



# Abyssal hills: Influence of topography on benthic foraminiferal assemblages



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## ABSTRACT

Abyssal plains, often thought of as vast flat areas, encompass a variety of terrains including abyssal hills, features that constitute the single largest landscape type on Earth. The potential influence on deep-sea benthic faunas of mesoscale habitat complexity arising from the presence of abyssal hills is still poorly understood. To address this issue we focus on benthic foraminifera (testate protists) in the >150- $\mu\text{m}$  fraction of Megacorer samples (0–1 cm layer) collected at five different sites in the area of the Porcupine Abyssal Plain Sustained Observatory (NE Atlantic, 4850 m water depth). Three sites are located on the tops of small abyssal hills (200–500 m elevation) and two on the adjacent abyssal plain. We examined benthic foraminiferal assemblage characteristics (standing stock, diversity, composition) in relation to seafloor topography (hills vs. plain). Density and rarefied diversity were not significantly different between the hills and the plain. Nevertheless, hills do support a higher species density (i.e. species per unit area), a distinct fauna, and act to increase the regional species pool. Topographically enhanced bottom-water flows that influence food availability and sediment type are suggested as the most likely mechanisms responsible for these differences. Our findings highlight the potential importance of mesoscale heterogeneity introduced by relatively modest topography in regulating abyssal foraminiferal diversity. Given the predominance of abyssal hill terrain in the global ocean, we suggest the need to include faunal data from abyssal hills in assessments of abyssal ecology.

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## 1. Introduction

The abyssal zone (~3500–6500 m water depth) occupies 27% of the entire ocean depth range as well as almost 65% and 85% of Earth's surface and ocean floor, respectively (Watling et al., 2013; Harris et al., 2014). However, only an estimated  $1.4 \times 10^{-9}\%$  of this large biome has been sampled to date (Stuart et al., 2008). Most of that sampling effort has been focused on abyssal plains, topographically flat (i.e. homogeneous) soft-bottom areas of the ocean (Heezen and Laughton, 1963). The plains are commonly regarded as the dominant topographic feature of the abyss, with the result that the terms abyssal plain and abyssal zone are often used interchangeably in the scientific literature (e.g. Ebbe et al., 2010; Ramirez-Llodra et al., 2010; Stuart et al., 2008). On the other hand, marine geologists and geophysicists have reported the presence of numerous abyssal hills, small topographic rises <1000 m in height, for almost 60 years (Heezen et al., 1959; Macdonald et al., 1996; Goff, 1998). Recently, Harris et al. (2014) estimated that hills (300–1000 m in height) cover almost 50% and >40% of the abyssal

and global seafloor, respectively, making them the most pervasive landform on Earth as well as in the abyss. It is clear that the widespread occurrence of abyssal hills in the oceans increases mesoscale (metre to kilometre) habitat heterogeneity and complexity in the abyss (Bell, 1979), with potentially significant effects on the density, diversity and distribution of deep-sea benthic organisms (Snelgrove and Smith, 2002; Rex and Etter, 2010).

Deep-sea studies investigating the effects of habitat heterogeneity on benthic faunas have focused mainly on small spatial scales (centimetres to metres) represented by biogenic structures and the patchy distribution of organic matter (Levin et al., 1986; Grassle and Morse-Porteous, 1987; Rice and Lamshead, 1994; Buhl-Mortensen et al., 2010; Hasemann and Soltwedel, 2011). Others have addressed broader scales by comparing assemblages from environmentally contrasting habitats (Thistle, 1983; Kaminski, 1985; Gage et al., 1995; Schönfeld, 1997, 2002b; Menot et al., 2010). However, only a few recent studies (e.g., Durden et al., 2015, on megafauna; Laguionie-Marchais, 2015, on macrofauna; Morris et al., 2016, on megafauna and organic matter supply) have considered the impacts of abyssal hills on deep-sea

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communities and none has focused on smaller organisms such as foraminifera.

Benthic foraminifera are single-celled eukaryotes (protists) that produce a ‘test’ (shell) and are very common in marine environments from intertidal mudflats to the greatest ocean depths. In the deep sea they often account for >50% of the meiofauna (32 or 63–300  $\mu\text{m}$ ) (Snider et al., 1984; Gooday, 2014), while larger species constitute a significant proportion of the macrofauna (300–1000  $\mu\text{m}$ ) (Tendal and Hessler, 1977; Bernstein et al., 1978) and even the megafauna (e.g., Gooday et al., 2011; Amon et al., 2016). Foraminifera play an important role in ecological processes on the seafloor (e.g. Gooday et al., 1992, 2008) and their abundance is closely related to levels of organic matter input and dissolved oxygen concentrations in the near-bottom water (e.g. Jorissen et al., 1995). In addition, calcareous benthic foraminifera have an excellent fossil record and are commonly utilized as proxies for reconstructing past ocean conditions (Gooday, 2003; Jorissen et al., 2007).

The aim of this study was to examine the potential effects of seafloor topography on benthic foraminiferal assemblages from the Porcupine Abyssal Plain Sustained Observatory area (PAP-SO, Hartman et al., 2012) in the Northeast Atlantic (4850 m water depth), a largely flat area populated by a number of abyssal hills. There has been a long history of research at the PAP-SO dating back to the 1980s (Lampitt et al., 2010a), including foraminiferal studies (Gooday et al., 2010; Stefanoudis and Gooday, 2015). However, the ecological significance of the abyssal hills in this area has only recently been appreciated (Durden et al., 2015; Morris et al., 2016). An earlier investigation established that differences in sediment characteristics between the hills and the adjacent plain had a significant effect in the agglutination patterns and test morphometry of certain benthic foraminifera (Stefanoudis et al., 2016). Here, we investigate whether abyssal hills: (i) modify standing stocks of benthic foraminifera, (ii) influence foraminiferal diversity, locally and/or regionally, and (iii) support distinct benthic foraminiferal communities compared to the adjacent plain.

## 2. Environmental characteristics of the study area

The water column overlying the PAP-SO area is subject to seasonal fluctuations in primary production and fluxes of organic matter to the seafloor (Rice et al., 1994). Deep ocean particle flux has been monitored since 1989 using sediment traps (Lampitt et al., 2010b; Frigstad et al., 2015). Sedimentation rates on the plain in the PAP-SO area are around 3.5  $\text{cm ky}^{-1}$  (Billett and Rice, 2001). Oxygen penetrates at least 25 cm into the sediment (Rutgers van der Loeff and Lavaleye, 1986). Both hill and plain sediments have a bimodal particle size distribution, with a trough at 22.9  $\mu\text{m}$  (Durden et al., 2015). The sediments are carbonate oozes with particles <23  $\mu\text{m}$  comprising mainly coccoliths, while the sediment fraction 23–1000  $\mu\text{m}$  is dominated by planktonic foraminiferal tests. However, sediments at the hill sites (H1, H2 and H4; Fig. 1) have a significantly higher fraction of coarser-grained material (>63  $\mu\text{m}$ ) than plain sites (P3, P4; Fig. 1) (38–64% on the hills vs. 25% on the plain; see Stefanoudis et al., 2016, Table 3 therein), for both the 0–1 and 0–5 cm sediment horizons (Durden et al., 2015; Stefanoudis et al., 2016). Some ice-rafted dropstones that serve as a hard substratum for sessile organisms are also known from the hills. Median seabed slope is greater and more variable at the abyssal hill sites compared to the plain. Potential organic matter input, expressed either as the percentage of the seafloor covered by phytodetritus or as median detrital aggregate size, did not vary between hills and plain (Durden et al., 2015) at the time samples for the present study were collected, although some variation has been detected subsequently (Morris et al., 2016).

