1 Running head: Abyssal hills shape megafaunal assemblages

2 **Title: Abyssal hills - hidden source of increased habitat heterogeneity, benthic megafaunal**

3 **biomass and diversity in the deep sea**

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14 **Highlights:**

15 • We used photos to assess abyssal megabenthic communities on hills and the plain.

16 • Megafaunal biomass was significantly greater on the hills than the adjacent plain.

17 • Differences in megabenthic communities were related to environmental conditions.

18 • Assemblage, and trophic, compositions were correlated with sediment particle size.

19

20

1 Abstract

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 to 19.36 $g.m^{-2}$) than the plain (4.34 $g.m^{-2}$, 95% CI 2.08 to 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.

Key words: Community composition; diversity; topography; deep sea; megafauna; benthic; habitat heterogeneity

1   **Regional index terms:** Porcupine Abyssal Plain, Northeast Atlantic Ocean

2   **2   Introduction**

3   Habitat heterogeneity resulting from broad-scale topographic features is responsible for

4 variations in the diversity and biomass of seafloor fauna in channels (Jones, Bett & Tyler, 2007),

5 canyons (De Leo, Smith, Rowden, Bowden & Clark, 2010; McClain & Barry, 2010; Ramirez-

6 Llodra, Company, Sardà & Rotllant, 2010; Sarda, Cartes & Company, 1994), trenches (Paterson,

7 Glover, Frojan, Whitaker, Budaeva et al., 2009), and on seamounts (McClain, 2007). Habitat

8 heterogeneity and benthic diversity has been examined in the deep sea, for example, by

9 comparing communities at sites between basins across the Mid-Atlantic Ridge (Alt, Rogacheva,

10 Boorman, Hughes, Billett et al., 2013; Priede, Bergstad, Miller, Vecchione, Gebruk et al., 2013)

11 and between the Porcupine and Madeira Abyssal Plains (PAP and MAP; Thurston, Rice & Bett,

12 1998). However, the heterogeneity of the abyssal plain habitat and corresponding seafloor

13 assemblage density, biomass and composition is little known at a sub-basin scale.

14   The abyss was once viewed as being practically homogenous, with lower habitat

15 heterogeneity than most other habitats globally. Nearly all previous work from abyssal depths,

16 including biodiversity and biomass estimation, uses data from the level abyssal plain (Jones,

17 Yool, Wei, Henson, Ruhl et al., 2014). However, the vast abyssal plains are populated by abyssal

18 hills, thought to be the most abundant landform on Earth (Harris, Macmillan-Lawler, Rupp &

19 Baker, 2014). Sediment-covered abyssal hills rise up to 1000 m above the seabed (seamounts by

20 definition reach >1000 m above the seafloor), and exist in similar densities in the Atlantic, Indian

21 and Pacific Oceans (Yesson, Clark, Taylor & Rogers, 2011). Despite their abundance, and

22 potential importance to spatial variation in benthic communities, abyssal hills have been rarely

23 studied. Even at the much-studied Porcupine Abyssal Plain (Hartman, Lampitt, Larkin, Pagnani,

1   Campbell et al., 2012), the ecology of abyssal hills have been tacitly avoided as they are

2   logistically challenging to study. Previous studies of the PAP, including a long-term time series,

3   have focussed on the level bottom (Bett, Malzone, Narayanaswamy & Wigham, 2001; Bett &

4   Rice, 1993; Billett, 1991; Billett, Bett, Rice, Thurston, Galeron et al., 2001; Billett & Rice, 2001;

5   Brunnegard, Grandel, Stahl, Tengberg & Hall, 2004; Danovaro, Dell'Anno & Fabiano, 2001;

6   Turnewitsch & Springer, 2001), but few have examined the potential spatial variation. Billett et

7   al. (2010) found detectable differences in megafaunal community composition between trawls

8   collected ~100 km apart on the PAP, but little synoptic data exists for quantitative study of

9   abyssal heterogeneity at the scale of hills.

10   Variations in local (alpha) species diversity in the deep sea have been related to

11   environmental gradients (Levin, Etter, Rex, Gooday, Smith et al., 2001), and the complex

12   interactions of these effects may lead to variations in diversity associated with habitat

13   heterogeneity. Seamounts, which can be considered as large analogues of abyssal hills, have

14   been the subject of considerable research on habitat variation in relation to bathymetry,

15   substratum, currents and topography (McClain, 2007). Seamounts appear to be characterised by

16   both high species richness and high standing stock biomass (Clark, Rowden, Schlacher,

17   Williams, Consalvey et al., 2009; McClain, 2007; Ramirez-Llodra, Brandt, Danovaro, De Mol,

18   Escobar et al., 2010; Rowden, Schlacher, Williams, Clark, Stewart et al., 2010). Causal factors

19   are thought to include: alteration of currents and near-bed flows (Hernandez-Molina, Maldonado

20   & Stow, 2008), with implications for sediment sorting and deposition of particulate organic

21   material (Graf, 1989); elevation of seafloor, providing habitat for species of limited bathymetric

22   range (Rex & Etter, 2010); reduced settling distance of particulate organic matter (Wei, Rowe,

23   Hubbard, Scheltema, Wilson et al., 2010); and greater substratum type diversity associated with

1   bathymetric features (Levin & Nittrouer, 1987). However, it is not clear how such heterogeneity

2   might extend to lesser topographic features, having only modest elevations (e.g. ~200 m above

3   the abyssal seafloor), and limited flank slope angles (<15°; Heezen & Laughton, 1963). Abyssal

4   hills and the adjacent plain provide an excellent model system for investigating the effects of

5   habitat heterogeneity, with minimal influence of spatial variation in the overhead supply of food

6   as particles sinking from surface waters. If abyssal hills do harbour a largely unappreciated

7   biological heterogeneity, regional abyssal biological diversity may be appreciably higher than

8   current estimates suggest.

9   Here we evaluate the role of landscape-scale habitat heterogeneity in structuring megafaunal

10   assemblages in the abyss. We hypothesize that abyssal hill features differ from the adjacent

11   abyssal plain in terms of physical habitat (sediment type and topography), but otherwise have

12   similar ecological structuring forces (common organic matter input). We expect that the density,

13   biomass, assemblage structure, alpha- and beta-diversity of megafaunal assemblages inhabiting

14   abyssal hills are significantly different from those on the plain. We test these hypotheses using

15   remote sensing (acoustics and photographic data) and direct sampling of the sedimentary

16   environment. We used these data to show how observed differences in habitat heterogeneity may

17   affect megafaunal assemblages, and contribute to our understanding of processes structuring the

18   broad-scale community and regulating biological diversity in the abyss.

19

20   **3   Methods**

21   **3.1   Study Area**

22   The PAP (NE Atlantic) has been a site of approximately annual study since 1985,

23   primarily for water column biogeochemistry, particulate organic carbon flux, and biochemistry

1   and ecology of the seabed. It was originally chosen as a study site for the absence of major

2   topographic features, and its substantial distance from the potential influences of both the

3   continental margin and the Mid-Atlantic Ridge (Billett, Lampitt, Rice & Mantoura, 1983; Billett

4   & Rice, 2001). The majority of the abyssal hills of the PAP rise approximately 300 m above the

5   plain, with one rising to ~1000 m (Klein & Mittelstaedt, 1992; Turnewitsch & Springer, 2001).

6   Eight locations were selected for the present study (Figure 1, Table 1): four on the plain (P1 to

7   P4), and four on hills of varying altitude and flank slope (H1 to H4). Site P1 corresponds with

8   the 'PAP Central' location frequently occupied in time-series studies of the sedimentary infauna

9   (Laguionie-Marchais, Billett, Paterson, Ruhl, Soto et al., 2013) and adjacent to the primary area

10   of trawl sampling of megabenthos studies (Billett et al., 2010).

11   **3.2   Assessment of habitat heterogeneity and food availability**

12   To test whether physical habitat and food availability differed on abyssal hills from the

13   plain, we collected environmental data (Table 2), including first-order derivatives from

14   bathymetric data (i.e. depth and slope), substratum characteristics, and measures of food

15   availability. Seafloor bathymetry was assessed using a hull-mounted Simrad EM12 multibeam

16   echo sounder during RRS *Charles Darwin* cruise 158 in June 2004 (Lampitt, 2010), processed to

17   a 50 m x 50 m pixel resolution for subsequent analyses. The water depth along each

18   photographic transect (see section 3.3) was expressed as the altitude above the abyssal plain

19   seabed normalised to standard score. Median seafloor slope for each location was determined

20   using a native function in ArcMAP(v10.0; ESRI) using a 100 m buffer around each photographic

21   transect (see section 3.3). Subsurface sediment structure was imaged using a Kongsberg Simrad

22   SBP120 subbottom profiler (chirp 2.5-7 kHz) during the RRS *James Cook* cruise 062 (Ruhl,

23   2012) in July and August 2011.

1   Physical surface sediment characteristics were assessed from multiple Megacorer samples

2   (59 and 100 mm internal diameter; Gage & Bett, 2005) collected at each location (Figure 1)

3   during research cruise JC062. Following visual inspection of the cores for the presence of

4   dropstones (Bennett, Doyle & Mather, 1996), sediment particle size distributions were measured

5   in each of three near-surface layers (0-10, 10-30, 30-50 mm) by laser diffraction using a Malvern

6   Mastersizer, after homogenisation (particles >2 mm removed), dispersal in a 0.05% $(NaPO_3)_6$

7   solution (Abbireddy & Clayton, 2009), and mechanical agitation. For subsequent analyses, the

8   mean particle size distribution for each site was computed for the combined 0-50 mm horizon.

9   As the particle size distributions were bimodal with a consistent trough between modes at

10   22.9 μm, the fraction of particles in the coarse mode (> 22.9 μm) was used for comparison to

11   biological data. No cores were available from site P2, so particle size data from P1 were used as

12   a proxy, given their close proximity and similarity in other observed and measured

13   environmental characteristics.

