# Abyssal hills – hidden source of increased habitat heterogeneity, benthic megafaunal biomass and diversity in the deep sea

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A R T I C L E   I N F O

A B S T R A C T

Abyssal hills are the most abundant landform on Earth, yet the ecological impact of the resulting habitat heterogeneity on the wider abyss is largely unexplored. Topographic features are known to influence food availability and the sedimentary environment in other deep-sea habitats, in turn affecting the species assemblage and biomass. To assess this spatial variation, benthic assemblages and environmental conditions were compared at four hill and four plain sites at the Porcupine Abyssal Plain. Here we show that differences in megabenthic communities on abyssal hills and the adjacent plain are related to environmental conditions, which may be caused by local topography and hydrodynamics. Although these hills may receive similar particulate organic carbon flux (food supply from the surface ocean) to the adjacent plain, they differ significantly in depth, slope, and sediment particle size distribution. We found that megafaunal biomass was significantly greater on the hills (mean 13.45 g m$^{-2}$, 95% confidence interval 9.25–19.36 g m$^{-2}$) than the plain (4.34 g m$^{-2}$, 95% CI 2.08–8.27 g m$^{-2}$; ANOVA $F(1,6) = 23.8$, $p < 0.01$). Assemblage and trophic compositions by both density and biomass measures were significantly different between the hill and plain, and correlated with sediment particle size distributions. Hydrodynamic conditions responsible for the local sedimentary environment may be the mechanism driving these assemblage differences. Since the ecological heterogeneity provided by hills in the abyss has been underappreciated, regional assessments of abyssal biological heterogeneity and diversity may be considerably higher than previously thought.

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## 1. Introduction

Habitat heterogeneity resulting from broad-scale topographic features is responsible for variations in the diversity and biomass of seafloor fauna in channels (Jones et al., 2007), canyons (De Leo et al., 2010; McClain and Barry, 2010; Ramirez-Llodra et al., 2010b; Sarda et al., 1994), trenches (Paterson et al., 2009), and on seamounts (McClain, 2007). Habitat heterogeneity and benthic diversity has been examined in the deep sea, for example, by comparing communities at sites between basins across the Mid-Atlantic Ridge (Alt et al., 2013; Priede et al., 2013) and between the Porcupine and Madeira Abyssal Plains (PAP and MAP; Thurston et al., 1998). However, the heterogeneity of the abyssal plain habitat and corresponding seafloor assemblage density, biomass and composition is little known at a sub-basin scale.

The abyss was once viewed as being practically homogenous, with lower habitat heterogeneity than most other habitats globally. Nearly all previous work from abyssal depths, including

biodiversity and biomass estimation, uses data from the level abyssal plain (Jones et al., 2014). However, the vast abyssal plains are populated by abyssal hills, thought to be the most abundant landform on Earth (Harris et al., 2014). Sediment-covered abyssal hills rise up to 1000 m above the seabed (seamounts by definition reach >1000 m above the seafloor), and exist in similar densities in the Atlantic, Indian and Pacific Oceans (Yesson et al., 2011). Despite their abundance, and potential importance to spatial variation in benthic communities, abyssal hills have been rarely studied. Even at the much-studied Porcupine Abyssal Plain (Hartman et al., 2012), the ecology of abyssal hills have been tacitly avoided as they are logistically challenging to study. Previous studies of the PAP, including a long-term time series, have focussed on the level bottom (Bett et al., 2001; Bett and Rice, 1993; Billett, 1991; Billett et al., 2001; Billett and Rice, 2001; Brunnegard et al., 2004; Danovaro et al., 2001; Turnewitsch and Springer, 2001), but few have examined the potential spatial variation. Billett et al. (2010) found detectable differences in megafaunal community composition between trawls collected ~100 km apart on the PAP, but little synoptic data exists for quantitative study of abyssal heterogeneity at the scale of hills.

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Variations in local (alpha) species diversity in the deep sea have been related to environmental gradients (Levin et al., 2001), and the complex interactions of these effects may lead to variations in diversity associated with habitat heterogeneity. Seamounts, which can be considered as large analogues of abyssal hills, have been the subject of considerable research on habitat variation in relation to bathymetry, substratum, currents and topography (McClain, 2007). Seamounts appear to be characterised by both high species richness and high standing stock biomass (Clark et al., 2009; McClain, 2007; Ramirez-Llodra et al., 2010a; Rowden et al., 2010). Causal factors are thought to include: alteration of currents and near-bed flows (Hernandez-Molina et al., 2008), with implications for sediment sorting and deposition of particulate organic material (Graf, 1989); elevation of seafloor, providing habitat for species of limited bathymetric range (Rex and Etter, 2010); reduced settling distance of particulate organic matter (Wei et al., 2010); and greater substratum type diversity associated with bathymetric features (Levin and Nittrouer, 1987). However, it is not clear how such heterogeneity might extend to lesser topographic features, having only modest elevations (e.g. ~200 m above the abyssal seafloor), and limited flank slope angles (<15°; Heezen and Laughton, 1963). Abyssal hills and the adjacent plain provide an excellent model system for investigating the effects of habitat heterogeneity, with minimal influence of spatial variation in the overhead supply of food as particles sinking from surface waters. If abyssal hills do harbour a largely unappreciated biological heterogeneity, regional abyssal biological diversity may be appreciably higher than current estimates suggest.

Here we evaluate the role of landscape-scale habitat heterogeneity in structuring megafaunal assemblages in the abyss. We hypothesize that abyssal hill features differ from the adjacent abyssal plain in terms of physical habitat (sediment type and topography), but otherwise have similar ecological structuring forces (common organic matter input). We expect that the density, biomass, assemblage structure, alpha- and beta-diversity of megafaunal assemblages inhabiting abyssal hills are significantly different from those on the plain. We test these hypotheses using remote sensing (acoustics and photographic data) and direct sampling of the sedimentary environment. We used these data to show how observed differences in habitat heterogeneity may affect megafaunal assemblages, and contribute to our understanding of processes structuring the broad-scale community and regulating biological diversity in the abyss.