However, significant temporal variations, both seasonal and inter-annual, in organic matter supply do occur (Bett et al., 2001), and may be influenced by seafloor topography (Turnewitsch et al., 2015).

## 3. Materials and methods

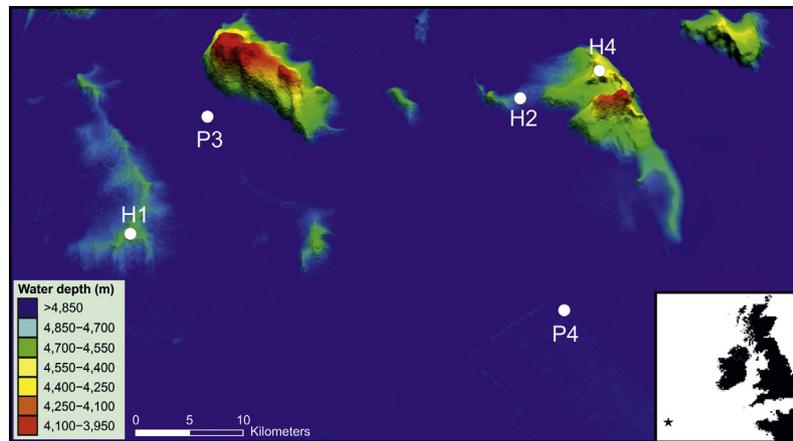
### 3.1. Sample collection

Samples were collected during RRS *James Cook* Cruise 062 (JC062, 24 July to 29 August 2011; Ruhl, 2012) at two abyssal plain sites (P1, P2) and three abyssal hill sites (H1, H2, H4) (Fig. 1) in the vicinity of the PAP-SO. Distances between sites were in the range of tens of kilometres (i.e. mesoscale). The samples were obtained using a Bowers and Connelly Megacorer (the specific instrument used in the present study is as illustrated as Fig. 7.16 in Gage and Bett, 2005), a multi-corer equipped with 59 mm internal diameter core tubes. The Megacorer represents a development of the original Scottish Marine Biological Association’s multi-corer (Barnett et al., 1984), itself a development of the Millport Marine Station Craib corer (Craib, 1965). Because the descent of the core tubes into the sediment is hydraulically dampened, multi-corers of this type are widely considered the instrument of choice for the collection of core samples from fine-grained, soft-sedimented habitats (Gage and Bett, 2005; Narayanaswamy et al., 2016). The reduced bow wave effect certainly improves their quantitative performance over box corers in sampling meiofauna, including foraminifera (Bett et al., 1994), and even in sampling the macrofauna (Gage and Bett, 2005). All cores used in this study were of excellent quality, 30–40 cm in length, having clear overlying water and no sign of sediment surface disturbance (see Appendix A). In order to avoid the problem of pseudo-replication (Hurlbert, 1984), single cores from multiple deployments of the corer were used as replicates at each site in this study (Blomqvist, 1991; Rose et al., 2005).

On board the ship the cores were sliced into 0.5-cm-thick layers down to 2-cm sediment depth, followed by 1-cm-thick layers from 2 to 10-cm depth. Each slice was transferred into 10% buffered formalin, a commonly used fixative and preservative for biological samples (Gage and Bett, 2005; Schiaparelli et al., 2016), including those used for meiofaunal research (Giere, 2009). Foraminiferal workers often use 70% ethanol to preserve samples (Schönfeld et al., 2012). However, we avoided the use of ethanol because it causes the shrinkage of some soft-shelled foraminifera, notably those with delicate organic test walls. Murray (2006, p. 13) lists borax-buffered formalin together with 70% ethanol and freezing as three commonly-used methods for preserving samples for foraminiferal analysis. The present study is based on material retained on a 150- $\mu\text{m}$ -mesh sieve from the 0 to 1 cm sediment horizon from 16 Megacore samples, with up to four replicates per site (Table 1).

### 3.2. Laboratory analysis

In the laboratory, the 0–0.5 cm and 0.5–1.0 cm slices of cores were gently washed through two sieves (mesh sizes 300 and 150  $\mu\text{m}$ ) using filtered tap water. Residues >300 and 150–300  $\mu\text{m}$  were stained with Rose Bengal (1 g dissolved in 1 L tap water) overnight and sorted for ‘live’ (stained) benthic foraminifera in water in a Petri dish under a binocular microscope. We did not include komokiaceans or small dome-like foraminifera associated with planktonic foraminiferal shells and mineral grains (Stefanoudis and Gooday, 2015), with the exception of two easily recognisable morphotypes (*Psammospaera* sp. 1 and ‘White domes’; see taxonomic notes in Appendix D). These forms are omitted because they are difficult to separate into species and do not stain well with Rose Bengal, making the recognition of ‘live’



**Fig. 1.** 3D topographic representation of the PAP-SO area (48.79–49.21°N, –16.03 to –16.93°W) indicating the approximate location and bathymetry of the five study sites H1, H2 and H4 (abyssal hill sites) and P3 and P4 (abyssal plain sites). The inset shows the general location (star) of the Porcupine Abyssal Plain in the Northeast Atlantic Ocean.

**Table 1**

Site and station information for each core used in the present study.

Site	Station	Topography	Water depth (m)	Latitude (°N)	Longitude (°E)
H1	JC062-53	Hill	4679	48.977	–16.727
	JC062-60	Hill	4673	48.977	–16.728
	JC062-61	Hill	4673	48.979	–16.728
H2	JC062-115	Hill	4669	48.978	–16.729
	JC062-129	Hill	4775	49.091	–16.314
	JC062-123	Hill	4382	49.074	–16.260
H4	JC062-126	Hill	4365	49.074	–16.264
	JC062-128	Hill	4339	49.076	–16.314
	JC062-66	Plain	4852	49.085	–16.666
P3	JC062-67	Plain	4851	49.083	–16.667
	JC062-101	Plain	4851	49.083	–16.667
	JC062-131	Plain	4851	49.082	–16.666
P4	JC062-73	Plain	4851	48.879	–16.294
	JC062-75	Plain	4849	48.877	–16.297
	JC062-76	Plain	4849	48.876	–16.292
	JC062-77	Plain	4851	48.875	–16.293

specimens problematic. For the rest, in order to ensure that the stained material was foraminiferal protoplasm, specimens were transferred to glass slides with glycerin and examined under a high-power compound microscope. This enabled us to distinguish ‘fresh’ cellular material from decayed cytoplasm, accumulations of bacteria, or inhabiting organisms. If necessary, thick-walled agglutinated tests were broken open to expose the material inside. Only specimens with most chambers stained were considered to be ‘live’. In the case of many monothalamids, the test contained numerous stercomata (waste pellets) that decay after death into a grey powder. We regarded the ‘fresh’ (undegraded) appearance of stercomata as an additional indication that specimens were alive when collected. Delicate taxa were either stored on glass cavity slides in glycerol or in 2-ml Nalgene cryovials in 10% buffered formalin (4% borax buffered formaldehyde solution).