14   To assess the food input to the abyssal hills and plain, we measured seafloor accumulations

15   of phytodetritus (Bett et al., 2001), the dominant allochthonous particulate organic matter input

16   to the PAP. The sizes of discrete aggregates were measured in seabed photographs using

17   methods described in section 3.3, and the percentage seabed cover was calculated, an approach

18   previously used by Smith et al. (2014).

19   **3.3   Assessment of megafaunal assemblages**

20   To examine differences in megafaunal assemblages, we used photographic surveys of the

21   seabed. We captured approximately 1460 non-overlapping photographs at 12-second intervals

22   with a vertically mounted still camera (Ocean Scientific International Limited Mk7) on the Wide

23   Angle Seabed Photography towed camera platform (WASP; Jones, Bett, Wynn & Masson, 2009)

7

1   during research cruise JC062. WASP was towed (~0.25 ms^{-1}) along each transect (Figure 1) at a

2   target altitude of 2 m above the seabed. Photographs were captured on film (35mm Kodak Vision

3   250D colour negative) that was processed and then scanned at high resolution (4096 x 6144

4   pixels) prior to analysis. Photographs that were out of focus, obscured, or taken at an altitude

5   above the seabed of >5.0 m were excluded from the analysis. The camera was positioned

6   approximately perpendicular to the sea floor and the area of seafloor observed was calculated

7   from altitude and camera acceptance angles of 35º and 50º (Jones et al., 2007; Jones et al., 2009).

8   Distinctly identifiable megafauna (generally >10 mm; consistent with Grassle et al. 1975)

9   were enumerated and classified to the lowest practicable taxonomic levels (Table 3, Figure 2).

10   Each specimen was measured using ImagePro Plus (Media Cybernetics), and these dimensions

11   converted to physical units using trigonometry (e.g. Jones et al., 2007). Pelagic taxa were

12   excluded from the analysis, although some benthopelagic species, such as the holothurian

13   *Enypniastes eximia* and cephalopods, were included. Benthic specimens that could not be

14   identified as living (e.g. gastropod shells and worm tubes) were also omitted. Feeding groups

15   were assigned based on existing literature (Table 3).

16   Biomass (wet weight) was estimated from measured faunal dimensions using conversions

17   developed from relationships established between the dimensions and wet weights of specimens

18   (Table 3) collected in trawls at PAP (August 1996-October 2002; Billett et al. 2010). In those

19   small, rare taxa for which insufficient trawl data were available, biomass was estimated using

20   conversions for congener taxa of similar body shape, or omitted if an appropriate analogue was

21   not available.

22   **3.4   Data analyses**

23   Faunal count and biomass data were standardized to unit area (m^{-2}), and were log(x+1)

1 transformed prior to parametric statistical analysis. Where percentage or proportional data were

2 employed, they were subject to arcsine transformation before further assessment. Normality was

3 tested by visual inspection of histograms and QQ plots, and using the Shapiro-Wilk normality

4 test. Comparisons of hill and plain sites were made using ANOVA, and potential correlations

5 examined using Spearman's rank method. Significance at the 5% level was reported.

6   Univariate diversity indices (Shannon H´ and Pielou J´; log base 2) were calculated as

7 described in Magurran (2004). The expected number of morphotypes by rarefaction was

8 calculated (Hurlbert, 1971) at the minimum number of individuals observed in a single transect.

9 The quantitative difference of density- from biomass-based cumulative dominance curves was

10 examined as a potential means of revealing relative levels of disturbance or successional state,

11 and the W-statistic used to assess the difference (Clarke, 1990).

12   Multivariate assessments of the faunal and environmental data were computed using

13 PRIMER6 (Clarke & Warwick, 2008). Bray-Curtis similarity matrices were generated for

14 $\log(x+1)$-transformed densities and biomass; Euclidean distance similarity matrices were

15 calculated for normalized environmental data (altitude, slope, coarse particle fraction, mean

16 phytodetritus cover, median phytodetritus aggregate size). Density and biomass similarity

17 matrices were compared between the hill and plain sites, and correlated with environmental data

18 using the ANOSIM and BEST routines in PRIMER, respectively. Two other PRIMER routines,

19 SIMPER ("similarity percentages") and RELATE, were used to assess dissimilarity between hill

20 and plain composition and the morphotypes contributing to within-group similarity, and to test

21 the null hypothesis of no relationship between the faunal similarity matrices and environmental

22 factors, respectively.

23

4 Results

4.1 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 characterized 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 ~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 (Figure 3), with peaks at approximately 4 and 200 μm, likely attributable to coccoliths and foraminiferan tests, respectively (Frenz, Baumann, Boeckel, Hoppner & Henrich, 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

1   particles (> 22.9 µm). The fraction of coarse particles was significantly correlated to altitude

2   ($r_s[8] = 0.83$, $p < 0.01$), and slope ($r_s[8] = 0.80$, $p < 0.05$). Habitat heterogeneity (all physical

3   factors assessed simultaneously) was significantly different between the hills and plain

4   (ANOSIM R = 0.69, $p < 0.05$).

5   Food availability did not vary spatially; phytodetrital cover (Table 2) was not statistically

6   different between hills and plain sites, nor was median phytodetritus aggregate size. The

7   phytodetritus observed was similar in nature to three groups previously identified by Lauerman

8   and Kaufman (1998): amorphous aggregates (light with distinct edges), mucus (elongate, grey,

9   collapsed cobwebs), and rolled aggregates (amorphous rolled into cylinder).

10

11   **4.2   Megafauna**

12   **4.2.1   Standing stocks**

13   Megafaunal density at the hill sites (0.40 ind.m^{-2}; 95% confidence interval 0.22 to 0.61

14   ind.m^{-2}) was greater than at the sites on the plain (0.26 ind.m^{-2}; 95% CI 0.14 to 0.55 ind.m^{-2};

15   Table 2), though not significantly. Megafaunal biomass was, however, significantly higher at the

16   hill sites (13.45 g.m^{-2}; 95% CI 9.25 to 19.36 g.m^{-2}) compared to the plain sites (4.34 g.m^{-2}; 95%

17   CI 2.08 to 8.27 g.m^{-2}; ANOVA F(1,6) = 23.8, $p < 0.01$; Table 2).

18   **4.2.2   Diversity**

19   Overall, 43 morphotypes were observed: 39 morphotypes on the plains, 6 of which were

20   only recorded there, and 37 on the hills, 4 of which were not recorded on the plain. Neither the

21   Shannon Index nor the expected number of morphotypes were significantly different between the

22   hill and plain sites. Rarefied morphotype richness curves differed on the hills from the plains

23   (Figure 4); the amalgamation of hill and plain data produced a slight reduction in apparent

1 richness relative to plain data alone.

2   Evenness (by density) on the plain was significantly higher than at the hill sites (ANOVA

3 $F(1,6) = 12.37$, $p < 0.05$; Table 2). At the plain sites, the difference in density between the first

4 and fifth-ranked species was almost an order of magnitude (Appendix B a-d). *Iosactis*

5 *vagabunda* and *Amperima* sp. were the first and second-ranked taxa by density, and Ophiuroidea

6 ranked third to fifth, depending on location. The large holothurians *Psychropotes longicauda*,

7 *Pseudostichopus aemulatus*, *Pseudostichopus villosus*, *Benthothuria* sp. and *Enypniastes eximia*

8 occurred at low densities on the plain. Many morphotypes were recorded as singletons at any one

9 site; this was true for half of the taxa at P4. By contrast, the hill sites (except H2) were

10 characterised by lower evenness (Table 2). *Amperima* sp. was again the first or second-ranked

11 species (Appendix B d-h), while *Iosactis vagabunda* was the third-ranked species at H1 and H2.

12 *Actinauge abyssorum* was prominent on the hills, ranked second at H2, H3 and H4. Ophiuroids

13 ranked fourth or fifth. Large holothurians were also present in all hill transects.

14   Megafaunal biomass on the plain was characterized by high evenness (Appendix C). The

15 large holothurians, particularly *Psychropotes longicauda* and *Pseudostichopus villosus*, were

16 major contributors to megafauna biomass; one of these was the first ranked species at each of the

17 sites on the plain. The small-bodied taxa *Amperima* sp. and *Iosactis vagabunda* were still

18 significant contributors to biomass as a result of their high densities. Individual body weights of

19 *Amperima* sp. were significantly higher on the plain than on the hills (ANOVA $F(1,338) = 4.70$,

20 $p < 0.05$) , though there was no difference in the individual body weights of *Iosactis vagabunda*.

21 Conversely, community biomass at the hill sites was dominated by only a few species,

22 particularly *Actinauge abyssorum* and the large-bodied species *Pseudostichopus villosus*.

23   Disparity between biomass- and abundance- based cumulative dominance was greater on

1 the hills than on the plain (Figure 5). The calculated W statistics (Table 2) were greater on the

2 hills, but not significantly so, and suggest minimal disturbance at H1, H3 and H4, limited at H2,

3 P1 and P3, and greatest at P2 and P4.

4.2.3 Assemblage composition

5 Faunal assemblage composition by density was significantly different between the hill

6 and plain sites (ANOSIM R = 0.70, p < 0.05; Figure 6; Appendix B). This dissimilarity in

7 composition (65%) was driven by *Iosactis vagabunda* (24%), Ophiuroidea (16%) and *Actinauge*

8 *abyssorum* (13%). Morphotypes recorded only on the hills were *Munidopsis* sp., Cnidaria sp.1

9 (both found at more than one hill). Variation in assemblage composition by density was best

10 correlated with coarse particle fraction ($r_s[5] = 0.77$). The mean similarity (56%) between plain

11 sites was driven by *Iosactis vagabunda* (57%), and *Amperima* sp. (22%), while mean similarity

12 (49%) between hill sites was driven by *Amperima* (20%), *Actinauge abyssorum* (17%), and

13 Ophiuroidea (15%). A significant relationship was detected between variations in faunal

14 composition by density and habitat heterogeneity (R = 0.42, p < 0.05).