## 2. Methods

### 2.1. Study area

The PAP (NE Atlantic) has been a site of approximately annual study since 1985, primarily for water column biogeochemistry, particulate organic carbon flux, and biochemistry and ecology of the seabed. It was originally chosen as a study site for the absence of major topographic features, and its substantial distance from the potential influences of both the continental margin and the Mid-Atlantic Ridge (Billett et al., 1983; Billett and Rice, 2001). The majority of the abyssal hills of the PAP rise approximately 300 m above the plain, with one rising to ~1000 m (Klein and Mittelstaedt, 1992; Turnewitsch and Springer, 2001). Eight locations were selected for the present study (Fig. 1, Table 1): four on the plain (P1–P4), and four on hills of varying altitude and flank slope (H1–H4). Site P1 corresponds with the 'PAP Central' location frequently occupied in time-series studies of the sedimentary infauna (Laguionie-Marchais et al., 2013) and adjacent to the primary area of trawl sampling of megabenthos studies (Billett et al., 2010).

### 2.2. Assessment of habitat heterogeneity and food availability

To test whether physical habitat and food availability differed on abyssal hills from the plain, we collected environmental data (Table 2), including first-order derivatives from bathymetric data (i.e. depth and slope), substratum characteristics, and measures of food availability. Seafloor bathymetry was assessed using a hull-mounted Simrad EM12 multibeam echo sounder during RRS *Charles Darwin* cruise 158 in June 2004 (Lampitt, 2010), processed to a 50 m × 50 m pixel resolution for subsequent analyses. The water depth along each photographic transect (see Section 2.3) was expressed as the altitude above the abyssal plain seabed normalised to standard score. Median seafloor slope for each location was determined using a native function in ArcMAP (v10.0; ESRI) using a 100 m buffer around each photographic transect (see Section 2.3). Subsurface sediment structure was imaged using a Kongsberg Simrad SBP120 subbottom profiler (chirp 2.5–7 kHz) during the RRS *James Cook* cruise 062 (Ruhl, 2012) in July and August 2011.

Physical surface sediment characteristics were assessed from multiple Megacorer samples (59 and 100 mm internal diameter; Gage and Bett, 2005) collected at each location (Fig. 1) during research cruise JC062. Following visual inspection of the cores for the presence of dropstones (Bennett et al., 1996), sediment particle size distributions were measured in each of three near-surface layers (0–10, 10–30, 30–50 mm) by laser diffraction using a Malvern Mastersizer, after homogenisation (particles >2 mm removed), dispersal in a 0.05% $(NaPO_3)_6$ solution (Abbireddy and Clayton, 2009), and mechanical agitation. For subsequent analyses, the mean particle size distribution for each site was computed for the combined 0–50 mm horizon. As the particle size distributions were bimodal with a consistent trough between modes at 22.9 μm, the fraction of particles in the coarse mode (>22.9 μm) was used for comparison to biological data. No cores were available from site P2, so particle size data from P1 were used as a proxy, given their close proximity and similarity in other observed and measured environmental characteristics.

To assess the food input to the abyssal hills and plain, we measured seafloor accumulations of phytodetritus (Bett et al., 2001), the dominant allochthonous particulate organic matter input to the PAP. The sizes of discrete aggregates were measured in seabed photographs using methods described in Section 2.3, and the percentage seabed cover was calculated, an approach previously used by Smith et al. (2014).

### 2.3. Assessment of megafaunal assemblages

To examine differences in megafaunal assemblages, we used photographic surveys of the seabed. We captured approximately 1460 non-overlapping photographs at 12-s intervals with a vertically mounted still camera (Ocean Scientific International Limited Mk7) on the Wide Angle Seabed Photography towed camera platform (WASP; Jones et al., 2009) during research cruise JC062. WASP was towed (~0.25 ms$^{-1}$) along each transect (Fig. 1) at a target altitude of 2 m above the seabed. Photographs were captured on film (35 mm Kodak Vision 250D colour negative) that was processed and then scanned at high resolution (4096 × 6144 pixels) prior to analysis. Photographs that were out of focus, obscured, or taken at an altitude above the seabed of >5.0 m were excluded from the analysis. The camera was positioned approximately perpendicular to the sea floor and the area of seafloor observed was calculated from altitude and camera acceptance angles of 35° and 50° (Jones et al., 2007, 2009).

Distinctly identifiable megafauna (generally >10 mm; consistent with Grassle et al., 1975) were enumerated and classified to the lowest practicable taxonomic levels (Table 3, Fig. 2). Each
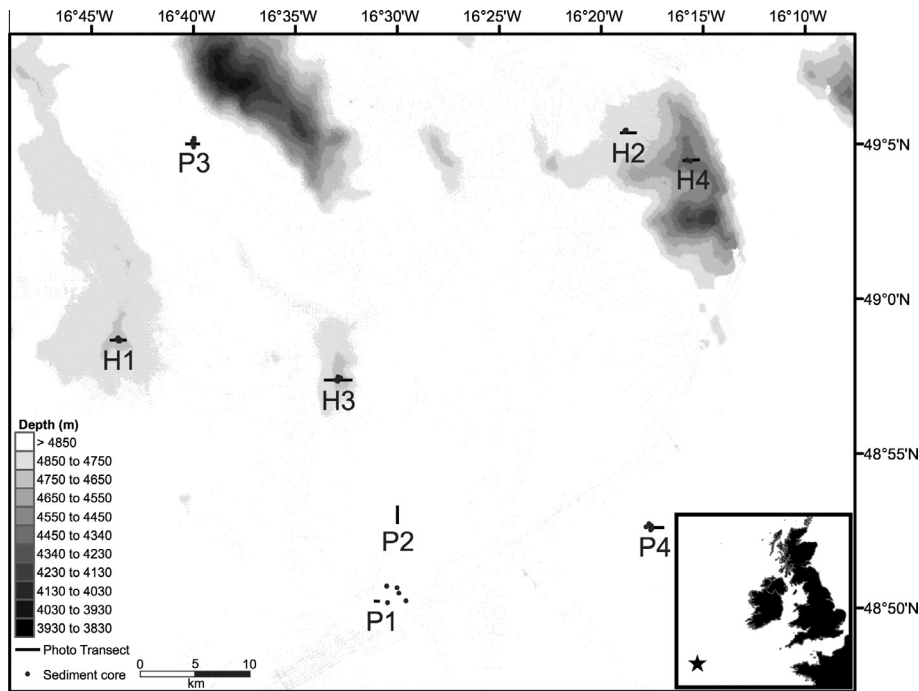
**Fig. 1.** Bathymetric map of the study area, with inset indicating general location of the Porcupine Abyssal Plain in the northeast Atlantic Ocean, and detail indicating the locations of study sites on the abyssal plain (P) and hills (H).

