2 and 1.5 times the values found at the H4 summit (20% and 50% higher, respectively). In this study the pattern was similar but the magnitude smaller: numerical density in depth groups 2 and 3 was 2–5% higher than in depth group 1 and 15% higher than in depth group 6, while biomass density in depth groups 2 and 4 was 15–56% higher than in depth group 1 and 30–78% higher than in depth group 6.

From evidence in both studies, local processes appear to be causing differences in sedimentary conditions. Increased coarse sediment content and reduced organic matter were found in this study at the top of the flank (as TOC in depth groups 0 and 1) and at the H3 hill summit (as detritus cover and aggregate size in Durden et al., 2015a), in comparison to the side of the hill (depth groups 2–5 in this study). These results are in common with findings by Turnewitsch et al. (2015) that hydrodynamic conditions resulted in increased winnowing on the summit and flank of the adjacent hill, with sediment redistribution elsewhere. The varying winnowing and sediment redistribution processes were suggested as the cause of differing inorganic carbon contents in sediments on hill flanks with similar depths, and may be the reason for the wide ranges in coarse sediment and TOC content within depth groups and grids (Table S1). Our results suggest that these local processes and sediment conditions may be causing the differences found in the communities on the hill, with the W-statistic (reflecting successional state/disturbance) greatest in the intermediate depth groups.

Benthic communities are altered by variations in seabed environmental conditions and the differing interactions of benthic organisms with the sedimentary environment. The substantial numerical density variations in *Iosactis vagabunda*, the most common megafaunal morphotype on the abyssal plain, whose density is more than halved by ascending one depth group, may be related to differences in sediment texture, given its frequent burrowing habit (Durden et al., 2015b). However, as a facultative surface deposit feeder, the numerical density difference may also be related to differences in sedimentary TOC content. It has previously been suggested that this anemone may feed primarily by predation on abyssal hills, and by deposit feeding on the abyssal plain (Durden et al., 2017).

Assemblage feeding modes were similarly modified in the depth group transitions up the hill, with suspension feeders increasing in numerical and biomass density, peaking in depth groups 1 and 2 respectively, likely related to increased suspended particulate organic matter availability in the water column from increased current speeds (Durden et al., 2015a; Durden et al., 2017; Morris et al., 2016), particularly on the flank of the hill. The peak in deposit feeder density (depth group 2) corresponded to a peak in sedimentary TOC. Fractionation of detritus on abyssal hills is suggested to result in differing compositions of the deposited detritus (Turnewitsch et al., 2015). Carbon flow modelling has further suggested that the detritus deposited on the hill may be more labile than that on the plain (Durden et al., 2017), despite the lower total sediment organic matter content. The dominance of Elpidiidae spp. on the hill may be related to such fractionation, as they are suspected to selectively feed on relatively 'fresh' detritus (Wigham, Hudson, Billett & Wolff, 2003).

4.2. Environmental drivers of spatial variation on the abyssal plain

The statistically significant differences detected in the ecological characteristics of the benthic communities in the North Plain and PAP Central fine grids, in terms of diversity (N_2) and community composition by numerical and biomass densities, were likely driven by subtle variations in the benthic environment. The most marked obvious difference in the communities was in the numerical density of the burrowing anemone, *I. vagabunda*, the PAP Central density of which was 150% that at the North Plain. Although the two areas lie on a continuous open abyssal plain of essentially identical water depth, the North Plain fine grid area is marginally deeper (~2 m). Note that differences in sedimentary TOC and coarse fraction content were not statistically significantly different between these areas. However, shipboard observations of all cores from the three coring sites in the North Plain fine grid noted that the profiles were homogeneous with unconsolidated sediment, and clearly different in character to all cores recovered from the PAP Central over the course of the PAP-SO benthic time series, which become substantially consolidated within ~10 cm of the sediment surface (Ruhl & scientists, 2013). As a result of its location, the North Plain grid area and surrounds may have been impacted by a mass wasting/slope failure event from the south-facing aspect of the adjacent hill to the north (Fig. 1). We postulate that the legacy of such an event is a surface sediment column that is highly variant to that of PAP Central area, having been emplaced en masse and not yet de-watered to the same extent.