15 Variations in faunal assemblage composition by biomass were also significantly different

16 between plain and hill sites (R = 0.69, p < 0.05; Appendix C), and best correlated with coarse

17 particle fraction ($r_s[5] = 0.59$). Morphotypes that contributed most to the mean dissimilarity in

18 biomass composition between hill and plain sites (66%) were *Actinauge abyssorum* (31%) and

19 *Pseudostichopus villosus* (14%), both of which contributed most to the mean similarity between

20 hill sites, and *Psychropotes longicauda* (12%), which contributed most to the mean similarity

21 between sites on the plain.

4.2.4 Trophic composition

23 Variation in trophic composition between plains and hill sites is illustrated in Figure 7

1 and listed in Table 2. The density of surface deposit feeders (ANOVA $F(1,6) = 6.76$, $p < 0.05$;

2 mean on hills 0.19 ind.m^{-2}, 95% CI 0.08 to 0.31 ind.m^{-2}; mean on plains 0.08 ind.m^{-2}, 95% CI

3 0.02 to 0.16 ind.m^{-2}) and the biomass of suspension feeders (ANOVA $F(1,6) = 26.83$, $p < 0.01$;

4 mean on hills 7.84 g.m^{-2}, 95% CI 2.40 to 21.99 g.m^{-2}; mean on plains 0.71 g.m^{-2}, 95% CI 0.25 to

5 1.36 g.m^{-2}) were significantly greater on the hills than the plain. The density of surface deposit

6 feeders was significantly correlated to the fraction of coarse particles ($r_s[8] = 0.85$, $p < 0.05$), as

7 was the biomass of suspension feeders ($r_s[8] = 0.93$, $p < 0.01$), which was also correlated to slope

8 ($r_s[8] = 0.79$, $p < 0.05$).

9   The relative proportions of trophic groups also varied with topography. The proportion of

10 suspension feeders and surface deposit feeders by density differed significantly between the hill

11 and plain sites (ANOVA $F(1,6) = 6.62$, $p < 0.05$ and $F(1,6) = 8.63$, $p < 0.05$, respectively), and

12 their proportions by biomass were also significantly different between the hill and plain sites

13 ($F(1,6) = 9.05$, $p < 0.05$ and $F(1,6) = 11.89$, $p < 0.05$, respectively). At the plain sites,

14 suspension feeders were dominant by density, while surface deposit feeders were dominant by

15 biomass. At the hill sites, suspension feeders were dominant by biomass at three sites (H2-H4).

16 Subsurface deposit feeders and predators / scavengers made minor contributions, with no

17 significant variations related to topography. The proportion of suspension feeders by biomass

18 was significantly correlated with the fraction of coarse particles ($r_s[8] = 0.99$, $p < 0.0001$), slope

19 ($r_s[8] = 0.83$, $p < 0.05$), and altitude ($r_s[8] = 0.85$, $p < 0.01$). The proportion of surface deposit

20 feeders by biomass was negatively correlated with the fraction of coarse particles ($r_s[8] = -0.69$,

21 $p < 0.1$).

22

1 **5   Discussion**

2 **5.1   Megafaunal assemblages of abyssal hill and plain sites**

3   We found significant differences in the megafaunal assemblages related to the variations in

4 environmental conditions on abyssal hills and the adjacent plain. These globally abundant hill

5 features likely play an important role in structuring abyssal communities. The significant

6 heterogeneity detected here occurs at physical scales less than the ~100 km scale examined by

7 Billett et al. (2010) for the broader abyssal plain, and provides new insights into factors affecting

8 abyssal community structure.

9   The difference in the megafaunal ecology between hills and the surrounding plain

10 manifests as changes in biomass, diversity (evenness of assemblages by abundance and

11 biomass), and assemblage composition. Changes in biomass related to the rank-switching of low-

12 individual biomass morphotypes, such as *Iosactis vagabunda*, from high density-dominance on

13 the plain to lower densities on the hills, and of moderate- and large- individual biomass

14 morphotypes, such as Other Cnidarians and *Pseudostichopus villosus*, from lower densities on

15 the plain to higher densities on the hills.

16   The results suggest that hill features significantly alter abyssal assemblages, and the

17 inclusion of hill features in the consideration of abyssal ecology changes the overall impression

18 of diversity and biomass in the deep sea. Sites on the hills have greater variation in the

19 megafaunal assemblage (i.e. beta-diversity) between them than variation between sites on the

20 plain, which is complemented by greater variation in the sediment conditions. In terms of the

21 gamma-diversity related to topography at the landscape scale, the total species pool is increased

22 when hills and plain are considered together, the assemblage composition becomes less even,

23 and rarefied richness somewhat reduced.

5.2   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 & Boyer, 1982; Snelgrove & Butman, 1994; Young, Richardson & Birggs, 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, Pearson & Ruswahyuni, 1987), and appears applicable to a wide range and size of taxa (Blanchard, LeLoc'h, Hily & Boucher, 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 & Clarke, 1994). Previous time-series studies have shown that some small abyssal surface deposit feeders are opportunistic (e.g Amperima sp.; Wigham, Tyler & Billett, 2003), while large taxa (e.g. *Oneirophanta* sp.) suffer

1   losses during booms of small opportunists (Billett et al., 2010; Ramirez-Llodra, Reid & Billett,

2   2005).

3   The W-statistic may act as a proxy for the occurrence and/or frequency of disturbing

4   events that alter the studied assemblages, we can speculate on the mechanisms that link habitat

5   heterogeneity to variation in megafaunal assemblages. Disturbance on the hills and plains may

6   have several sources that differ in magnitude, including differences in organic particle

7   accumulation rates and sorting dynamics, and the influence of rare but pervasive impacts from

8   debris flows or turbidity currents. Food supply is a key structuring feature in abyssal

9   communities (Rex, Etter, Morris, Crouse, McClain et al., 2006), but seafloor coverage by

10   phytodetritus found here was low, and no significant difference was noted between the hills and

11   plain. However, our data provide only a snapshot of this dynamic temporal process that is

12   known to exhibit substantial intra- and inter-annual variation (Bett et al., 2001). It may be that

13   differences in phytodetritus accumulation became more evident in seabed photographs during

14   periods of higher input than we observed.

15   Physical disturbance on the plain is likely related to sediment movement as a result of local

16   hydrodynamics, including historical turbidity currents and contemporary sediment movement by

17   currents. The dark bands observed in the cores from P1, P2 and P4, where the sediment was

18   stratified on the sub-bottom profile, are likely a preserved redox potential discontinuity layer as a

19   result of an historical turbidity flow (Thomson, Colley, Higgs, Hydes, Wilson et al., 1987), an

20   event suggested to reduce densities and biomass in the abyss, with recovery taking thousands of

21   years (Young & Richardson, 1998; Young et al., 2001). Sedimentation differed at P3 (no band

22   observed in cores, no stratification in sub-bottom profile) from the other sites on the plain,

23   possibly owing to the run out of slope failures from the adjacent steep hill. In contrast, physical

1   disturbance to the sediment on abyssal hills is likely a result of the hydrodynamic erosion of finer

2   particles (winnowing), where fine sediments accumulate in areas of lower flow velocity than

3   coarse sediments. The topography of abyssal hills increases the near bed flow, by as much an

4   order of magnitude (Klein & Mittelstaedt, 1992). The resulting lower sediment accumulation

5   rates on the hills is evident from the visible surface drop stones in cores and photographs from

6   the hill sites and lack thereof on the plain. The chaotic structure of mixed sediments in cores

7   from H2, located on the flank of a hill, suggests differing processes may dominate the physical

8   disturbance there other than vertical particulate sedimentation; it is likely that the extreme

9   variability in sediment observed in the cores is an indication of debris flow.

10   **5.3   Trophic structure**

11   The trophic structure of the megabenthos at the PAP differs on the hills and plain, and

12   appears to be related to habitat heterogeneity. Potential topographically-generated increases in

13   the near-bed flow may increase the flux of suspended organic particles, a food resource not

14   necessarily reflected in our quantification of the detritus on the seabed. Such current-related

15   organic matter fluxes have previously been suggested to benefit seamount communities of

16   suspension feeders (Rowden et al., 2010).

17   The strict separation of taxa by feeding type is difficult at the PAP as a result of the likely

18   non-linear food web structure (van Oevelen, Soetaert & Heip, 2012), overlap in food sources and

19   adaptation to compete for food (Iken, Brey, Wand, Voigt & Junghans, 2001). For example,

20   cnidarians are not solely suspension feeders; they have widened their trophic niche to include

21   predation on polychaetes and crustaceans. The increased mobility of some species, such as

22   *Iosactis vagabunda* (a hemisessile sea anemone) (Riemann-Zürneck, 1997)*,* has led to carnivory.

23   Stable isotope studies place this species at the top of the cnidarian trophic range at the PAP (Iken

1 et al., 2001). This morphotype has an important influence on the interpretation of our results.

2 The proportional density of suspension feeders was higher than deposit feeders on the plain, with

3 *I. vagabunda* comprising the majority of the suspension feeders on the plain. The biomass of

4 suspension feeders was greater on the hills than on the plain, but the biomass of *I. vagabunda*

5 was greater on the plain, and the contribution of *I. vagabunda* to the suspension feeder biomass

6 was greater on the plain than on the hills. When *I. vagabunda* is removed from the trophic

7 analysis, the fraction of suspension feeders is significantly less on the plains than on the hills

8 (ANOVA $F(1,6) = 13.5$, $p < 0.05$), and the biomass of suspension feeders is significantly greater

9 on the hills than on the plain (ANOVA $F(1,6) = 13.1$, $p < 0.05$). The preference of this

10 suspension feeder for the plains may be related to two lifestyle factors. Firstly, *Iosactis*

11 *vagabunda* employs both mixed feeding methods on the plain (Durden, Bett & Ruhl, submitted),

12 while other strict suspension feeders are more prominent on the hills. Secondly, this animal

13 burrows in the soft sediment that is found on the plains, rather than attaching to hard substrata,

14 found on the hills.