**Table 1**
Details of the photographic and sediment core sampling programs at eight abyssal sites, four on the plain (P) and four on hills (H) at the Porcupine Abyssal Plain.

| Site | Centre latitude (°) | Centre longitude (°) | Water Depth (m) | Seabed slope[a] (°) | Useable photos | Seabed area imaged (m²) | Sediment cores |
|------|---------------------|----------------------|-----------------|---------------------|----------------|--------------------------|----------------|
| P1 | 48.837 | −16.516 | 4848–4851 | 0.4–0.6 | 85 | 423 | 5 |
| P2 | 48.884 | −16.500 | 4848–4850 | 0.6–1.4 | 236 | 1164 | 0 |
| P3 | 49.083 | −16.667 | 4851–4854 | 0.5–0.9 | 183 | 1424 | 5 |
| P4 | 48.877 | −16.293 | 4846–4850 | 0.5–0.7 | 222 | 934 | 5 |
| H1 | 48.978 | −16.728 | 4672–4691 | 3.4–5.1 | 217 | 831 | 5 |
| H2 | 49.089 | −16.313 | 4750–4781 | 1.8–2.6 | 253 | 1083 | 5 |
| H3 | 48.956 | −16.547 | 4633–4658 | 5.8–10.6 | 149 | 583 | 5 |
| H4 | 49.074 | −16.243 | 4339–4392 | 7.0–9.6 | 116 | 444 | 3 |

[a] Interquartile range.

specimen was measured using ImagePro Plus (Media Cybernetics), and these dimensions converted to physical units using trigonometry (e.g. Jones et al., 2007). Pelagic taxa were excluded from the analysis, although some benthopelagic species, such as the holothurian *Enypniastes eximia* and cephalopods, were included. Benthic specimens that could not be identified as living (e.g. gastropod shells and worm tubes) were also omitted. Feeding groups were assigned based on existing literature (Table 3).

Biomass (wet weight) was estimated from measured faunal dimensions using conversions developed from relationships established between the dimensions and wet weights of specimens (Table 3) collected in trawls at PAP (August 1996–October 2002; Billett et al., 2010). In those small, rare taxa for which insufficient trawl data were available, biomass was estimated using conversions for congener taxa of similar body shape, or omitted if an appropriate analogue was not available.

### 2.4. Data analyses

Faunal count and biomass data were standardized to unit area (m⁻²), and were log($x$ + 1) transformed prior to parametric statistical analysis. Where percentage or proportional data were employed, they were subject to arcsine transformation before

further assessment. Normality was tested by visual inspection of histograms and QQ plots, and using the Shapiro–Wilk normality test. Comparisons of hill and plain sites were made using ANOVA, and potential correlations examined using Spearman's rank method. Significance at the 5% level was reported.

Univariate diversity indices (Shannon H′ and Pielou J′; log base 2) were calculated as described in Magurran (2004). The expected number of morphotypes by rarefaction was calculated (Hurlbert, 1971) at the minimum number of individuals observed in a single transect. The quantitative difference of density- from biomass-based cumulative dominance curves was examined as a potential means of revealing relative levels of disturbance or successional state, and the W-statistic used to assess the difference (Clarke, 1990).

Multivariate assessments of the faunal and environmental data were computed using PRIMER6 (Clarke and Warwick, 2008). Bray–Curtis similarity matrices were generated for log($x$ + 1)-transformed densities and biomass; Euclidean distance similarity matrices were calculated for normalised environmental data (altitude, slope, coarse particle fraction, mean phytodetritus cover, median phytodetritus aggregate size). Density and biomass similarity matrices were compared between the hill and plain sites, and correlated with environmental data using the ANOSIM and BEST

**Table 2**
Summary of environmental and megafaunal data for each location, including altitude and slope from bathymetric data, sedimentary characteristics from Megacorer samples, with food availability, faunal density, biomass, density-based diversity metrics ($H_2'$: Shannon Index; $J_2'$: Pielou's evenness; $EM_{103}$: Rarefied taxon richness), and density and biomass for the two major megafaunal feeding groups (SF: suspension feeders; SDF: surface deposit feeders) from seabed photographs.

| Site | Altitude (m above P3) | Median seabed slope (°) | Coarse sediment fraction (>22.9 μm, %) | Seabed detritus cover (%) | Median detritus aggregate size (cm²) | Density (ind m⁻²) | Biomass (g wet m⁻²) | $H_2'$ | $J_2'$ | $EM_{103}$ | W | SF Density (ind m⁻²) | SF Biomass (g wet m⁻²) | SDF Density (ind m⁻²) | SDF Biomass (g wet m⁻²) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| P1 | 3 | 0.5 | 40.9 | 0.29 | 8.72 | 0.24 | 2.42 | 1.79 | 0.11 | 17 | 0.168 | 0.16 | 0.54 | 0.07 | 1.87 |
| P2 | 3 | 1.0 | – | 0.18 | 51.96 | 0.35 | 5.23 | 2.69 | 0.10 | 14.9 | −0.003 | 0.22 | 1.24 | 0.12 | 3.71 |
| P3 | 0 | 0.8 | 38.9 | 1.23 | 38.72 | 0.10 | 6.68 | 2.35 | 0.09 | 22.1 | 0.174 | 0.06 | 0.42 | 0.03 | 3.57 |
| P4 | 4 | 0.7 | 39.1 | 2.32 | 9.99 | 0.36 | 3.98 | 2.10 | 0.09 | 12.3 | 0.022 | 0.24 | 0.77 | 0.12 | 0.79 |
| H1 | 163 | 4.0 | 52.4 | 0.69 | 15.08 | 0.26 | 11.39 | 2.22 | 0.07 | 22.4 | 0.244 | 0.10 | 2.74 | 0.15 | 2.62 |
| H2 | 73 | 2.2 | 59.0 | 2.51 | 32.69 | 0.55 | 18.82 | 2.26 | 0.08 | 16.6 | 0.089 | 0.24 | 12.93 | 0.30 | 1.63 |
| H3 | 196 | 7.6 | 58.8 | 0.16 | 9.19 | 0.37 | 11.84 | 2.04 | 0.08 | 20.1 | 0.275 | 0.21 | 8.12 | 0.17 | 0.76 |
| H4 | 462 | 8.6 | 69.2 | 0.32 | 21.49 | 0.45 | 12.83 | 1.76 | 0.08 | 17.3 | 0.272 | 0.28 | 11.81 | 0.15 | 0.57 |

routines in PRIMER, respectively. Two other PRIMER routines, SIMPER ("similarity percentages") and RELATE, were used to assess dissimilarity between hill and plain composition and the morphotypes contributing to within-group similarity, and to test the null hypothesis of no relationship between the faunal similarity matrices and environmental factors, respectively.