### 3.3. Light and scanning electron microscopy

Specimens placed in glycerol on a glass cavity slide were photographed using either a NIKON Coolpix 4500 camera mounted on an Olympus SZX10 compound microscope or a Leica Z16-APO incident light microscope. Selected specimens were dried onto aluminium stubs and examined by scanning electron microscopy (SEM) using a LEO 1450VP (variable pressure) or an environmental Zeiss EVO LS10 (variable pressure) instrument. The taxonomic scheme we followed was a combination of those proposed by Loeblich and Tappan (1987) and Pawlowski et al. (2013).

### 3.4. Statistical analysis

In order to test for differences in density with respect to topography (hills vs. plain) or site at either the assemblage level (for complete and fragmentary specimens separately) or the species level we performed analysis of variance (ANOVA), where necessary followed by Tukey’s or Games-Howell (for homogeneous and non-homogeneous data, respectively) pairwise comparisons (SPSS v22) on log (x + 1) transformed count data (see e.g. Sokal and Rohlf, 2012). For the species-level comparisons we used only species with complete tests that were ‘common’ (relative abundance >2% in at least one sample). In an attempt to reduce the reporting of ‘false positive’ results, we followed the method of Benjamini and Hochberg (1995) in controlling the false discovery rate (SPSS v22). We calculated the reciprocal Berger-Parker dominance index ( $N/N_{\max}$ ) (Magurran, 2004), where  $N_{\max}$  and  $N$  are the number of individuals of the most abundant species and all species combined in a sample, respectively. An increased value of the index accompanies an increase in diversity and a reduction in dominance. Rank-density plots were constructed for all species in order to detect changes in dominance and ranking order between habitats.

Rarefied alpha diversity indexes (species richness, exponential Shannon index, inverse Simpson index, Chao 1; see e.g. Magurran, 2004) were calculated using the EstimateS 9 software package (Colwell, 2013), based on count data for complete specimens, and compared against seafloor topography (hills vs. plain) or site using ANOVA and Tukey’s post hoc pairwise comparisons

(SPSS v22). Subsequently, we created two sets of sample-based rarefaction curves scaled by sampled seabed area and by number of individuals to examine species density (i.e. number of species per unit area). Species density is an important concept that may be particularly valuable in comparisons of contrasting organic matter supply regimes, and species richness (i.e. number of species per individuals), respectively (Chazdon et al., 1998; Gotelli and Colwell, 2001). In addition, we estimated beta diversity ( $\beta_w$ ) for the eight hill and the eight plain samples separately as well as for all 16 samples of our dataset combined, using the formula proposed by Whittaker (1960, 1972), and commonly referred to as Whittaker's diversity index (Magurran, 2004):

$$\beta_w = \gamma / \bar{\alpha}.$$

In our case  $\bar{\alpha}$  is the average sample diversity rarefied to 50 individuals (the lowest number of individuals found in a single sample that could be placed into a morphospecies), and  $\gamma$  is the total diversity (i.e. combining all samples of a category) rarefied to 400 individuals (i.e. eight replicate samples of 50 individuals). This form of beta diversity quantifies how many times as rich the entire dataset is compared to its constituent sampling units (Tuomisto, 2010), and hence, is a measure of variability in community structure among samples (Anderson et al., 2011). We calculated beta diversity based on three of Hill's numbers (Chao et al., 2014a): species richness  ${}^0D = S$ , exponential Shannon index  ${}^1D = \exp(-\sum p_i \log p_i)$  and inverse Simpson index  ${}^2D = 1/\sum p_i^2$  (see also Chao et al., 2012, 2014b; Jost, 2006), where  $p_i$  is the proportional abundance of the  $i$ -th morphospecies. As indicated by Gotelli and Chao (2013),  ${}^0D$  takes into account the number of species in the assemblage but not their relative abundances;  ${}^1D$  weights species in proportion to their frequency of occurrence, and can be interpreted as the number of 'typical species' in the assemblage; and  ${}^2D$  is weighted towards the most common (i.e. abundant) species and represents the number of very abundant species in the assemblage.

Trends in the structure of foraminiferal communities were explored using multivariate statistics such as global and pairwise analysis of similarities (ANOSIM) and non-metric multidimensional scaling (MDS) ordinations in PRIMER 6 (Clarke and Gorley, 2006). The analyses were based on Bray Curtis dissimilarity of raw (i.e. untransformed) and transformed ( $\log[x + 1]$  transformed, square-root transformed, fourth-root transformed, presence-absence) density data for complete specimens. To examine the impact of rarity we considered three versions of these data: (i) all species, (ii) only species with a relative abundance >2% in at least one sample, and (iii) only species with a relative abundance >5% in at least one sample. The PRIMER routine, SIMPER (similarity percentages) was used to assess dissimilarity in foraminiferal composition by topography and site and identify those species contributing to within-group similarity. Spearman's rank correlation was used to assess the strength of the association between MDS ordination and proportion of the coarse sediment particle fraction (>63  $\mu\text{m}$ ) at each site, using particle size data as presented by Durden et al. (2015) and Stefanoudis et al. (2016).

## 4. Results

### 4.1. Density

#### 4.1.1. Total fauna

A total of 2102 obviously complete and 'live' (Rose-Bengal-stained) foraminiferal specimens was picked from the 16 Megacorer samples (Table 2). The density of complete specimens from abyssal hill samples ranged from 62 to 322 (mean  $155 \pm 76$  standard deviation) individuals per sample (i.e.  $25.5 \text{ cm}^2$ ) compared with 70–175 (mean  $108 \pm 35$ ) indiv. per sample on the plain

(Table 2 and Appendix B.1). Hill sites had higher mean densities than plain sites, especially in the case of site H4, situated on top of a large hill (Fig. 1). However, statistical comparisons of density against topography or site did not reveal any significant differences (ANOVA,  $p > 0.05$ ).

In addition to the complete specimens, we recorded 2447 fragmented stained tests from all samples. Almost all (~99%) represented tubular morphospecies. Numbers varied considerably, ranging from 0 to 197 (mean  $92 \pm 79$ ) indiv. per sample on the hills, against 2–1183 (mean  $214 \pm 409$ ) indiv. per sample on the plain (Table 2; Appendix B.1). Again, statistical comparisons of density by seafloor topography or site did not detect significant differences in densities (ANOVA,  $p < 0.05$ ).