15 **5.4   Comparison to seamounts**

16   The changes in sediment conditions and megafaunal assemblages between abyssal hills

17 and the adjacent plain suggest that abyssal hills share some similarities with seamounts, in terms

18 of faunal biomass, diversity and environmental conditions. The higher megabenthic biomass on

19 the abyssal hills of the PAP echoed the elevated benthic biomass on seamounts found by Rogers

20 (1994). Habitats on abyssal hills are influenced by the same environmental conditions as those

21 on seamounts: seamount geomorphology, substratum type, hydrodynamic regime. Our finding

22 that megafaunal assemblages were linked to sediment coarse particle fraction were analogous to

23 results in Levin and Thomas (1989) and Lundsten (2009) where the patchiness of soft-sediment

1   fauna was influenced by topographically-induced currents and sediment coarseness on

2   seamounts. Accelerated currents caused by topography can increase the horizontal transport of

3   food, which favours suspension feeders. In terms of biomass, our results at the PAP are in

4   common with the findings of Jones, Bett and Tyler (2007) that suspension feeders favored coarse

5   sediments and deposit feeders finer sediments, and also those of Rowden et al. (2010), that the

6   biomass on seamounts is dominated by suspension feeders and dominated by deposit feeders on

7   the continental slope. Similarly, Jones et al. (2013) found increased suspension feeder and

8   reduced deposit feeder numbers with increasing slope on a bathyal knoll feature.

9   **5.5   Conclusions**

10   We have quantified the differences in megafaunal assemblages between abyssal hills and the

11   adjacent plain, and have linked them to changes in environmental conditions, testing a

12   fundamental ecological heterogeneity paradigm in the most common habitat on the planet. Our

13   findings suggest that the biomass and structure of megafaunal assemblages are related to

14   differences in sedimentary conditions, rather than to differences in depth or in sinking particulate

15   organic carbon inputs from the surface ocean. The work indicates that abyssal hills may increase

16   beta and gamma-diversity in the abyss, suggesting that previous interpretations based on plains

17   alone may contain significant biases, and underestimate this heterogeneity at the global scale.

18   However, key questions remain regarding the scale of environmental heterogeneity and the

19   processes controlling it. Further work is required to quantify the detailed contributions of factors

20   that cause such heterogeneity, such as slope, hydrodynamic regime, sedimentation events (both

21   sinking from the surface and re-suspended sediments), and bioturbation. To understand the roles

22   of these factors in structuring megabenthic communities, the topography of abyssal hills must be

23   examined in higher resolution.

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20

1 **Table 1.** Details of the photographic and sediment core sampling programs at eight abyssal sites,

2 four on the plain (P) and four on hills (H) at the Porcupine Abyssal Plain.

Site	Centre latitude (º)	Centre longitude (º)	Water Depth (m)	Seabed slope[1] (°)	Useable photos	Seabed area imaged (m^2)	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

3 [1]interquartile range

4

1 **Table 2.** Summary of environmental and megafaunal data for each location, including altitude and slope from bathymetric data,

2 sedimentary characteristics from Megacorer samples, with food availability, faunal density, biomass, density-based diversity metrics

3 (H_2': Shannon Index; J_2': Pielou's evenness; EM_{103}: Rarefied taxon richness), and density and biomass for the two major megafaunal

4 feeding groups (SF: Suspension feeders; SDF: Surface Deposit feeders) from seabed photographs.

5

6

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

1   **Table 3.** Morphotypes identified in seabed photographs, with factors in the model m=A×L$^{\text{E}}$

2   for biomass estimation (m is wet weight in grams, L is dimension in mm), and feeding type

3   used in trophic analysis (P/S: Predator/scavenger, SF: Suspension feeder, SDF: Surface dep

4   feeder, SSDF: Subsurface deposit feeder).

Group	Morphotype	A	B	R^2	Feedi
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[d]	2.6779[c]	0.91	SF [a]
	Umbellula sp.1[b], sp.2[b]				SF
Echinodermata	Brisingid[b]				P/S [a]
	Ophiuroidea	0.0091[e]	1.4503[e]	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.[e]	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
	Mesothuria candelabri	0.0017	2.2409	0.62	SSDF
	Paroriza sp.	0.0002	2.5389	0.92	SSDF
	Psychropotes longicauda	0.0002	2.6518	0.94	SDF [a]
	Holothuroid sp.2[f]	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,f]				
Unknown	Unknown sp.C (ploughs sediment)[b]				SSDF
	Unknown sp.R (Circle scriber)[b]				SDF

5   [a] Iken et al (2001); [b] Not included in biomass estimate; [d] Length-wet weight relationship for

6   *Kadosactis* sp.; [e] Length-wet weight relationship for *Benthodytes* sp.; [f] Feeding type unknov

1 **Figures**

2 **Figure 1.** Bathymetric map of the study area, with inset indicating general location of the

3 Porcupine Abyssal Plain in the northeast Atlantic Ocean, and detail indicating the locations of

4 study sites on the abyssal plain (P) and hills (H).

5 **Figure 2**. Selected megafauna observed in seabed photographs from the study sites: Cnidarians

6 (a) *Iosactis vagabunda*, (b) *Sicyonis* sp., (c) Cnidaria sp.10; (d) Polychaeta; Holothurians (e)

7 *Amperima* sp., (f) *Benthothuria* sp., (g) Oneirophanta sp., (h) Pseudostichopus villosus, (i)

8 Psychropotes longicauda; (j) Brisingid; (k) Ophiuroid; (l) Echiura.

9 **Figure 3**. Average particle size distributions of surface sediments (0-5 cm) from Megacores

10 collected at sites on (a) the plain and (b) the hills.

11 **Figure 4.** Individual-based rarefied megabenthic morphotype richness determined from seabed

12 photographs on the plains (sites grouped), hills and in all images. Shaded areas represent 95%

13 confidence intervals.

14 **Figure 5.** Difference in biomass- and density-based k-dominance plots at sites on the plain (solid

15 lines) and on the hills (dashed lines).

16 **Figure 6.** 2-dimensional non-metric multidimensional scaling ordination plots of megabenthic

17 taxon composition by (a) density and (b) biomass at abyssal plain (P) and hill (H) sites.

18 **Figure 7.** The proportions of megafaunal density and biomass by feeding types (suspension