## 3. Results

### 3.1. Habitat heterogeneity and food availability

The water depths of sites on the plain were similar, and calculated seabed slopes were slight (Table 1). Median slopes (Table 2) were significantly higher on the hill sites (ANOVA $F(1,6) = 17.4$, $p < 0.01$). The elevations (Table 2) of H1 and H3 were similar (163 and 196 m), but the slope of H3 (7.6°) was greater than that of H1 (4.0°). The slope of the highest hill (H4, 8.6°) was also relatively steep, while the elevation and slope at site H2 (2.2°), located on the flank of the same hill, was much less than on the other hills.

Plain sites were characterised by soft sediments, with evidence of burrowing activity in the cores and seabed photographs. Cores from P1, P2 and P4 all contained an apparently common dark band at $\sim 300$ mm below the sediment surface, with soft, light-coloured sediment above (Appendix A). This band was not present at P3. Cores from all hill sites contained pebble-sized clinker from steamships and iceberg-rafted drop-stones, which both function as coarse particles/hard substratum. Pebble- to cobble-sized particles were also visible on the sediment surface in seabed photographs from the hills. Core profiles from the hill sites were visually more variable than the plain sites; those from H2, located on the flank of a hill, had a particularly mixed structure. This was supported by acoustic subbottom profile imagery that showed sediments at H2 were not stratified in the near-surface layers, as was the case at the sites on the plain.

Particle size distributions were bimodal at all sites (Fig. 3), with peaks at approximately 4 and 200 μm, likely attributable to coccoliths and foraminiferan tests, respectively (Frenz et al., 2005). The fraction of coarse particles (Table 2) was significantly greater on the hills than the plain (ANOVA $F(1,6) = 9.8$, $p < 0.05$). H4 was located at the top of the highest and steepest hill (Table 1), and contained the greatest fraction of coarse particles (>22.9 μm). The fraction of coarse particles was significantly correlated to altitude ($r_s[8] = 0.83$, $p < 0.01$), and slope ($r_s[8] = 0.80$, $p < 0.05$). Habitat heterogeneity (all physical factors assessed simultaneously) was significantly different between the hills and plain (ANOSIM $R = 0.69$, $p < 0.05$).

Food availability did not vary spatially; phytodetrital cover (Table 2) was not statistically different between hills and plain sites, nor was median phytodetritus aggregate size. The phytodetritus observed was similar in nature to three groups previously identified by Lauerman and Kaufmann (1998): amorphous aggregates (light with distinct edges), mucus (elongate, grey, collapsed cobwebs), and rolled aggregates (amorphous rolled into cylinder).

### 3.2. Megafauna

#### 3.2.1. Standing stocks

Megafaunal density at the hill sites (0.40 ind m⁻²; 95% confidence interval 0.22–0.61 ind m⁻²) was greater than at the sites on the plain (0.26 ind m⁻²; 95% CI 0.14–0.55 ind m⁻²; Table 2), though not significantly. Megafaunal biomass was, however, significantly higher at the hill sites (13.45 g m⁻²; 95% CI 9.25–19.36 g m⁻²) compared to the plain sites (4.34 g m⁻²; 95% CI 2.08–8.27 g m⁻²; ANOVA $F(1,6) = 23.8$, $p < 0.01$; Table 2).

**Table 3**
Morphotypes identified in seabed photographs, with factors in the model $m = A \times L^B$ used for biomass estimation ($m$ is wet weight in grams, $L$ is dimension in mm), and feeding types used in trophic analysis (P/S: predator/scavenger, SF: suspension feeder, SDF: surface deposit feeder, SSDF: subsurface deposit feeder).

| Group | Morphotype | $A$ | $B$ | $R^2$ | Feeding type |
|---|---|---|---|---|---|
| Annelida | Polynoidae | 0.0002 | 2.3073 | 0.76 | |
| Arthropoda | *Munidopsis* sp. | 0.0009 | 2.5742 | 0.87 | SDF[a] |
| | Pycnogonida | 0.000006 | 2.8427 | 0.98 | SDF[a] |
| Tunicata | Tunicata[b] | | | | |
| | Stalked tunicate[b] | | | | SF[a] |
| Cnidaria | *Iosactis vagabunda*, Cnidaria sp.1, Cnidaria sp.7, Cnidaria sp.9 | 0.0788 | 0.9614 | 0.22 | SF[a] |
| | *Sicyonis* sp. | 53.079 | 0.2348 | 0.1 | SF[a] |
| | *Daontesia* sp. | 0.0159 | 1.6962 | 0.46 | SF[a] |
| | *Actinauge abyssorum*, Cnidaria sp.4 | 0.0009 | 2.802 | 0.90 | SF[a] |
| | *Amphianthus* sp. | 0.0012 | 2.5776 | 0.89 | SF[a] |
| | Unclassified Cnidaria | 0.0005[c] | 2.6779 | 0.91 | SF[a] |
| | *Umbellula* sp.1[b], sp.2[b] | | | | SF |
| Echinodermata | Brisingid[b] | | | | P/S[a] |
| | Ophiuroidea | 0.0091[d] | 1.4503[d] | 0.41 | SDF[a] |
| | Crinoidea[b], Crinoidea2[b] | | | | SF[a] |
| | *Amperima* sp., Elasipod sp.1, sp.2 | 0.0006 | 2.5078 | 0.97 | SDF[a] |
| | *Peniagone* sp., *Enypniastes eximia* | 0.0015 | 1.9989 | 0.84 | SDF[a] |
| | *Benthothuria* sp.[d] | 0.0003 | 2.4513 | 0.94 | SDF |
| | *Deima* sp. | 0.0027 | 2.2564 | 0.88 | SDF[a] |
| | *Oneirophanta* sp. | 0.0004 | 2.5082 | 0.93 | SDF[a] |
| | *Pseudostichopus villosus* and *Pseudostichopus aemulatus* | 0.00005 | 2.8575 | 0.92 | SSDF[a] |
| | *Mesothuria candelabri* | 0.0017 | 2.2409 | 0.62 | SSDF[a] |
| | *Paroriza* sp. | 0.0002 | 2.5389 | 0.92 | SSDF[a] |
| | *Psychropotes longicauda* | 0.0002 | 2.6518 | 0.94 | SDF[a] |
| | Holothuroid sp.2[e] | 0.0004 | 2.3586 | 0.65 | |
| Echiura | Echiura | 0.0281 | 0.9895 | 0.52 | SDF[a] |
| Mollusca | Cephalopoda | 0.0003 | 2.4378 | 0.60 | P/S[a] |
| Porifera | Porifera sp.A[b], sp.B[b], Unclassified[b] | | | | SF[a] |
| Protozoa | Foraminifera[b,e] | | | | |
| Unknown | Unknown sp.C (ploughs sediment)[b] | | | | SSDF |
| | Unknown sp.R (Circle scriber)[b] | | | | SDF |

[a] Iken et al. (2001).
[b] Not included in biomass estimate.
[c] Length-wet weight relationship for *Kadosactis* sp.
[d] Length-wet weight relationship for *Benthodytes* sp.
[e] Feeding type unknown.