#### 4.1.2. Major taxa and groupings

The complete individuals that could be assigned to morphospecies (either described or undescribed) comprised the majority (85%) of all picked specimens, the remainder being indeterminate. As some species could not be placed easily in any higher taxon, the major groupings in Table 3 (for data per site see Appendices B.2 and B.3) represent a pragmatic mix of formal taxa (mainly multi-chambered groups) and informal morphology-based groupings (most monothalamids). More than half belonged to two multi-chambered agglutinated groups, the Hormosinacea and the Trochamminacea, and the calcareous Rotaliida. Among the monothalamids (single-chambered taxa; *sensu* Pawlowski et al., 2013), species of the genus *Lagenammina* were the most abundant. Delicate and soft-walled agglutinated spheres without apertures (including representatives of the Psammosphaeridae), 'saccaminids' (agglutinated flasks and similar morphotypes with apertures) and organic-walled taxa ('allogromiids'), were never very abundant either in absolute or relative terms (Table 3). Many other monothalamids (grouped as 'Others' in Table 3) could not be assigned easily to recognised taxa. The only group that was significantly more abundant in one topographic setting comprised the *Nodellum*-like forms (tubular or 'segmented' organic-walled taxa of uncertain affinity), which overall were more common on the hills than the plain (ANOVA,  $p < 0.05$ ; Table 3).

Hormosinaceans (i.e. *Reophax*, *Hormosina* and similar uniserial agglutinated genera) and rotaliids were the most speciose groups at both hills and plain sites. In general, all groups had similar numbers of species at different sites and in different topographic settings, except for trochamminaceans, which were more speciose at H4 than at the other sites (pairwise comparisons,  $p < 0.05$  in all cases; see also Appendix B.3).

The overwhelming majority (~99%) of fragmentary specimens were agglutinated tubes (i.e., tubular monothalamids). These also represented a significant proportion (15–19%) of the total number of species found in each setting (Table 3 and Appendix B.3), highlighting the importance of considering fragments in assessments of abyssal benthic foraminiferal diversity.

#### 4.1.3. Key species

Appendices B.4–B.6 summarise the ten most abundant morphospecies with complete and fragmentary tests, respectively, in all samples and in each topographic setting. These taxa are briefly described and illustrated in Appendices D and E, respectively. The densities of 'common' species (relative abundance >2% in at least one sample) were not significantly different between hill and plain sites (ANOVA,  $p < 0.05$ ). However, there were significant differences in relation to site (ANOVA and pairwise comparisons,  $p < 0.05$ ) for four species: *Nodellum*-like sp. (H4 > P3, P4), *Psammosphaera* sp. 1 (H4 > H1, P3, P4), *Reophax* sp. 23 (H1, P4 > P3), and *Portatrochammina murrayi* (H4 > P4). Six species (*Adercotryma glomerata*, *Lagenammina* aff. *arenulata*, *Reophax* sp. 21, *Nodulina dentaliniformis*, *Epistominella exigua*, *Thurammina albicans*) were

**Table 2**  
Mean density of 'live' (Rose-Bengal-stained) specimens (complete and fragmentary) and mean number of species, per site and topographic setting (hills, plain). (N: density of complete specimens, NF: density of fragments,  $S_N$ : number of species with complete tests,  $S_{N+NF}$ : number of species including fragmentary tests). Densities per 10 cm<sup>2</sup> are included in order to facilitate comparisons with other studies.

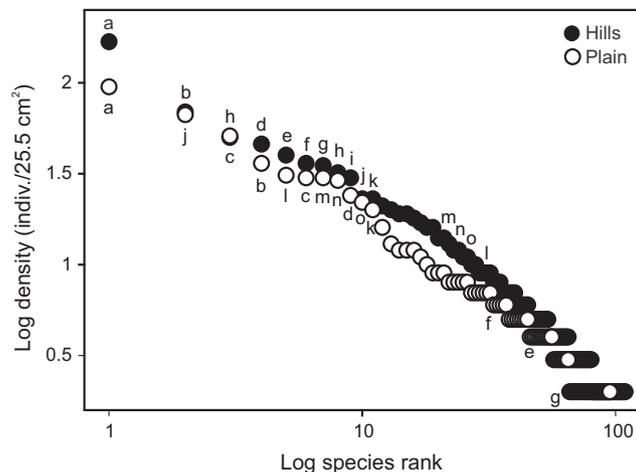
	H1	H2	H4	Hills	P3	P4	Plain
<i>Density</i>							
N 25.5 cm <sup>2</sup>	115	134	215	155	112	104	108
N 10 cm <sup>2</sup>	45	53	84	61	44	41	42
NF 25.5 cm <sup>2</sup>	77	11	138	92	387	41	214
NF 10 cm <sup>2</sup>	30	4	54	36	152	16	84
<i>Species richness</i>							
$S_N$	35	39	47	40	34	35	34
$S_{N+NF}$	41	41	56	47	38	38	39

**Table 3**  
Absolute and relative (%) densities (number of specimens per eight Megacorer samples, i.e. 204 cm<sup>2</sup>) of the major taxa and informal groupings based on complete (N) and fragmentary (NF) 'live' (Rose-Bengal-stained) specimens for each topographic setting. ( $S_{N+NF}$ : number of species including complete and fragmentary specimens, \*significant difference between hill and plain samples, ANOVA,  $p < 0.05$ ). The informal term 'saccaminids' is used for flask-shaped monothalamids with one or two apertures.

Major grouping	Hills					Plain				
	N	N%	NF	NF%	$S_{N+NF}$	N	N%	NF	NF%	$S_{N+NF}$
<i>Monothalamids</i>										
Lagenammina	88	7.1	0	0.0	8	114	13.2	0	0.0	8
Nodellum-like	45*	3.6	0	0.0	3	8*	0.9	0	0.0	2
Organic-walled	36	2.9	0	0.0	3	7	0.8	3	0.2	3
'Saccaminids'	44	3.6	0	0.0	6	36	4.2	0	0.0	8
Spheres (no aperture)	65	5.2	0	0.0	5	19	2.2	0	0.0	3
Tubular	7	0.6	725	98.8	24	2	0.2	1704	99.4	16
Others	143	11.6	1	0.1	3	77	8.9	0	0.0	3
<i>Multichambered</i>										
Ammodiscacea	1	0.1	0	0.0	1	2	0.2	0	0.0	2
Hormosinacea	273	22	5	0.7	24	234	27.1	3	0.2	20
Lageniida	10	0.8	0	0.0	6	14	1.6	0	0.0	8
Milioliida	34	2.7	0	0.0	5	15	1.7	0	0.0	4
Rotaliida	137	11.1	0	0.0	20	145	16.8	0	0.0	18
Textulariida	68	5.5	0	0.0	11	43	5	3	0.2	9
Trochamminacea	288	23.2	3	0.4	11	147	17	0	0	6
Total numbers	1239		734		130	863		1713		110

among the top 10 on the hills and on the plain, although their ranking was not consistent between settings (Fig. 2; Appendix B.5). Overall, hill assemblages seemed to exhibit slightly higher levels

of dominance compared to the plain, mainly driven by the high density of *A. glomerata* (Fig. 2), although this difference was not statistically significant (inverse Berger-Parker index, ANOVA,  $p > 0.05$ ). Similarly, six of the top 10 species with fragmentary tests (*Rhizammina algaiformis* and five other tubular spp.) were recorded in both hill and plain samples (Appendix B.6).