19 feeder, surface deposit feeder, and subsurface deposit feeder; predator/scavenger proportion
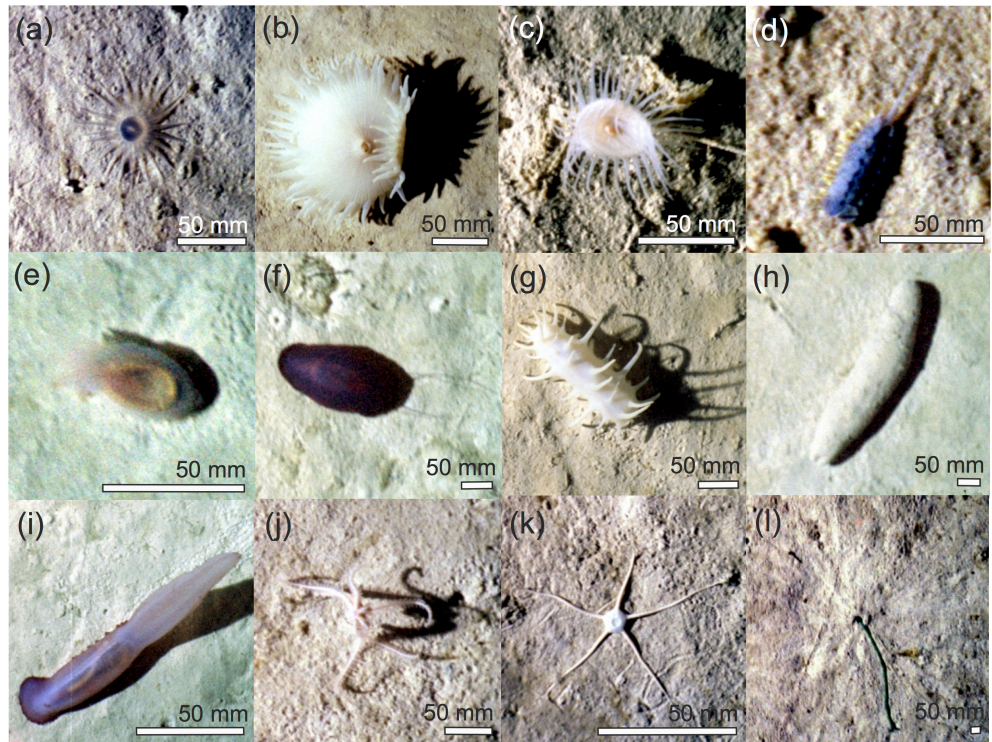
20 negligible and omitted).
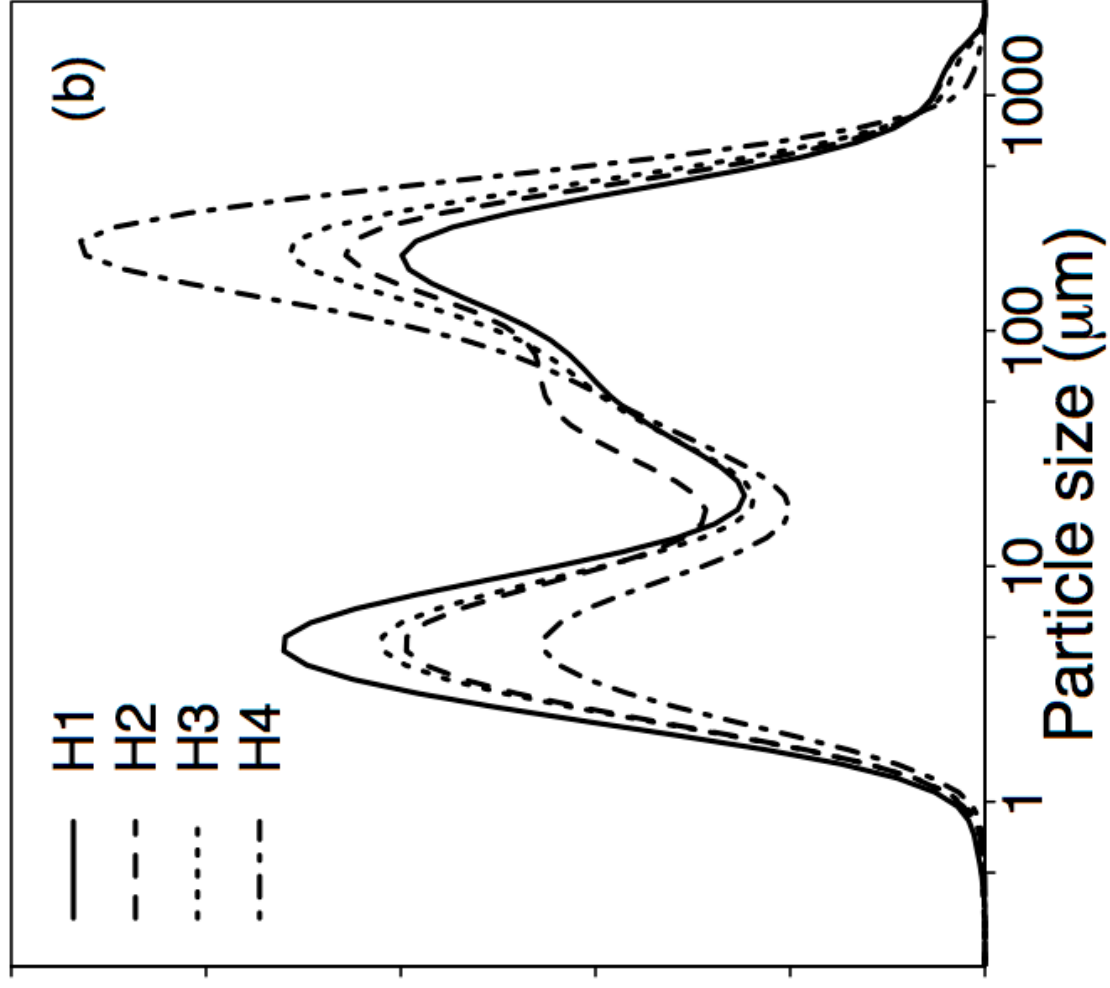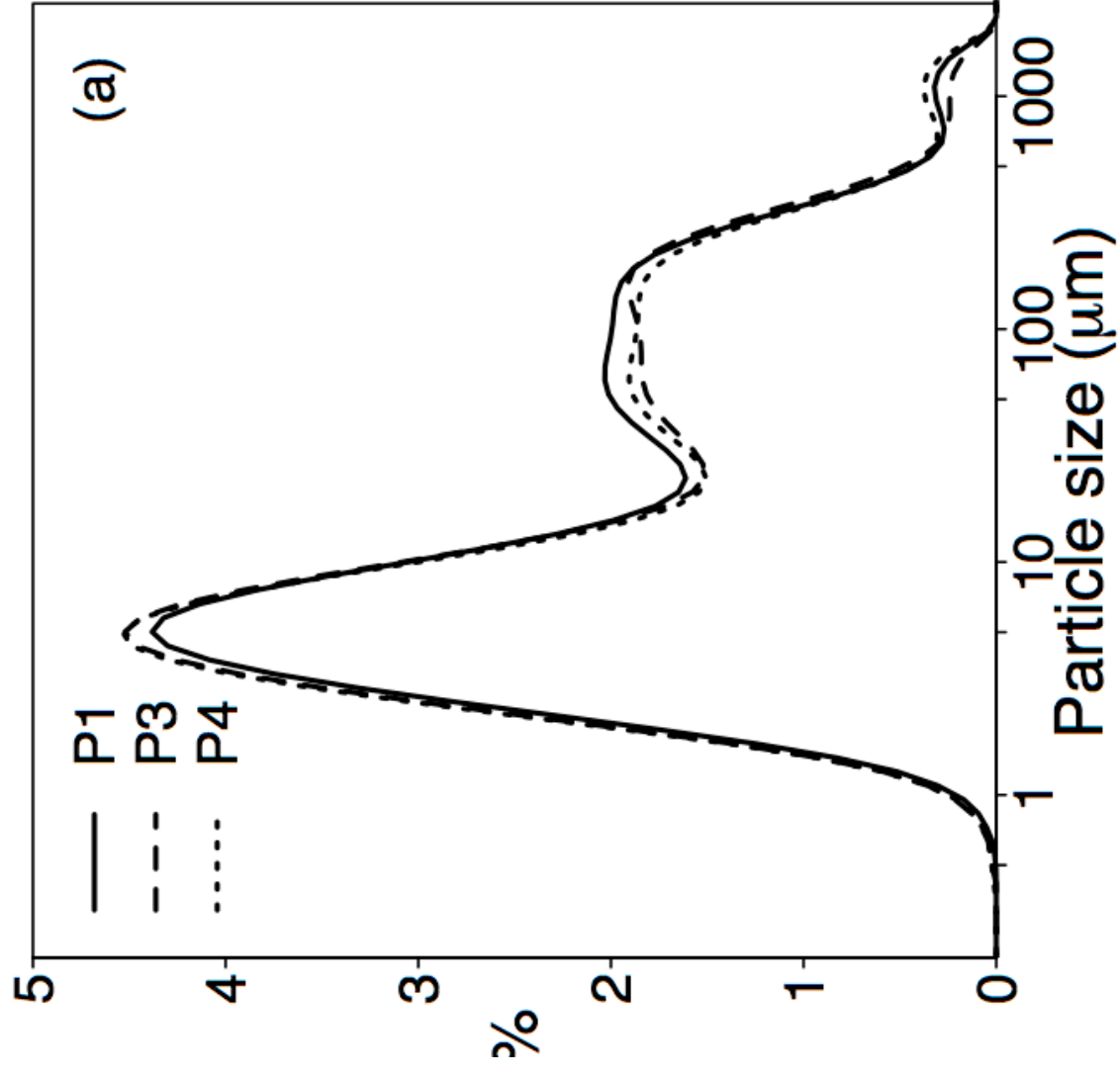
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1 **Supplemental Materials**

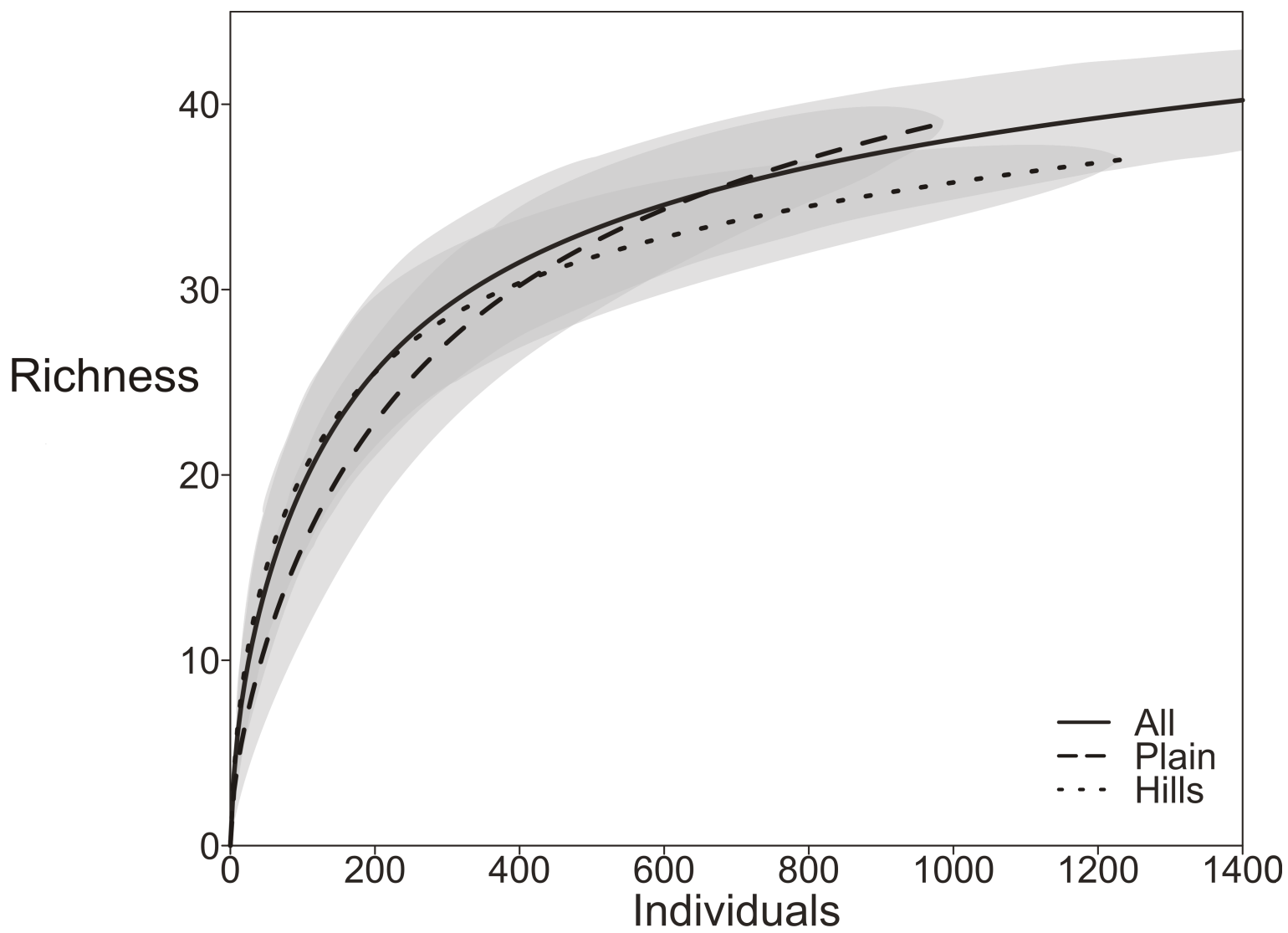2 **Appendix A**. Photographs of representative sediment megacore profiles for the study sites.