### 3.2.2. Diversity

Overall, 43 morphotypes were observed: 39 morphotypes on the plains, 6 of which were only recorded there, and 37 on the hills, 4 of which were not recorded on the plain. Neither the Shannon Index nor the expected number of morphotypes were significantly different between the hill and plain sites. Rarefied morphotype richness curves differed on the hills from the plains (Fig. 4); the amalgamation of hill and plain data produced a slight reduction in apparent richness relative to plain data alone.

Evenness (by density) on the plain was significantly higher than at the hill sites (ANOVA $F(1,6) = 12.37$, $p < 0.05$; Table 2). At the plain sites, the difference in density between the first and fifth-ranked species was almost an order of magnitude (Appendix B a–d). *Iosactis vagabunda* and *Amperima* sp. were the first and second-ranked taxa by density, and Ophiuroidea ranked third to fifth, depending on location. The large holothurians *Psychropotes longicauda*, *Pseudostichopus aemulatus*, *Pseudostichopus villosus*, *Benthothuria* sp. and *E. eximia* occurred at low densities on the plain. Many morphotypes were recorded as singletons at any one site; this was true for half of the taxa at P4. By contrast, the hill sites (except H2) were characterised by lower evenness (Table 2). *Amperima* sp. was again the first or second-ranked species (Appendix B d–h), while *I. vagabunda* was the third-ranked species at H1 and H2. *Actinauge abyssorum* was prominent on the hills, ranked second at H2, H3 and H4. Ophiuroids ranked fourth or fifth. Large holothurians were also present in all hill transects.

Megafaunal biomass on the plain was characterised by high evenness (Appendix C). The large holothurians, particularly *Psychropotes longicauda* and *Pseudostichopus villosus*, were major contributors to megafauna biomass; one of these was the first ranked species at each of the sites on the plain. The small-bodied taxa *Amperima* sp. and *I. vagabunda* were still significant contributors to biomass as a result of their high densities. Individual body weights of *Amperima* sp. were significantly higher on the plain than on the hills (ANOVA $F(1,338) = 4.70$, $p < 0.05$), though there was no difference in the individual body weights of *I. vagabunda*. Conversely, community biomass at the hill sites was dominated by only a few species, particularly *A. abyssorum* and the large-bodied species *Pseudostichopus villosus*.

Disparity between biomass- and abundance-based cumulative dominance was greater on the hills than on the plain (Fig. 5). The calculated W statistics (Table 2) were greater on the hills, but not significantly so, and suggest minimal disturbance at H1, H3 and H4, limited at H2, P1 and P3, and greatest at P2 and P4.

### 3.2.3. Assemblage composition

Faunal assemblage composition by density was significantly different between the hill and plain sites (ANOSIM $R = 0.70$, $p < 0.05$; Fig. 6; Appendix B). This dissimilarity in composition (65%) was driven by *I. vagabunda* (24%), Ophiuroidea (16%) and *A. abyssorum* (13%). Morphotypes recorded only on the hills were *Munidopsis* sp., Cnidaria sp.1 (both found at more than one hill).
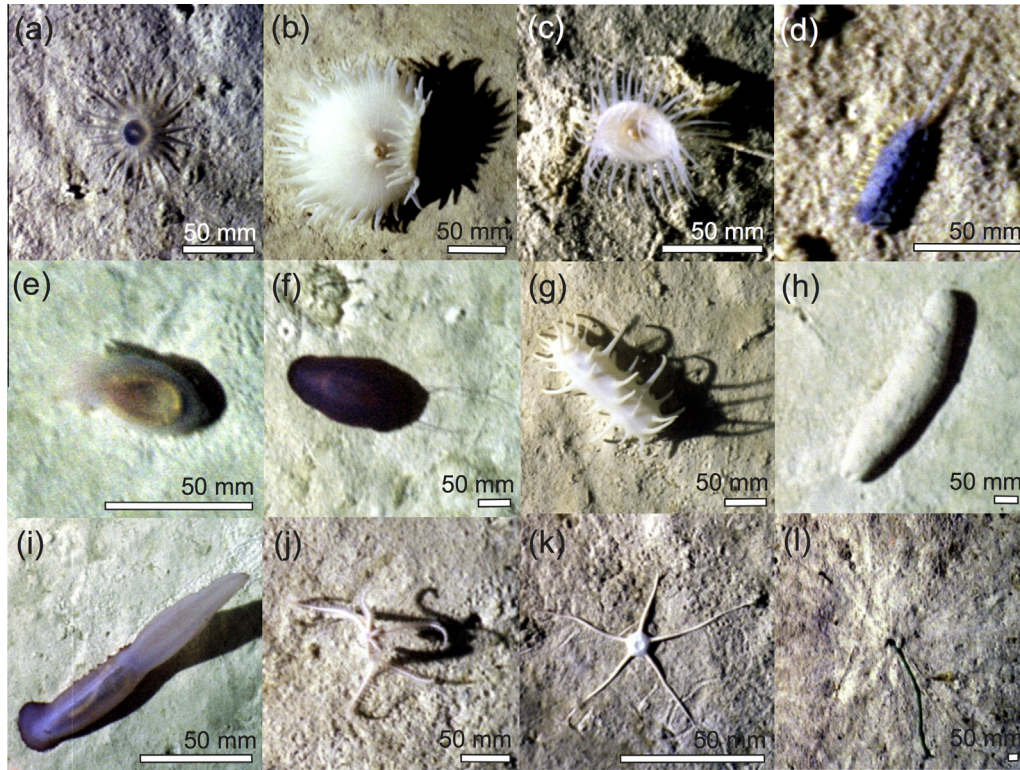
**Fig. 2.** Selected megafauna observed in seabed photographs from the study sites: Cnidarians (a) *Iosactis vagabunda*, (b) *Sicyonis* sp., (c) Cnidaria sp.10; (d) Polychaeta; Holothurians (e) *Amperima* sp., (f) *Benthothuria* sp., (g) Oneirophanta sp., (h) *Pseudostichopus villosus*, (i) *Psychropotes longicauda*; (j) Brisingid; (k) Ophiuroid; (l) Echiura.
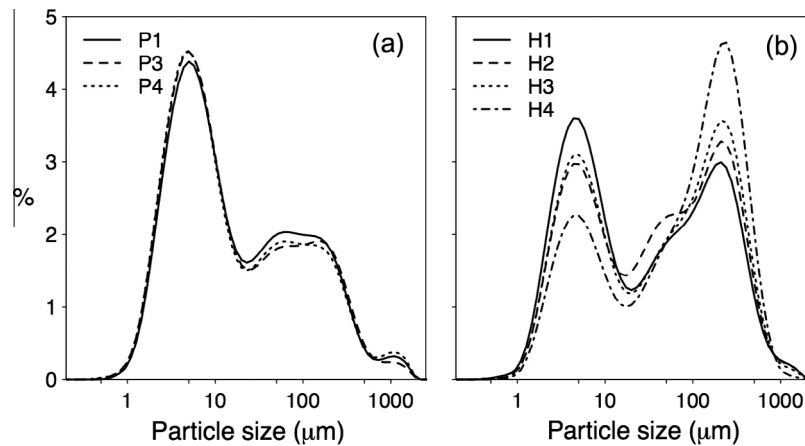