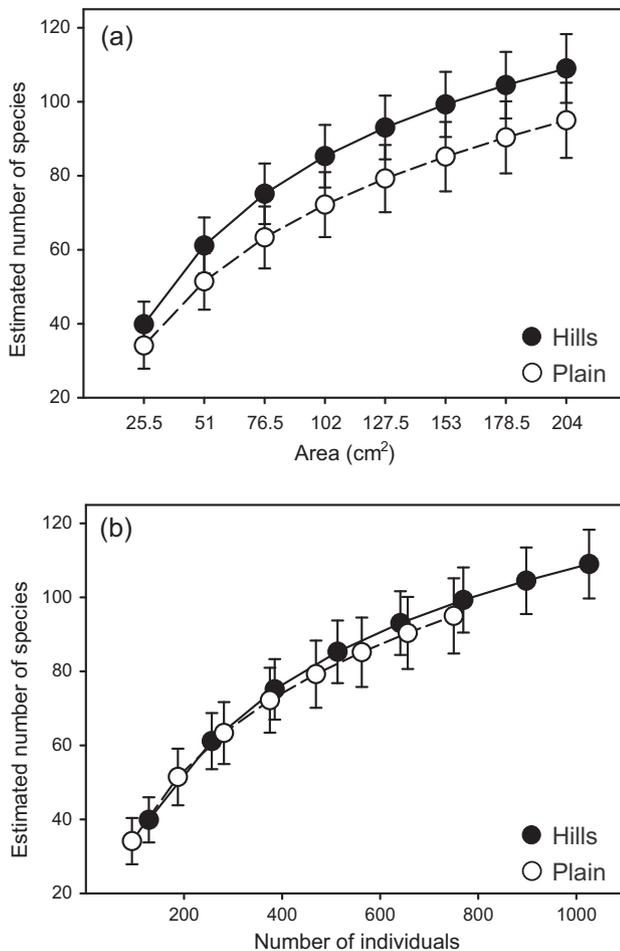


**Fig. 2.** Species ranked by density (individuals per 25.5 cm<sup>2</sup>). Hill (filled circles) and plain (open circles) are indicated separately, with abundant species keyed as follows: (a) *Adercotryma glomerata*, (b) *Reophax* sp. 21, (c) *Nodulina dentaliniformis*, (d) *Lagenammina* aff. *arenulata*, (e) *Psammospaera* sp. 1, (f) *Nodellum*-like sp., (g) Organic-walled domes, (h) *Epistominella exigua*, (i) *Recurvirodes* sp. 1, (j) *Thurammina albicans*, (k) *Lagenammina* sp. 19, (l) *Reophax bilocularis*, (m) *Reophax* sp. 19, and (n) *Reophax* sp. 28.

#### 4.2. Diversity

A total of 158 morphospecies (complete and fragmentary tests) was recognised in all samples (see Appendix C for the complete dataset), 130 from the hill samples and 110 from the plain samples (Table 3). Eighty-two species were found in both habitats, while 48 and 28 species were found exclusively on the hills and the plain, respectively. A detailed taxonomic appendix and illustrations for each species can be found in the Supplementary Material (Appendices D and E).

Rarefied sample (alpha;  $\alpha$ ) diversity indexes (species richness, exponential Shannon index, inverse Simpson index, Chao 1) showed no significant variation with respect to topographic setting (hills vs. plain) or site (ANOVA and Tukey's test,  $p > 0.05$ ). Sample-based rarefaction curves suggested that hills had a somewhat higher species density (number of species per unit area) (Fig. 3a) but when scaled to number of individuals (species richness) both settings were almost identical (Fig. 3b). Based on the eight samples we analysed from each topographic setting, Chao 1 (an asymptotic estimator of species richness) indicated that there were still species to be discovered on the hills (expected species number:



**Fig. 3.** Sample-based rarefied benthic foraminiferal morphospecies richness scaled by (a) area sampled (species density) and (b) number of individuals assessed (species richness) for combined hill (filled circles) and plain (open circles) samples.

119–172, mean = 134) and the plain (expected species number: 112–205, mean = 138).

According to the three metrics ( ${}^0D$ ,  ${}^1D$ ,  ${}^2D$ ), rarefied  $\bar{\alpha}$  diversity was marginally higher on the hills compared to the plain and the combined hill and plain samples. However,  $\beta_w$  and rarefied  $\gamma$  diversity appeared to be consistently higher in the combined hill and plain samples than in the hills or the plain samples analysed separately (Table 5). In qualitative terms, this may indicate that hills harbor some species not often encountered on the plain. Taken together with the rank abundance distribution (Fig. 2), these results suggest that the benthic foraminiferal assemblages on hills are somewhat richer in species than the plain assemblages, but have comparable numbers of ‘typical’ (in terms of frequency of occurrence) as well as ‘common’ (in terms of density) species.

#### 4.3. Assemblage composition

Differences in benthic foraminiferal assemblage composition with topography and site was assessed by ANOSIM based on three different sets of density data (all species with complete specimens; only species with a relative abundance >2% in at least one sample; only species with a relative abundance >5% in at least one sample) for the 134 species with complete tests (see Appendix C). In all pairwise cases, topography appeared to exert a significant (ANOSIM,  $p < 0.05$ ) effect on composition, with significant (ANOSIM,  $p < 0.05$ ) variation between sites detected in 14 of the 15 cases

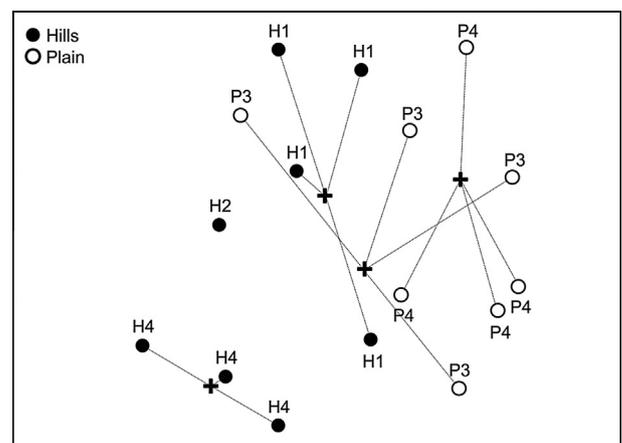
tested (Table 5). Where a significant difference was detected between sites, site H4 (large hill) was always distinct (ANOSIM,  $p < 0.05$ ) from one or both of the plain sites P3 and P4, and on five occasions from site H1 (Table 5).

