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Relationship between 'live' and dead benthic foraminiferal assemblages in the abyssal NE Atlantic

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Abstract

Dead foraminiferal assemblages within the sediment mixed layer provide an integrated, time-averaged view of the foraminiferal fauna, while the relationship between dead and live assemblages reflects the population dynamics of different species together with taphonomic processes operating over the last few hundred years. Here, we analysed four samples for 'live' (Rose-Bengal-stained) and dead benthic foraminifera (0–1 cm sediment layer, >150 μm) from four sites in the area of the Porcupine Abyssal Plain Sustained Observatory (PAP-SO; NE Atlantic, 4850 m water depth). Two sites were located on abyssal hills and two on the adjacent abyssal plain. Our results indicate that the transition from live to dead benthic foraminiferal assemblages involved a dramatic loss of delicate agglutinated and organic-walled tests (e.g. *Lagenammina*, *Nodellum*, *Reophax*) with poor preservation potential, and to a lesser extent that of some relatively fragile calcareous tests (mostly miliolids), possibly a result of dissolution. Other processes, such as the transport of tests by bottom currents and predation, are unlikely to have substantially altered the composition of dead faunas. Positive live to dead ratios suggest that some species (notably *Epistominella exigua* and *Bolivina spathulata*) may have responded to recent phytodetritus input. Although the composition of live assemblages seemed to be influenced by seafloor topography (abyssal hills vs. plain), no such relation was found for dead assemblages. We suggest that PAP-SO fossil assemblages are likely to be comparable across topographically contrasting sites, and dominated by calcareous and some robust agglutinated forms with calcitic cement (e.g. *Eggerella*).

Keywords:

abyssal hills; agglutinated foraminifera; L/D ratio; Porcupine Abyssal Plain; taphonomic loss.

Introduction

Benthic foraminifera are a hugely successful group of unicellular eukaryotes within the Supergroup Rhizaria (Ruggiero et al., 2015), most of which form a 'test' (shell) made of organic matter, agglutinated sediment particles or secreted calcium carbonate. They are extremely common in most marine sediments but particularly in the deep sea (>200 m water depth) where they often account for >50% of the meiofauna (32–300 μm) (Gooday, 2014; Snider et al., 1984) and a significant proportion of the macrofauna (>300 μm) (Gooday et al., 2007; Tendal and Hessler, 1977). Robust secreted (calcitic) or agglutinated foraminiferal tests are preserved in marine sediments in excellent condition and provide a continuous fossil record starting in the early Cambrian (McIlroy et al., 2001). This characteristic, in combination with their high sensitivity to environmental conditions, which in the deep sea include bottom current velocities, oxygenation and carbonate corrosiveness of bottom waters, and organic matter flux to the seafloor (quantity, quality and seasonality), makes foraminiferal tests widely used as proxies for reconstructing ancient oceans (Fischer and Wefer, 1999; Gooday, 2003; Jorissen et al., 2007).

The use of benthic foraminifera as tools in paleoceanographic studies necessitates a good knowledge of the ecology of modern species as well as the bias that is introduced during the transition from a living community into a dead and subsequently fossil assemblage. For a theoretical approach to assemblage formation see the works of Loubere and Gary (1990), Loubere et al. (1993) and Loubere (1997). Dead assemblages are found within the surface mixed layer where sediment is being bioturbated by macrofaunal and megafaunal organisms. A mixture of life and taphonomic processes controls dead assemblage composition. Life processes include species-specific rates of test production (i.e. reproduction and death), which dictate the contribution of tests from the living fauna to the sediment (de Stigter et al., 1999; Murray, 1976). Taphonomy occurs over the course of months to years and includes the following processes. 1) Microbial decomposition of fragile agglutinated tests that contain easily degradable organic cement (e.g. komokiaceans, organic-walled and most agglutinated taxa) (Schröder, 1988), and the dissolution of thin-walled calcareous tests within the lysocline (Berger et al., 1982) and below the carbonate compensation depth (CCD) (Saidova, 1965, 1966). (2) Post-mortem transport of small-sized tests by bottom currents (Murray, 2003; Snyder et al., 1990). (3) Destruction of tests by metazoan predation, passive ingestion by deposit-feeding organisms, and other forms of biological activity (Culver and Lipps, 2003). (4) Mixing by bioturbation (Bouchet et al., 2009; Moodley, 1990). The surface mixed layer overlies the 'fossil sediment' where the dead assemblage, now buried below the reach of biological activity, is transformed into the fossil assemblage. Additional changes in faunal composition are predominantly governed by pore-water geochemistry and sediment compaction (Mackensen and Douglas, 1989; Schröder, 1988).