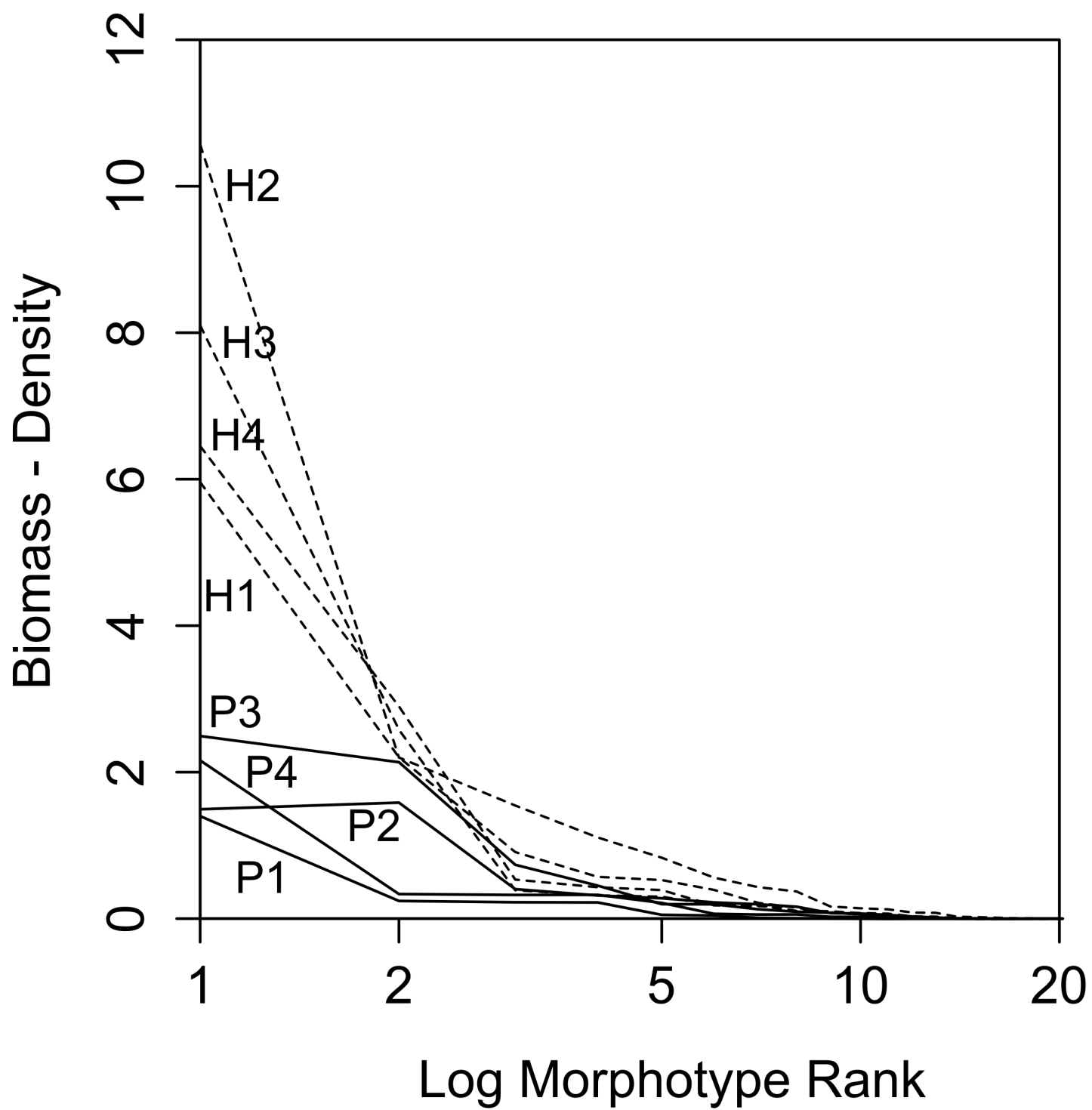3 **Appendix B.** Megabenthic morphotypes ranked by density from the study sites.

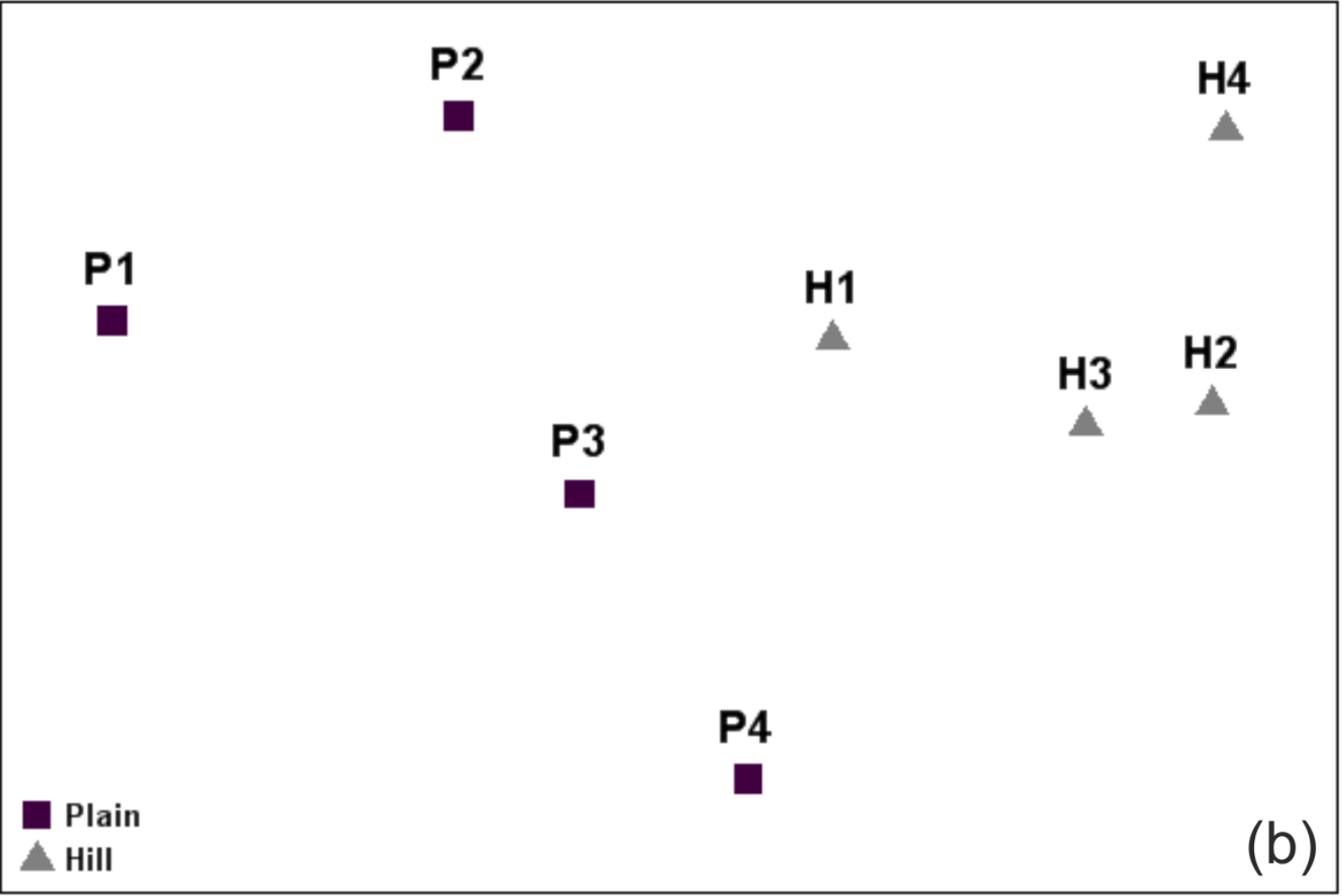4 **Appendix C.** Megabenthic morphotypes ranked by biomass from the study sites.
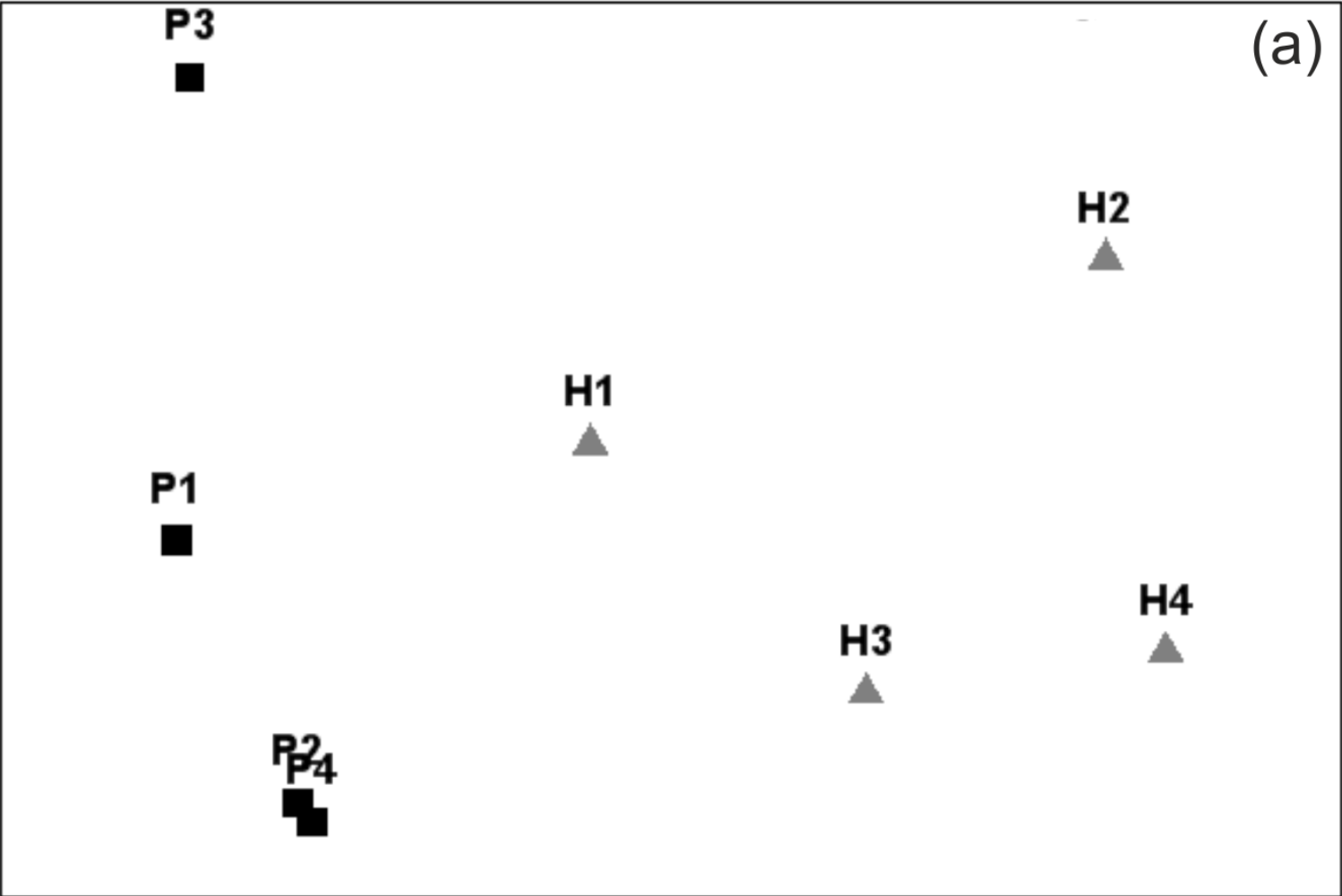
(a)   (b)   (c)   (d)
50 mm   50 mm   50 mm   50 mm