An MDS ordination plot based on  $\log(x + 1)$ -transformed data of all 134 species was constructed to visualise differences in assemblage composition (Fig. 4; Table 5). On an MDS plot the distance between two points corresponds to their degree of similarity in composition (i.e. closely spaced points are compositionally similar). The stress value of the resultant plot was somewhat high (0.22), i.e. the full variation in the dataset was not well captured in two dimensions. There is considerable overlap of some hill and plain samples (H1, P3) and significant topographic variation in assemblage composition is not apparent. Nevertheless, the large hill (H4) was well separated from both the plain sites (P3, P4) and the other hill sites (H1, H2), reflecting the distinctive nature of the H4 assemblage. Spearman’s rank correlation of the MDS x-ordinates, which best separate hill and plain sites, and the coarse sediment (>63  $\mu\text{m}$ ) particle fraction in each site, resulted in a significant ( $p = 0.01$ ) relationship between foram species composition and local sedimentology. SIMPER analysis (see Appendix F for detailed results by topography and site) on the same dataset showed that the mean similarity (43%) among hill samples was driven most by *A. glomerata* (13%), *Reophax* sp. 21, *N. dentaliniformis* and *Lagenammina* aff. *arenulata* (all 7%), while mean similarity (44%) among plain samples was driven most by *A. glomerata* (11%), *Lagenammina* sp. 19 (9%), *Reophax* sp. 21 and *E. exigua* (both 8%). In contrast, mean dissimilarity (59%) between hill and plain samples was driven by several species, each contributing modestly to that dissimilarity (0.4–2.5%; Appendix F).

## 5. Discussion

### 5.1. Limitations of dataset

This study was limited to foraminiferal tests retained on a 150- $\mu\text{m}$ -mesh sieve. Analysis of finer sieve fractions would have yielded additional information on smaller, shallow-infaunal species that can be more responsive to freshly deposited organic matter (Gooday, 1988, 1993; Sun et al., 2006). However, previous studies based on >150- $\mu\text{m}$  residues have succeeded in establishing ecologically meaningful links between patterns in benthic foraminiferal assemblages (density, diversity, community composition) and environmental parameters (Fontanier et al., 2002; Barras



**Fig. 4.** MDS ordination plot of 16 Megacorer samples in the PAP-SO area, including all 134 species with complete tests. Filled circles represent hill samples, open circles the plain samples, site replicates are shown linked to their corresponding centroids (solid crosses). (Based on Bray-Curtis dissimilarity of  $\log[x + 1]$  transformed density).

et al., 2010; Mojtabid et al., 2010; Goineau et al., 2012; Cauille et al., 2015), while size-fractionated data from the NE Atlantic (>150 and >63  $\mu\text{m}$ ) resulted in similar correlations between diversity measures and benthic foraminiferal densities (Gooday et al., 2012). The main advantage of analysing the >150- $\mu\text{m}$  sieve fractions is that it is less time-consuming than finer fractions, making it possible to process a larger number of replicates.

The majority (~60%) of the species in this study are new to science. In general, foraminifera are a relatively well-known taxon (Murray, 2007) and this high proportion of undescribed species could be considered surprising. However, many of our new species are single-chambered monothalamids, a poorly known and frequently overlooked group that is very common in the deep sea, particularly at abyssal depths. It should also be noted that deep-sea and especially abyssal settings are grossly understudied (e.g. McClain and Hardy, 2010) and >50% (sometimes >90%) of species in a particular taxon are often undescribed (e.g. Grassle and Maciolek, 1992; Glover et al., 2002; Brandt et al., 2007; George et al., 2014). As a result, studies of deep-sea community ecology often involve a large proportion of undescribed ('putative') species. In order to facilitate comparisons with benthic foraminiferal faunas from other deep-water localities, we have provided an illustrated taxonomic appendix with short descriptions and illustrations of all species recognised in this study (Appendices D and E in the Supplementary material).

## 5.2. Influence of abyssal hills on foraminiferal faunas

Topographic features on the scale of hills are associated with turbulent mixing above the seabed (Kunze and Llewellyn-Smith, 2004; Garrett and Kunze, 2007; Nash et al., 2007). This process modifies the distribution, settling and availability of organic matter (Genin et al., 1986; Clark et al., 2010), the quantity and quality of which influence benthic foraminiferal standing stocks (Caralp, 1989; Altenbach et al., 1999; Fontanier et al., 2002; Koho et al., 2008).

Although we lack specific near-bottom current-speed data for our study sites, we can use the proportion of coarser sediments particles (>63  $\mu\text{m}$ ) on the PAP-SO abyssal hills (Durden et al., 2015) as a proxy of enhanced flows. This is based on the assumption that particles <63  $\mu\text{m}$  are more readily transported by currents (McCave et al., 1995; McCave and Hall, 2006), as has been empirically established for another abyssal hill within the PAP-SO area (Turnewitsch et al., 2004, 2013). A recent study in the PAP-SO area by Turnewitsch et al. (2015) found less, but fresher, organic material in hill sediments when compared to adjacent plain sediments. The authors suggested that organic material deposited on the hill was readily advected and redeposited downstream, and/or that the reduced surface area of the coarser particles comprising hill sediments could have decreased the potential for sorptive organic-matter preservation (Arnarson and Keil, 2001; Curry et al., 2007). Another recent study of the PAP-SO area reported that there was no difference in apparent organic matter supply (seafloor phytodetritus cover; median detrital aggregate size) to the hills or the plain, but that seabed cover was minimal (between 0 and ~3%) (Durden et al., 2015). That survey occurred after the seasonal peak in deposition. A more detailed study of a single PAP-SO hill by Morris et al. (2016) revealed a much higher phytodetritus cover (c. 45%) and showed that modest topography (80 m elevation) had fractionally higher cover than the adjacent plain. Morris et al. (2016) also supported the previous observations of Durden et al. (2015) of a substantially higher biomass of megabenthos on the hill than the plain. Both studies strongly suggest that lateral transport of organic matter plays a major role in the benthic ecology of abyssal hill communities. Taken together, these observations suggest that total organic matter availability is generally

greater on the hills than on the plain, but that its residence may be reduced.

### 5.2.1. Density

Higher organic matter availability on the hills could partially explain the higher foraminiferal densities compared to the surrounding plain in the PAP-SO area (Table 2), although statistical comparisons suggested that these differences were not significant (ANOVA,  $p > 0.05$ ). Enhanced current velocities and therefore increased organic matter supply on the hills could also lead to more suspension-feeding organisms (e.g. Kaufmann et al., 1989). Both Durden et al. (2015) and Morris et al. (2016) recorded 3- to 5-fold increases in megabenthic biomass between PAP-SO plain and hill sites, with much of the increase attributable to suspension feeding taxa. This suggests that densities of epifaunal foraminiferal species inferred to be suspension feeders, notably tubular monothalamids (Jones and Charnock, 1985; Mullineaux, 1987; Veillette et al., 2007; Murray et al., 2011; Kaminski et al., 2015) and certain calcareous species (e.g. *Cibicides* spp., *Cibicidoides* spp., *Discanomalina* spp.) (Lutze and Altenbach, 1988; Lutze and Thiel, 1989; Linke and Lutze, 1993; Schönfeld, 1997, 2002a), might be higher on the hills. However, with the exception of the *Nodelum*-like group, which is unlikely to include suspension feeders, we did not find any significant increase in the density of any taxonomic or morphology-based groups, including the tubular monothalamids, linked to seafloor topography (Table 3).