The substantial changes to the ecological characteristics of megabenthic communities over modest bathymetric differences is important in the consideration of landscape-scale ecology. Previously, the abyssal plain has been considered to be an essentially homogeneous benthic habitat. However, seamounts and abyssal hills punctuate the vast abyssal plains (e.g. Harris et al., 2014), and bathymetric variations on the scale investigated here are likely extremely numerous and underestimated or ignored at basin and global scales. Our results suggest that the inclusion of small topographic changes, such as the small knoll and low ridge in the present study, increases diversity and reduces numerical dominance of the community of the abyssal plain. Thus, the beta and gamma diversity in the abyss may be increased. The understanding of spatial heterogeneity in the abyss would be further strengthened by additional study of the influence of topographical features across spatial scales.

4.3. Perspectives for monitoring abyssal benthic communities

Such substantive alterations to the ecological characteristics of the benthic community over subtle topographic variations in the deep sea could be particularly important to the detection and quantification of anthropogenic impacts (e.g. from oil and gas or deep-sea mining) in the context of such natural variation. Habitats typically considered to be

homogeneous continuous level-bottom systems may frequently include depth variations of more than 10 m. For example, an area in the eastern Clarion Clipperton Zone recently deemed similar to those designated for possible future polymetallic nodule mining, with negligible seabed slope (< 3°), encompassed a 63 m bathymetric range at a spatial scale of 10 km on the abyssal plain ('Flat' area in Simon-Lledo et al., 2019), a depth difference equivalent to five of the depth groups studied here. Consideration of this scale of bathymetric variation would therefore be important to survey design in such an area (see below), as it would be for biogeography and modelling of impacts, including those from climate change (e.g. Luoto & Heikkinen, 2008). Furthermore, the location of fixed-point observatories (Levin et al., 2019), and the results of studies conducted there should be considered in the context of such spatial variation.

Consideration of habitat variation, be it substantive or subtle, such as that evident in the modest topographic elevations studied here, is important to robust survey design. The differences in the communities of the North Plain and PAP Central fine grids also suggests that these two locations could be effectively considered as different habitats, despite their similar water depths, seabed slopes, and sampled sediment particle size distribution that would conventionally lead to them being considered a single continuous habitat. Locally complex terrain, such as areas that represent a mixture of two or more habitat types, may alias the characteristics of the component habitats if surveyed as a notionally uniform habitat. Disentangling such 'cryptic habitats' and their ecological characteristics may be accomplished through formation of appropriately sized and located sampling units after the data acquisition phase, a form of *a posteriori* environmental stratification as advocated by Benoist et al. (2019), with recording of environmental and biological data at suitable scale (i.e. individual photo scale).

5. Conclusions

It has been long understood that the abyss is not a quiescent, temporally, and spatially homogeneous environment (Billett et al., 1983; Heezen & Hollister, 1971; Rex & Etter, 2010). We have quantified such heterogeneity in terms of significant ecological differences in abyssal megabenthic communities with subtle topographic elevations (order 10 m) and mesoscale spatial variations (order 1–10 km) of non-bathymetric origin. Previous concepts of the abyssal environment underestimate this heterogeneity, and thus beta- and gamma-diversity in the abyss may be higher than estimated. A contemporary understanding of abyssal benthic ecology must acknowledge that abyssal plains may be far from 'plain', but comprise a complex spatial mosaic of benthic habitats. To be robust, designs for surveys and monitoring programmes must take this spatial ecological variation in account, and further consider that the abyssal benthos are further influenced by temporal disturbances (Billett, Bett, Reid, Boorman & Priede, 2010; Billett, Bett, Rice, Thurston, Galeron et al., 2001; Durden et al., 2020) and largely unresolved interspecific interactions (e.g. Mitchell et al., accepted for publication) that introduce additional spatial variation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank the captain, crew and scientists of RRS *Discovery* research cruise 377. The manuscript benefitted from the comments of two anonymous reviewers. This work contributes to ongoing observations at the Porcupine Abyssal Plain – Sustained Observatory of the Natural Environment Research Council (NERC, UK), through the NERC-funded

projects Autonomous Ecological Surveying of the Abyss (NE/H021787/1) and the Climate Linked Atlantic Sector Science (CLASS) project supported by NERC National Capability funding (NE/R015953/1).

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.pocan.2020.102395>.

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