**Fig. 3.** Average particle size distributions of surface sediments (0–5 cm) from Megacores collected at sites on (a) the plain and (b) the hills.

Variation in assemblage composition by density was best correlated with coarse particle fraction ($r_s[5] = 0.77$). The mean similarity (56%) between plain sites was driven by *I. vagabunda* (57%), and *Amperima* sp. (22%), while mean similarity (49%) between hill sites was driven by *Amperima* (20%), *A. abyssorum* (17%), and Ophiuroidea (15%). A significant relationship was detected between variations in faunal composition by density and habitat heterogeneity ($R = 0.42$, $p < 0.05$).

Variations in faunal assemblage composition by biomass were also significantly different between plain and hill sites ($R = 0.69$, $p < 0.05$; Appendix C), and best correlated with coarse particle fraction ($r_s[5] = 0.59$). Morphotypes that contributed most to the mean dissimilarity in biomass composition between hill and plain sites (66%) were *A. abyssorum* (31%) and *Pseudostichopus villosus* (14%),

both of which contributed most to the mean similarity between hill sites, and *Psychropotes longicauda* (12%), which contributed most to the mean similarity between sites on the plain.

### 3.2.4. Trophic composition

Variation in trophic composition between plains and hill sites is illustrated in Fig. 7 and listed in Table 2. The density of surface deposit feeders (ANOVA $F(1,6) = 6.76$, $p < 0.05$; mean on hills 0.19 ind m$^{-2}$, 95% CI 0.08–0.31 ind m$^{-2}$; mean on plains 0.08 ind m$^{-2}$, 95% CI 0.02–0.16 ind m$^{-2}$) and the biomass of suspension feeders (ANOVA $F(1,6) = 26.83$, $p < 0.01$; mean on hills 7.84 g m$^{-2}$, 95% CI 2.40–21.99 g m$^{-2}$; mean on plains 0.71 g m$^{-2}$, 95% CI 0.25–1.36 g m$^{-2}$) were significantly greater on the hills than the plain. The density of surface deposit feeders was significantly
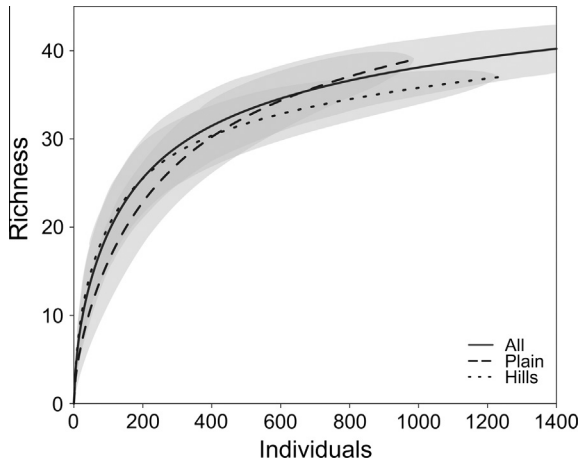
**Fig. 4.** Individual-based rarefied megabenthic morphotype richness determined from seabed photographs on the plains (sites grouped), hills and in all images. Shaded areas represent 95% confidence intervals.
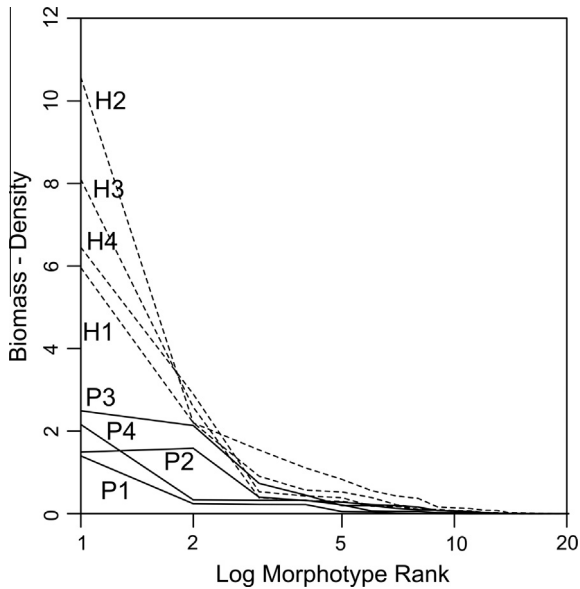


**Fig. 5.** Difference in biomass- and density-based k-dominance plots at sites on the plain (solid lines) and on the hills (dashed lines).



**Fig. 6.** 2-Dimensional non-metric multidimensional scaling ordination plots of megabenthic taxon composition by (a) density and (b) biomass at abyssal plain (P) and hill (H) sites.



**Fig. 7.** The proportions of megafaunal density and biomass by feeding types (suspension feeder, surface deposit feeder, and subsurface deposit feeder; predator/scavenger proportion negligible and omitted).

correlated to the fraction of coarse particles ($r_s[8] = 0.85$, $p < 0.05$), as was the biomass of suspension feeders ($r_s[8] = 0.93$, $p < 0.01$), which was also correlated to slope ($r_s[8] = 0.79$, $p < 0.05$).