Positive relationships between bottom currents and faunal density have been invoked to explain faunal density patterns in the deep sea. For example, Kaminski (1985) compared two abyssal locations with contrasting current regimes in the NW Atlantic and found that agglutinated benthic foraminiferal abundance was greater where bottom-water flow was enhanced at the HEBBLE site, which is subject to episodic high-velocity current flows ('benthic storms'), than at the nearby tranquil HEBBLE Shallow site. Kaminski (1985) attributed this difference to sediment heterogeneity and did not consider potential differences in food supply between the two areas. Thistle et al. (1985) reported that macrofaunal and meiofaunal abundance was higher at the high-energy HEBBLE site than on the Horizon Guyot perimeter. The authors concluded that the strong near-bottom currents at the HEBBLE site promoted bacterial growth and an enhanced flux of suspended food particles. Seamounts have been shown to support enhanced densities of epibenthic megafaunal biomass when compared to slope habitats (Rowden et al., 2010) due to an elevated food supply in the former. On the other hand, current-swept regions can also be characterised by depressed faunal densities. For example, Koho et al. (2007) found low standing stocks of benthic foraminifera in the highly disturbed axis of the upper Nazaré Canyon, which experiences frequent sediment resuspension and gravity flows. Similarly, strong near-bottom flows have been shown to depress the abundance of metazoan macrofauna (Levin and Thomas, 1989) and meiofauna (Thistle and Levin, 1998) on seamounts.

The literature reviewed above suggests that the effect of near-bottom currents on benthic faunas can be either negative or positive depending on the faunal group and the intensity of the disturbance (Levin et al., 2001). Strong, erosive currents will negatively impact benthic faunal density, including that of foraminifera, by eroding surficial sediments and the individuals living in them (Aller, 1997). Moderate currents, such as those present on the hills in the PAP-SO area, will increase food supply by delivering organic matter and promoting bacteria growth (Thistle et al., 1985; Aller, 1989), potentially leading to enhanced benthic faunal density.

### 5.2.2. Diversity

In general, the hills supported more species than the plain (130 vs. 110) (Table 3). Alpha, beta, and gamma measures of diversity

were in most cases marginally higher on hills than on the plain (Table 4). However, statistical comparisons of rarefied alpha diversity indexes (species richness, exponential Shannon index, inverse Simpson index, Chao 1) by topography and site did not reveal any significant differences (ANOVA,  $p > 0.05$ ). Taking our samples as a whole, hills had similar dominance values (inverse Berger-Parker index results; Fig. 2) but higher species density (i.e. more species per unit area) (Fig. 3a), and when added to samples from the plain acted to increase regional beta and gamma diversity (Table 4). The increased species density suggests enhanced organic matter supply (Section 5.2; also Levin et al., 2001; Rowden et al., 2010), while the increase in regional diversity may be indicative of additional habitat heterogeneity (e.g. variation in sediment particle size distributions; Durden et al., 2015; Stefanoudis et al., 2016).

Comparisons of benthic foraminiferal diversity between contrasting habitats are relatively scarce. In coastal waters, variation of organic-matter supply is reported to be a major driver of foraminiferal diversity (Mojtahid et al., 2009). In deeper waters, foraminiferal communities are less diverse in areas disturbed by high intensity bottom-water currents and with coarser sediments, than at undisturbed locations (Kaminski, 1985). As in the case of density, data on the effects of currents on deep-sea metazoan species diversity are rather contradictory. Macrofaunal diversity appears markedly depressed by high current flow (Gage et al., 1995; Harriague et al., 2014). On the other hand, meiofaunal diversity is reported to be similar at hydrodynamically contrasting sites (Thistle, 1983; Harriague et al., 2014), although enhanced diversity due to strong near-bottom flow has also been recorded (Thistle, 1998). Comparisons between seamounts and adjacent slope sites have revealed similar levels of mollusk, coral and ophiuroid species richness and/or rates of endemism (Hall-Spencer et al., 2007; O'Hara, 2007; Castelin et al., 2011).

These results suggest that the response to hydrodynamically-induced disturbance of diversity, like that of density, can be both negative and positive and may vary between faunal groups (see also Thistle et al., 1991). Levin et al. (2001) predicted a unimodal relationship between flow strength and diversity, whereby diversity is maximal at intermediate flows rates, although they added that there are few direct observations to support this model. The different aspects of diversity are variously impacted and controlled by different factors, including habitat heterogeneity, disturbance, and productivity (McClain and Barry, 2010) several of which may operate in our study area. We suspect that different sediment characteristics, together with moderately increased near-bottom water flows, and hence enhanced organic matter supply, are all likely to influence diversity in the PAP-SO area, although it is difficult to disentangle their separate influences (e.g., Svensson et al., 2012).

### 5.2.3. Assemblage characteristics

There were significant differences in benthic foraminiferal community composition related to seafloor topography (hills vs. plain). Assessments by ANOSIM and MDS suggested that relatively distinct assemblages occupy the hills, particularly the largest hill (H4) (Table 5; Fig. 4). Around 48 species, most of them uncommon (Table 5, Appendix F), were only recorded in hill samples (hills: 130

vs. plain: 110; Table 3, Appendix C). More importantly, there were relatively subtle changes between the two settings in the density of individual species that collectively make the assemblages distinctive (Table 5; Fig. 4), although these were significant only in the case of *Nodellum*-like sp. [H4 > P3, P4], *Psammosphaera* sp. 1 [H4 > H1, P3, P4], *Reophax* sp. 23 [H1, P4 > P3], and *Portatrochammina murrayi* [H4 > P4] (Table 3; Fig. 2; Appendix F).

Substratum heterogeneity has often been used to explain deep-sea diversity patterns and changes in benthic community composition (Kaufmann et al., 1989; Hecker, 1990; Etter and Grassle, 1992; Levin et al., 1994; Sautya et al., 2011; Leduc et al., 2012), including benthic foraminifera (Kaminski, 1985; Murray, 2006). For example, Mackensen et al. (1985) reported a distinct foraminiferal assemblage dominated by *Trifarina angulosa* on the upper part of the Norwegian continental slope, apparently linked to the coarse-grained sediments and strong prevailing bottom currents. Similarly, Schönfeld (1997, 2002a,b) recorded distinct foraminiferal assemblages from the Gulf of Cadiz and the southern Portuguese continental margin related to local hydrography and sedimentary facies. In the South Atlantic Ocean, Mackensen et al. (1995) found that the hydrodynamic properties of the benthic environment, and the related sediment grain size parameters, to be among the main environmental factors controlling foraminiferal faunas. Schmiedl et al. (1997) also concluded that the grain size characteristics influenced the distribution pattern of agglutinated foraminifera such as *Lagenammina*, *Psammosphaera*, *Reophax*, *Rhizammina*, all of which are present in our study area.