(e)   (f)   (g)   (h)
50 mm   50 mm   50 mm   50 mm

(i)   (j)   (k)   (l)
50 mm   50 mm   50 mm   50 mm

(a)

P3

H2

H1

P1

H4

H3

P2
P4

(b)

P2

H4

P1

H1

H3
H2

P3

P4
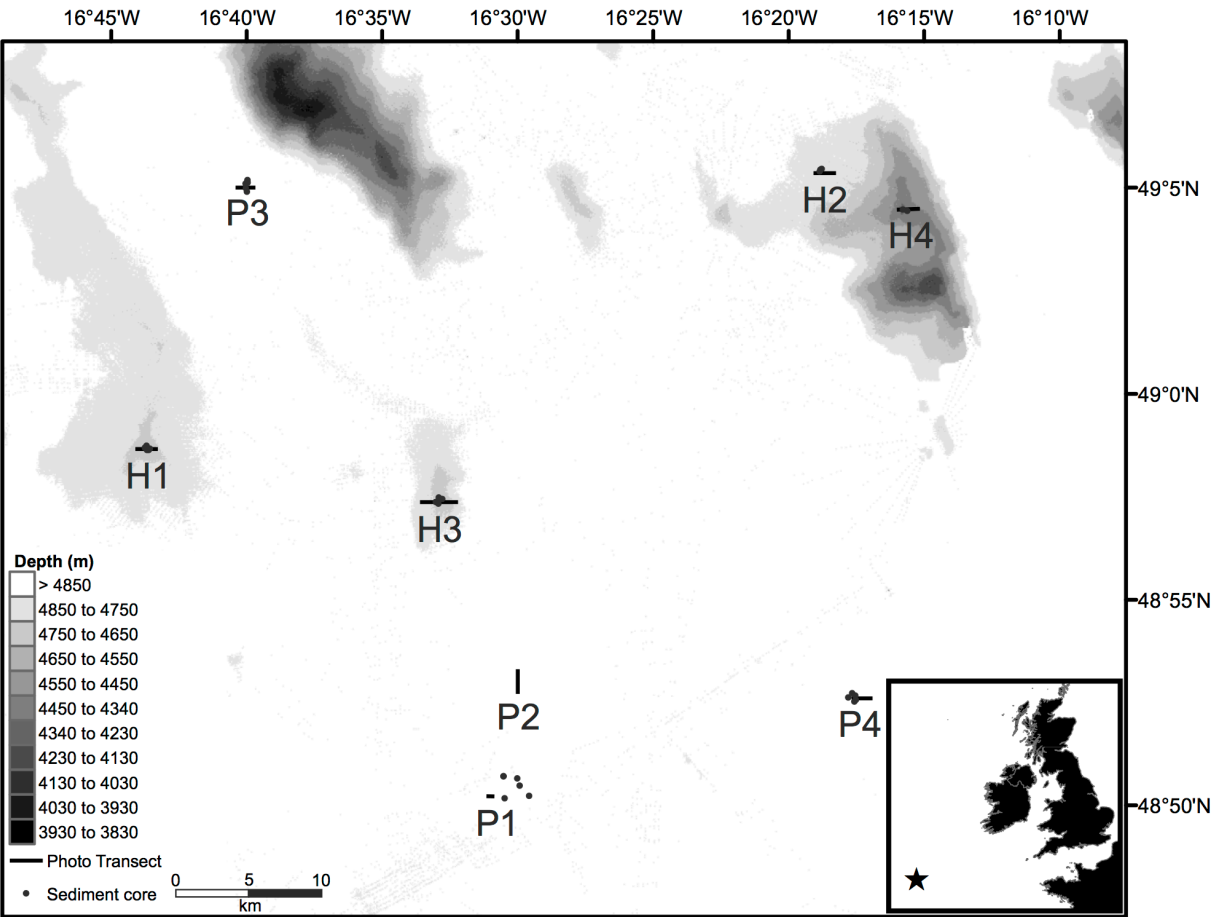
■ Plain
▲ Hill

Subsurface deposit feeders

Density on plains sites
Density on hills
Biomass on plains sites
Biomass on hills

Suspension feeders

Surface deposit feeders
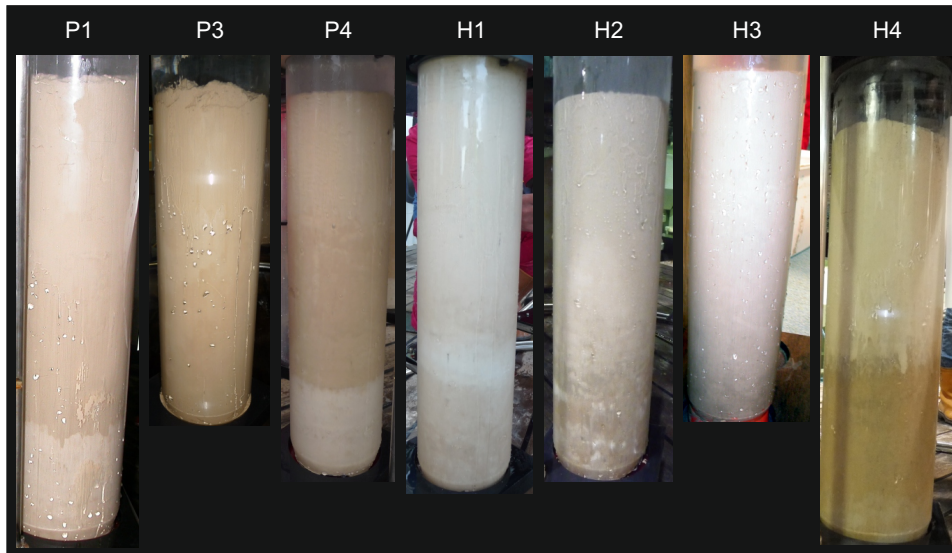
1   Appendices

2

3   **Appendix A**. Photographs of representative sediment megacore profiles for sites on the abyssal

4   plain (P) and hills (H).

5   **Appendix B.** Megabenthic morphotypes ranked by density from sites on the abyssal plain (a-d)

6   and hills (e-h), determined from seabed photographs.

7   **Appendix C**. Megabenthic morphotypes ranked by biomass from sites on the abyssal plain (a-d)