The relative proportions of trophic groups also varied with topography. The proportion of suspension feeders and surface deposit feeders by density differed significantly between the hill and plain sites (ANOVA $F(1,6) = 6.62$, $p < 0.05$ and $F(1,6) = 8.63$, $p < 0.05$, respectively), and their proportions by biomass were also significantly different between the hill and plain sites ($F(1,6) = 9.05$, $p < 0.05$ and $F(1,6) = 11.89$, $p < 0.05$, respectively). At the plain sites, suspension feeders were dominant by density, while surface deposit feeders were dominant by biomass. At the hill sites, suspension feeders were dominant by biomass at three sites (H2–H4). Subsurface deposit feeders and predators/scavengers made minor contributions, with no significant variations related to topography. The proportion of suspension feeders by biomass was significantly correlated with the fraction of coarse particles ($r_s[8] = 0.99$, $p < 0.0001$), slope ($r_s[8] = 0.83$, $p < 0.05$), and altitude ($r_s[8] = 0.85$, $p < 0.01$). The proportion of surface deposit feeders by biomass was negatively correlated with the fraction of coarse particles ($r_s[8] = -0.69$, $p < 0.1$).
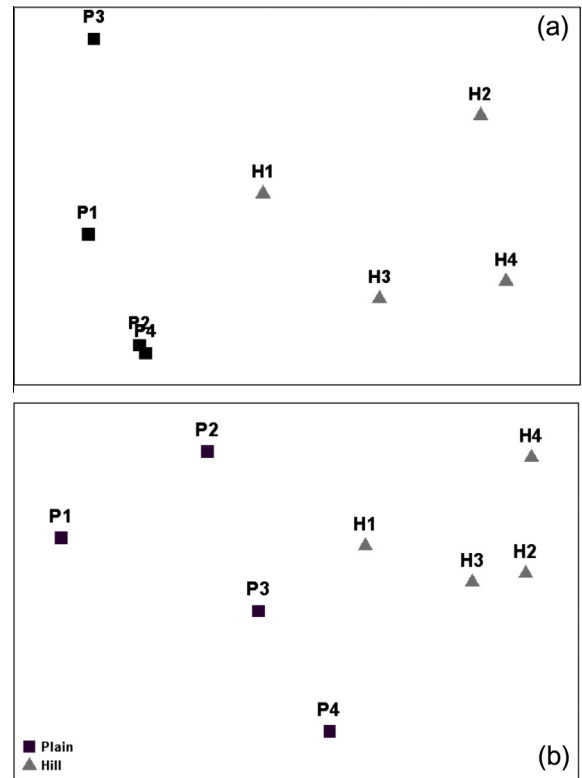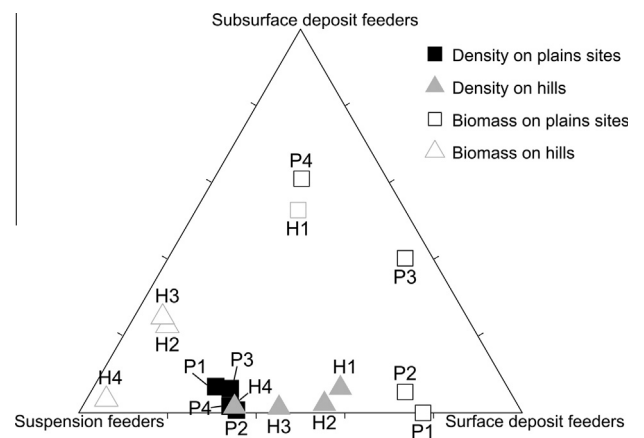
## 4. Discussion

### 4.1. Megafaunal assemblages of abyssal hill and plain sites

We found significant differences in the megafaunal assemblages related to the variations in environmental conditions on abyssal hills and the adjacent plain. These globally abundant hill features likely play an important role in structuring abyssal communities. The significant heterogeneity detected here occurs at physical scales less than the ~100 km scale examined by Billett et al. (2010) for the broader abyssal plain, and provides new insights into factors affecting abyssal community structure.

The difference in the megafaunal ecology between hills and the surrounding plain manifests as changes in biomass, diversity (evenness of assemblages by abundance and biomass), and assemblage composition. Changes in biomass related to the rank-switching of low-individual biomass morphotypes, such as *I. vagabunda*, from high density-dominance on the plain to lower densities on the hills, and of moderate- and large-individual biomass morphotypes, such as Other Cnidarians and *Pseudostichopus villosus*, from lower densities on the plain to higher densities on the hills.

The results suggest that hill features significantly alter abyssal assemblages, and the inclusion of hill features in the consideration of abyssal ecology changes the overall impression of diversity and biomass in the deep sea. Sites on the hills have greater variation in the megafaunal assemblage (i.e. beta-diversity) between them than variation between sites on the plain, which is complemented by greater variation in the sediment conditions. In terms of the gamma-diversity related to topography at the landscape scale, the total species pool is increased when hills and plain are considered together, the assemblage composition becomes less even, and rarefied richness somewhat reduced.

### 4.2. Habitat heterogeneity and processes regulating megafaunal assemblages

We have established that abyssal hills provide heterogeneity to the overall abyssal habitat. This suggests that with abyssal hills, as with other topographic features, local processes causing differences in organic matter settling and sedimentary conditions may be the factors related to differences in communities (Rhoads, 1974; Rhoads and Boyer, 1982; Snelgrove and Butman, 1994; Young et al., 2001).

The observed differences between biomass and density in cumulative dominance plots suggest that plain sites may have a higher disturbance regime than the hill sites. There were also differences in the W-statistics suggesting variation among hills and within the plains. The abundance–biomass comparison method of detecting disturbance is based on succession theory, and was originally developed as an indicator of disturbance to macrobenthic communities resulting from pollution (Warwick, 1986). It is now widely used to evaluate other types of disturbance to the benthos, including biological and physical disturbances (Warwick et al., 1987), and appears applicable to a wide range and size of taxa (Blanchard et al., 2004). The application of this method to the examination of disturbance in assemblages assumes that the communities under comparison are the same, but in different successional states. This may hold true at the PAP, where the majority of morphotypes found at the hills and plain sites were the same, with only a few singletons or low-density morphotypes restricted to either setting. The succession of the community at PAP in response to disturbance may be comparable to that of the shallow-water macrobenthos (Warwick et al., 1987), with opportunists favoured in disturbed areas (Warwick and Clarke, 1994). Previous time-series studies have shown that some small abyssal surface deposit feeders are opportunistic (e.g. *Amperima* sp.; Wigham et al., 2003), while large taxa (e.g. *Oneirophanta* sp.) suffer losses during booms of small opportunists (Billett et al., 2010; Ramirez-Llodra et al., 2005).