Although there is some evidence for a difference in organic matter supply to hill and plain sites in the PAP-SO area (Durden et al., 2015; Turnewitsch et al., 2015; Morris et al., 2016), we suggest that substratum variation (i.e. coarser sediments on hills; see Durden et al., 2015; Stefanoudis et al., 2016) is most likely the main driver of differences in foraminiferal assemblage composition (as distinct from density and diversity changes). This is supported by the statistically significant correlation between MDS x-ordinates and the coarser (>63  $\mu\text{m}$ ) particle fraction at each site. Durden et al. (2015) reached a similar conclusion for the PAP-SO megafauna. However, sediment granulometry and sedimentary organic carbon typically covary, with coarser sediments having a lower organic carbon content than finer ones (Arnarson and Keil, 2001; Curry et al., 2007). Hence grain size may only be influencing foraminiferal community attributes indirectly.

If substratum is the main driver of foraminiferal community composition, then the fact that the assemblages on the large hill (H4) and the plain are significantly different, whereas those on the two small hills (H1, H2) and the plain are much closer (Table 5), suggests that there should be little difference in sediment granulometry between the small hills and the plain. Nevertheless, Stefanoudis et al. (2016) found significant granulometric differences (ANOSIM,  $p < 0.05$ ) between H1 and the two plain sites (P3 and P4). Although we had too few sediment samples from H4 ( $n = 2$ ) to perform similar statistical comparisons, the fact that there is a higher percentage of coarse particles (>63  $\mu\text{m}$ ) in H4 than in H1 sediments (63% and 38%, respectively; Stefanoudis et al., 2016), is a good indication that sediments at H4 differ granulomet-

**Table 4**

Assessment of beta diversity via rarefaction with Hill numbers ( $^0D$ , species richness;  $^1D$ , exponential Shannon;  $^2D$ , inverse Simpson),  $\alpha$  rarefied to 50 individuals, and  $\gamma$  rarefied to 400 individuals.  $\beta_w = \gamma/\alpha$ .

	$^0D$			$^1D$			$^2D$		
	$\alpha$	$\beta_w$	$\gamma$	$\alpha$	$\beta_w$	$\gamma$	$\alpha$	$\beta_w$	$\gamma$
Hills	25.1	3.2	81.1	19	2.1	40.3	14.4	1.5	21.1
Plain	24.8	3.1	77.4	18.8	2.1	38.8	14	1.6	22.7
Hills and plain	25	3.4	83.9	18.9	2.3	43.1	14.2	1.7	23.6

**Table 5**  
Variation in benthic foraminiferal assemblage composition between hill and plain samples (Topo) and between sites as assessed by ANOSIM. Results are tabulated for three versions of the dataset and five data transformations (see text), and indicate the global result (Topo/Site) and significant ( $p < 0.05$ ) pairwise tests between individual sites.

Dataset	Factor	Transformation				
		None	Log	Sqrt	Fr <sub>t</sub>	P/A
All	Topo	<0.05	<0.05	<0.05	<0.05	<0.05
	Site	<0.01	<0.01	<0.01	<0.05	<0.05
		H4 vs. H1, P3, P4	H4 vs. P3, P4	H4 vs. P3, P4	H4 vs. P3, P4	H4 vs. P4
>2%	Topo	<0.05	<0.05	<0.05	<0.05	<0.01
	Site	<0.01	<0.01	<0.01	<0.05	<0.05
		H4 vs. H1, P3, P4	H4 vs. P3, P4	H4 vs. P3, P4	H4 vs. P3, P4	H4 vs. P3, P4
>5%	Topo	<0.05	<0.05	<0.01	<0.05	<0.05
	Site	<0.01	<0.01	<0.01	<0.05	Ns
		H4 vs. H1, P3, P4	H4 vs. H1, P3	H4 vs. H1, P3, P4	H4 vs. P3	

rically from those of the plains. This is also clear from an MDS plot of granulometric profiles from H1, H4, P1 and P2 (Stefanoudis et al., 2016, Fig. 3b therein), which shows that the particle size composition of H4 is distinct from the plain and quite possibly from H1 as well. These considerations suggest that topographically enhanced bottom currents, and hence coarser sediments, on the hills modify the composition of the foraminiferal communities when compared to the finer-grained sediments and more quiescent conditions on the abyssal plain. These differences are most evident (i.e. statistically significant) when comparing the large hill (H4) and the flat P3 and P4 sites. The two smaller hills (H1, H2), where the sediments contain less coarse-grained material than at H4 and foraminiferal assemblages have an intermediate composition (Fig. 4; SIMPER results between sites in Appendix F), fall between these extremes.

Assemblage characteristics might be further influenced by the occurrence at the sediment surface of dropstones (ice-rafted glacial erratics; Lisitzin, 2002), found exclusively on the hills. Although not present in samples analysed for this study, dropstones are an important source of small-scale habitat heterogeneity, providing 'islands' of solid substratum against a background of soft sediment. They typically host sessile species not found in the sediments (Gooday et al., 2015), and hence largely absent from abyssal plain samples.

### 5.3. Concluding remarks

The questions we sought to answer in this study were: do abyssal hills modify the (i) density, (ii) diversity, (iii) and species composition of foraminiferal assemblages, and if so, (iv) is mesoscale diversity enhanced? Although we recorded enhanced density and diversity on hills, these differences were not statistically significant. However, we did demonstrate that hills had a higher species density (potentially related to increased organic matter supply), and harbored species not found on the plain (most likely related to sediment characteristics), thereby increasing the pool of benthic foraminiferal species within the PAP-SO area. Most importantly, by combining data from abyssal hills and the neighboring plain the regional diversity was enhanced. These findings highlight the influence of mesoscale heterogeneity, linked to relatively modest topography, on the benthic foraminiferal communities of the PAP-SO area.

Abyssal hill terrain is the dominant feature of the abyssal realm (Harris et al., 2014), and represents an important source of habitat heterogeneity. Deep-sea macrohabitat diversity has been argued to be a significant contributor to global nematode diversity (Vanreusel et al., 2010), continental margin and slope diversity (Levin and Dayton, 2009; Levin and Sibuet, 2012) and regional deep-sea diversity (Levin et al., 2001). Our results support those general conclusions, and suggest that we need to also consider

the influence of abyssal hills on abyssal biodiversity. Although these features pose some practical challenges in terms of sample collection, the increased availability of remotely operated and autonomous underwater vehicles, and dynamically positioned research vessels with good swath bathymetry capability, as well as modern, hydraulically damped sediment coring systems, should make such studies more common. The juxtaposition of habitat heterogeneity, physical disturbance, and productivity variations over relatively small spatial scales, and generally remote from human impacts, at least in the Atlantic Ocean, suggests that abyssal hill terrain can be an effective focus for ecological hypothesis testing.

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### Supplementary material

Supplementary data associated with this article (Appendices A–F) can be found, in the online version, at <http://dx.doi.org/10.1016/j.pocean.2016.09.005>.

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