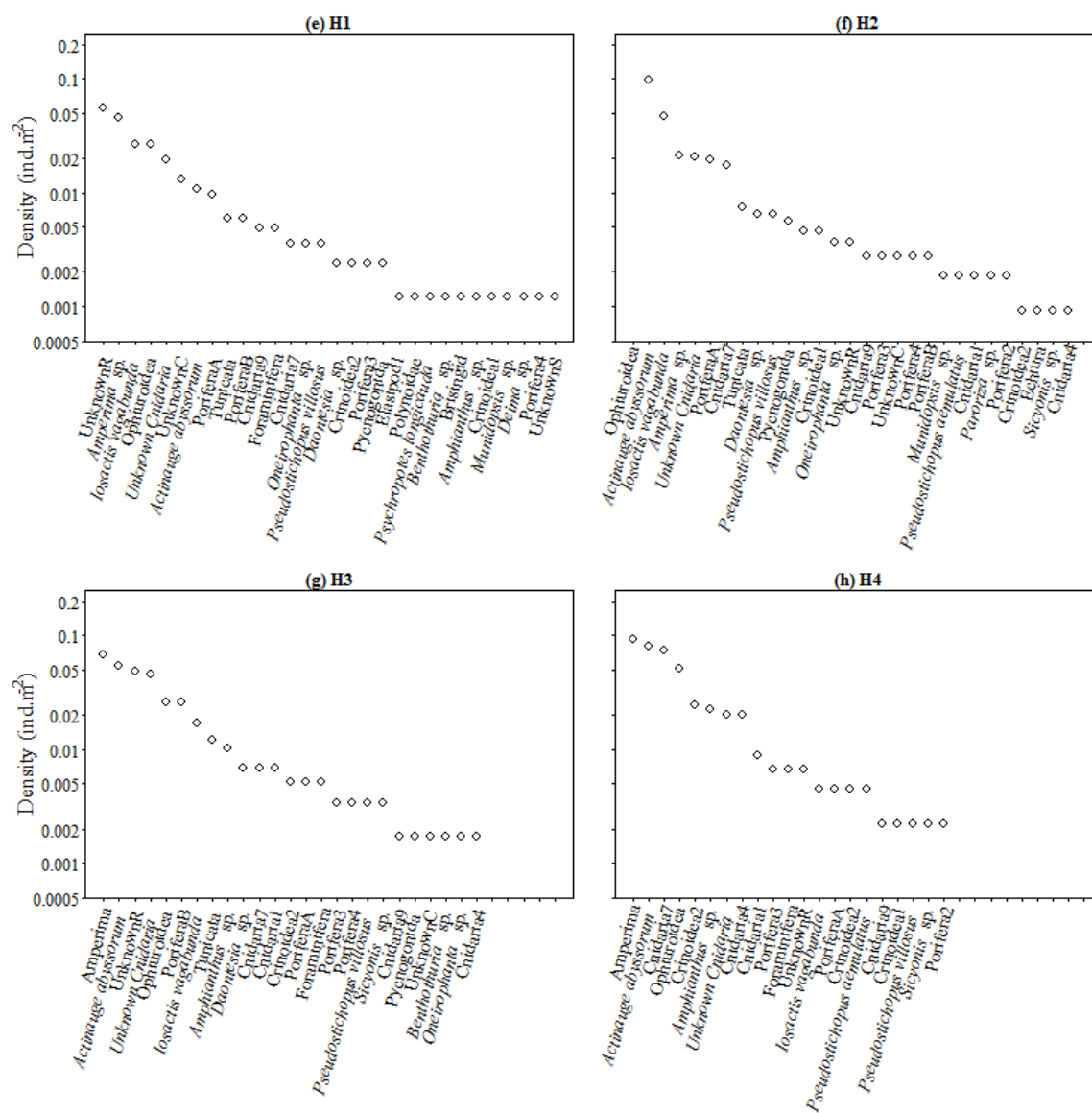8   and hills (e-h), determined from seabed photographs.
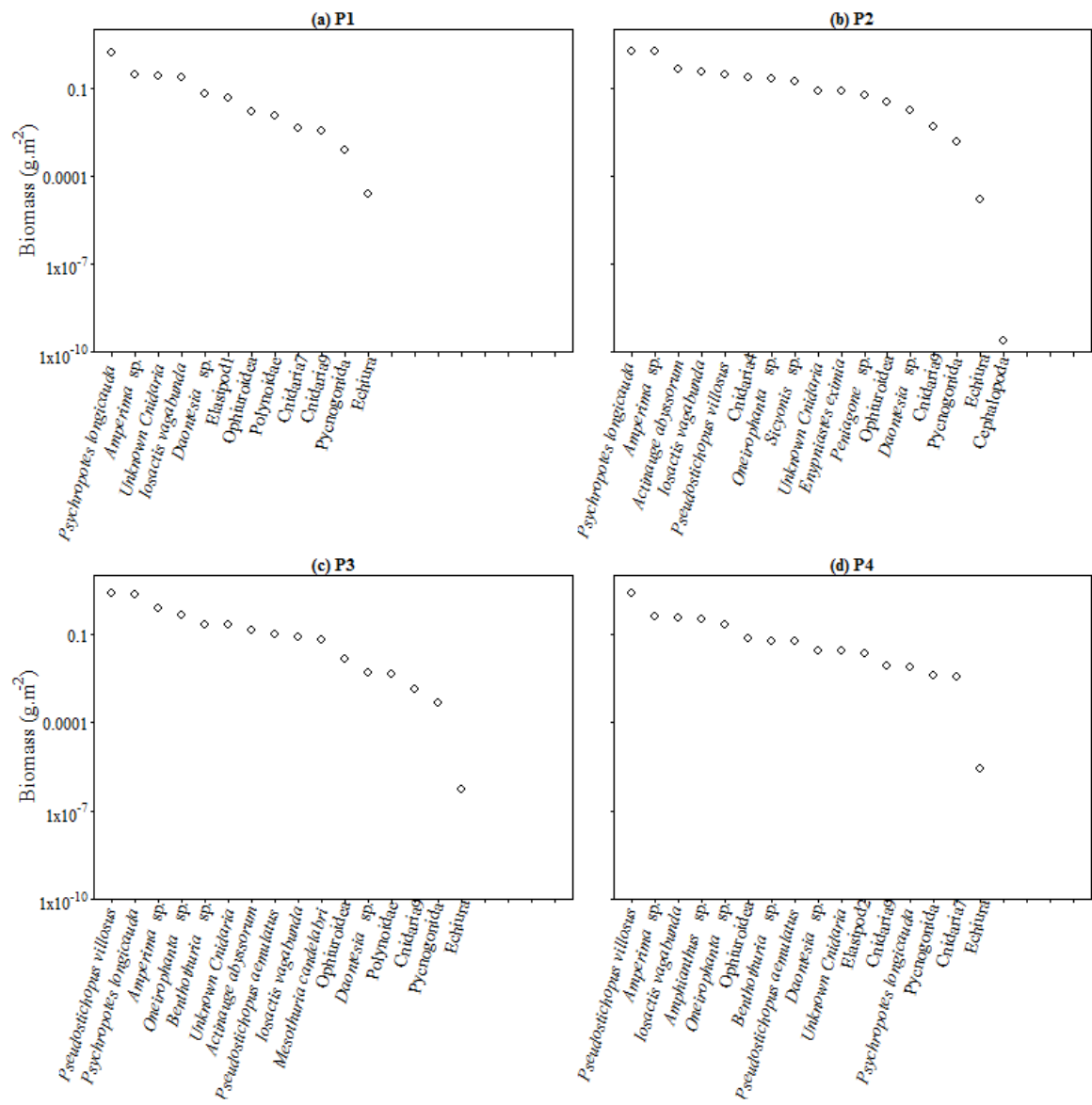
1   Appendix A.

2

3

1   Appendix B.

2

3

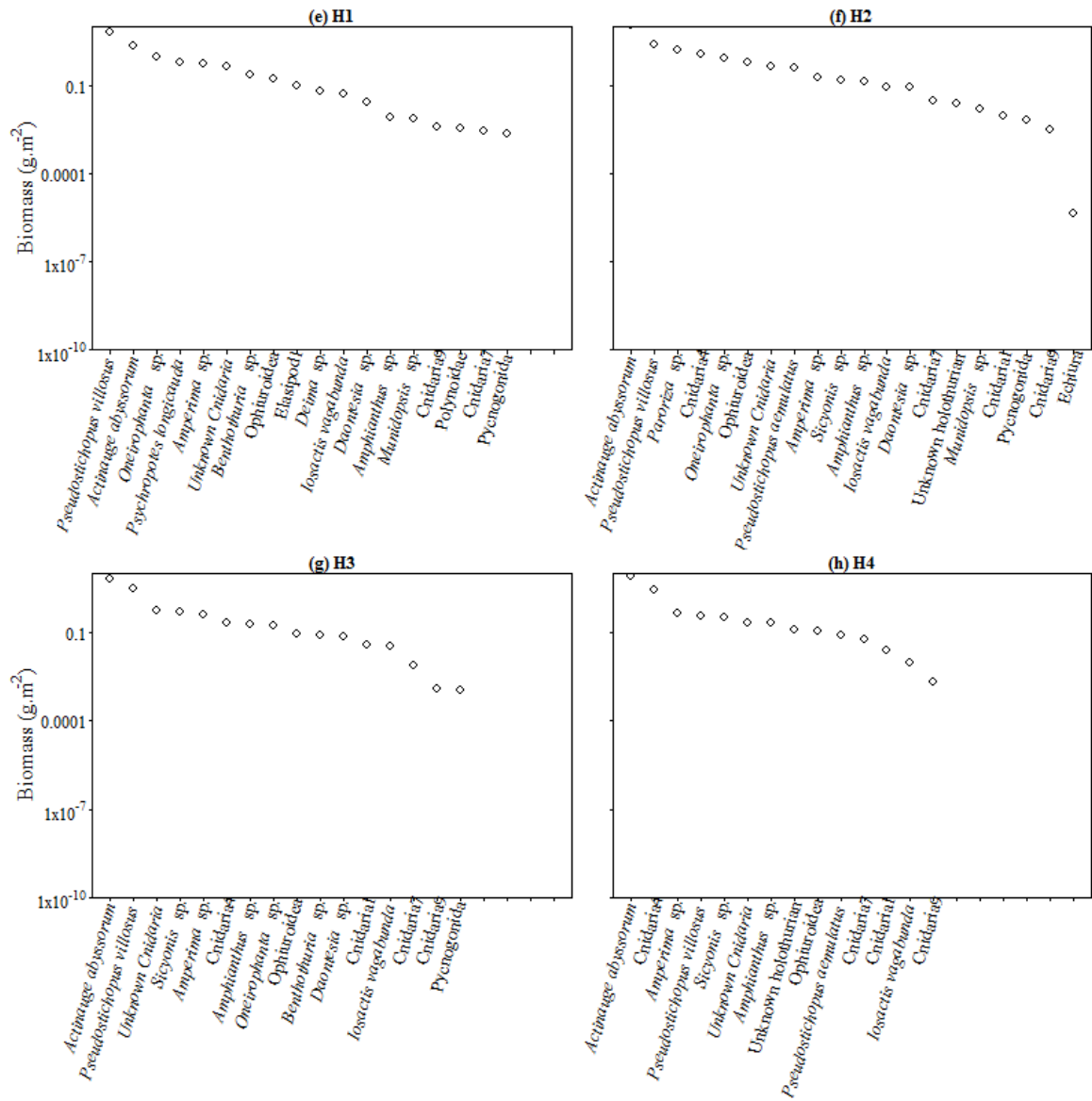4

1   Appendix B continued.

(e) H1

(f) H2

(g) H3

(h) H4

2

1 Appendix C.

1   Appendix C continued.

2

3