The W-statistic may act as a proxy for the occurrence and/or frequency of disturbing events that alter the studied assemblages, we can speculate on the mechanisms that link habitat heterogeneity to variation in megafaunal assemblages. Disturbance on the hills and plains may have several sources that differ in magnitude, including differences in organic particle accumulation rates and sorting dynamics, and the influence of rare but pervasive impacts from debris flows or turbidity currents. Food supply is a key structuring feature in abyssal communities (Rex et al., 2006), but

seafloor coverage by phytodetritus found here was low, and no significant difference was noted between the hills and plain. However, our data provide only a snapshot of this dynamic temporal process that is known to exhibit substantial intra- and inter-annual variation (Bett et al., 2001). It may be that differences in phytodetritus accumulation became more evident in seabed photographs during periods of higher input than we observed.

Physical disturbance on the plain is likely related to sediment movement as a result of local hydrodynamics, including historical turbidity currents and contemporary sediment movement by currents. The dark bands observed in the cores from P1, P2 and P4, where the sediment was stratified on the sub-bottom profile, are likely a preserved redox potential discontinuity layer as a result of an historical turbidity flow (Thomson et al., 1987), an event suggested to reduce densities and biomass in the abyss, with recovery taking thousands of years (Young and Richardson, 1998; Young et al., 2001). Sedimentation differed at P3 (no band observed in cores, no stratification in sub-bottom profile) from the other sites on the plain, possibly owing to the run out of slope failures from the adjacent steep hill. In contrast, physical disturbance to the sediment on abyssal hills is likely a result of the hydrodynamic erosion of finer particles (winnowing), where fine sediments accumulate in areas of lower flow velocity than coarse sediments. The topography of abyssal hills increases the near bed flow, by as much an order of magnitude (Klein and Mittelstaedt, 1992). The resulting lower sediment accumulation rates on the hills is evident from the visible surface drop stones in cores and photographs from the hill sites and lack thereof on the plain. The chaotic structure of mixed sediments in cores from H2, located on the flank of a hill, suggests differing processes may dominate the physical disturbance there other than vertical particulate sedimentation; it is likely that the extreme variability in sediment observed in the cores is an indication of debris flow.

### 4.3. Trophic structure

The trophic structure of the megabenthos at the PAP differs on the hills and plain, and appears to be related to habitat heterogeneity. Potential topographically-generated increases in the near-bed flow may increase the flux of suspended organic particles, a food resource not necessarily reflected in our quantification of the detritus on the seabed. Such current-related organic matter fluxes have previously been suggested to benefit seamount communities of suspension feeders (Rowden et al., 2010).

The strict separation of taxa by feeding type is difficult at the PAP as a result of the likely non-linear food web structure (van Oevelen et al., 2012), overlap in food sources and adaptation to compete for food (Iken et al., 2001). For example, cnidarians are not solely suspension feeders; they have widened their trophic niche to include predation on polychaetes and crustaceans. The increased mobility of some species, such as *I. vagabunda* (a hemisessile sea anemone) (Riemann-Zürneck, 1997), has led to carnivory. Stable isotope studies place this species at the top of the cnidarian trophic range at the PAP (Iken et al., 2001). This morphotype has an important influence on the interpretation of our results. The proportional density of suspension feeders was higher than deposit feeders on the plain, with *I. vagabunda* comprising the majority of the suspension feeders on the plain. The biomass of suspension feeders was greater on the hills than on the plain, but the biomass of *I. vagabunda* was greater on the plain, and the contribution of *I. vagabunda* to the suspension feeder biomass was greater on the plain than on the hills. When *I. vagabunda* is removed from the trophic analysis, the fraction of suspension feeders is significantly less on the plains than on the hills (ANOVA $F(1,6) = 13.5$, $p < 0.05$), and the biomass of suspension feeders is significantly greater on the hills than on the plain (ANOVA

$F(1,6) = 13.1$, $p < 0.05$). The preference of this suspension feeder for the plains may be related to two lifestyle factors. Firstly, *I. vagabunda* employs both mixed feeding methods on the plain (Durden et al., 2015), while other strict suspension feeders are more prominent on the hills. Secondly, this animal burrows in the soft sediment that is found on the plains, rather than attaching to hard substrata, found on the hills.

### 4.4. Comparison to seamounts

The changes in sediment conditions and megafaunal assemblages between abyssal hills and the adjacent plain suggest that abyssal hills share some similarities with seamounts, in terms of faunal biomass, diversity and environmental conditions. The higher megabenthic biomass on the abyssal hills of the PAP echoed the elevated benthic biomass on seamounts found by Rogers (1994). Habitats on abyssal hills are influenced by the same environmental conditions as those on seamounts: seamount geomorphology, substratum type, hydrodynamic regime. Our finding that megafaunal assemblages were linked to sediment coarse particle fraction were analogous to results in Levin and Thomas (1989) and Lundsten et al. (2009) where the patchiness of soft-sediment fauna was influenced by topographically-induced currents and sediment coarseness on seamounts. Accelerated currents caused by topography can increase the horizontal transport of food, which favours suspension feeders. In terms of biomass, our results at the PAP are in common with the findings of Jones et al. (2007) that suspension feeders favored coarse sediments and deposit feeders finer sediments, and also those of Rowden et al. (2010), that the biomass on seamounts is dominated by suspension feeders and dominated by deposit feeders on the continental slope. Similarly, Jones et al. (2013) found increased suspension feeder and reduced deposit feeder numbers with increasing slope on a bathyal knoll feature.

## 5. Conclusions

We have quantified the differences in megafaunal assemblages between abyssal hills and the adjacent plain, and have linked them to changes in environmental conditions, testing a fundamental ecological heterogeneity paradigm in the most common habitat on the planet. Our findings suggest that the biomass and structure of megafaunal assemblages are related to differences in sedimentary conditions, rather than to differences in depth or in sinking particulate organic carbon inputs from the surface ocean. The work indicates that abyssal hills may increase beta and gamma-diversity in the abyss, suggesting that previous interpretations based on plains alone may contain significant biases, and underestimate this heterogeneity at the global scale.

However, key questions remain regarding the scale of environmental heterogeneity and the processes controlling it. Further work is required to quantify the detailed contributions of factors that cause such heterogeneity, such as slope, hydrodynamic regime, sedimentation events (both sinking from the surface and re-suspended sediments), and bioturbation. To understand the roles of these factors in structuring megabenthic communities, the topography of abyssal hills must be examined in higher resolution.

## Acknowledgements

## Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.pocean.2015.06.006.

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