The comparison of live and dead assemblages can provide important information about the

population dynamics of foraminiferal assemblages, as well as about taphonomic processes. However, most studies of this kind have been restricted to coastal (Goineau et al., 2015; Murray and Alve, 1999; Murray and Pudsey, 2004), shelf (Douglas et al., 1980; Mendes et al., 2013) or bathyal settings (Duros et al., 2012; Duros et al., 2014; Fontanier et al., 2014; Mackensen and Douglas, 1989; Schumacher et al., 2007), with only a handful conducted partly or entirely at abyssal depths (i.e. >3500 m) (Bernstein and Meador, 1979; Schröder, 1988; Mackensen et al., 1990, 1993; Harloff and Mackensen, 1997; Loubere and Rayray, 2016).

The area of the Porcupine Abyssal Plain Sustained Observatory (PAP-SO, Hartman et al., 2012), located in the northeast Atlantic (4850 m water depth), has been studied for almost three decades (Lampitt et al., 2010a). Although the live foraminiferal faunas are well known (Gooday, 1996; Gooday et al., 2010; Stefanoudis et al., 2016a), and post-glacial (the last 15,000 years) fossil faunas in a long core were analysed by Smart (2008), the dead faunas at the PAP-SO site have never been examined. Studies of dead core-top assemblages, and their relationship to corresponding live assemblages, provide insights into initial post-mortem changes unaffected by diagenetic effects. With this in mind, we analysed the top sediment layer (0–1 cm) of four samples for 'live' (Rose-Bengal-stained) and dead benthic foraminifera from four sites in the PAP-SO area, two on tops of abyssal hills and two on the adjacent abyssal plain. We then asked the following questions. (1) To what extent are dead foraminiferal assemblages representative of the original live fauna? (2) Based on these comparisons, which factors seem to influence the composition of dead assemblages? (3) Are faunal differences between the hill and plain settings reflected in the dead assemblages?

2. Materials and methods

2.1 Characteristics of the study area

The PAP-SO area is subject to seasonal fluctuations in surface ocean primary production and consequent fluxes of organic matter to the seafloor (Rice et al., 1994). Particle flux has been monitored since 1989 using sediment traps, with a peak typically occurring in summer (Frigstad et al., 2015; Lampitt et al., 2001; Lampitt et al., 2010b). Long-term sediment accumulation rates on the plain are around 3.5 cm ky^{-1} (Rice et al., 1991; Thomson et al., 1993), with oxygen penetrating to at least 25 cm sediment depth (Rutgers van der Loeff and Lavaleye, 1986), and the sediment mixed layer being around 11 cm thick (Smith and Rabouille, 2002). The lysocline has been estimated to lie between 4700–4900 m (Biscaye et al., 1976; Rutgers van der Loeff and Lavaleye, 1986) and the CCD at about 5200 m (Biscaye et al., 1976). Ice-rafted dropstones are frequently exposed on hills but not on the plain (Durden et al., 2015; Ruhl, 2012). The silt and clay content of hill sediments is appreciably lower than plain sediments (Durden et al., 2015; Stefanoudis et al.,

2016b). These observations strongly suggest significant winnowing of fine particles from hill sediments, and consequently reduced sediment accumulation rates on hills. The strong seasonal signal in organic matter supply to the seafloor (e.g. Bett et al., 2001), coupled with the substantial variation in the silt and clay content of hill and plain sediments, complicates the interpretation of sedimentary organic matter content (Turnewitsch et al., 2015). It appears that total organic carbon and nitrogen content of the sediment is less in hill than in plain sediments (Morris et al., 2016), possibly as a result of winnowing. However, phytodetritus cover is slightly higher, and the suspended particle concentration in the benthic boundary layer substantially higher, on the hills than on the plain. This, together with a ~3-fold increase in total megafaunal biomass (5-fold and 2.5-fold for suspension and non-suspension feeders, respectively) on hill compared to plain locations suggests that the hills receive more organic matter from the water column (Durden et al., 2015; Morris et al., 2016).

2.2 Sample collection

Samples were collected during RSS *James Cook* cruise 062 (JC062, 24 July to 29 August 2011; Ruhl, 2012) and were obtained using a Bowers and Connelly Megacorer (Gage and Bett, 2005) fitted with 59 mm internal diameter cores tubes, from two abyssal plain sites (P1, P2) and two abyssal hill sites (H1, H4) (Fig. 1). On recovery the cores were sliced into 0.5 cm layers to 2 cm sediment depth, followed by 1 cm layers from 2 to 10 cm depth, and each slice fixed in 10% Borax buffered formalin. The present contribution is based on material retained on a 150-µm sieve from the 0–1 cm sediment horizon from four samples, one from each site (Table 1).

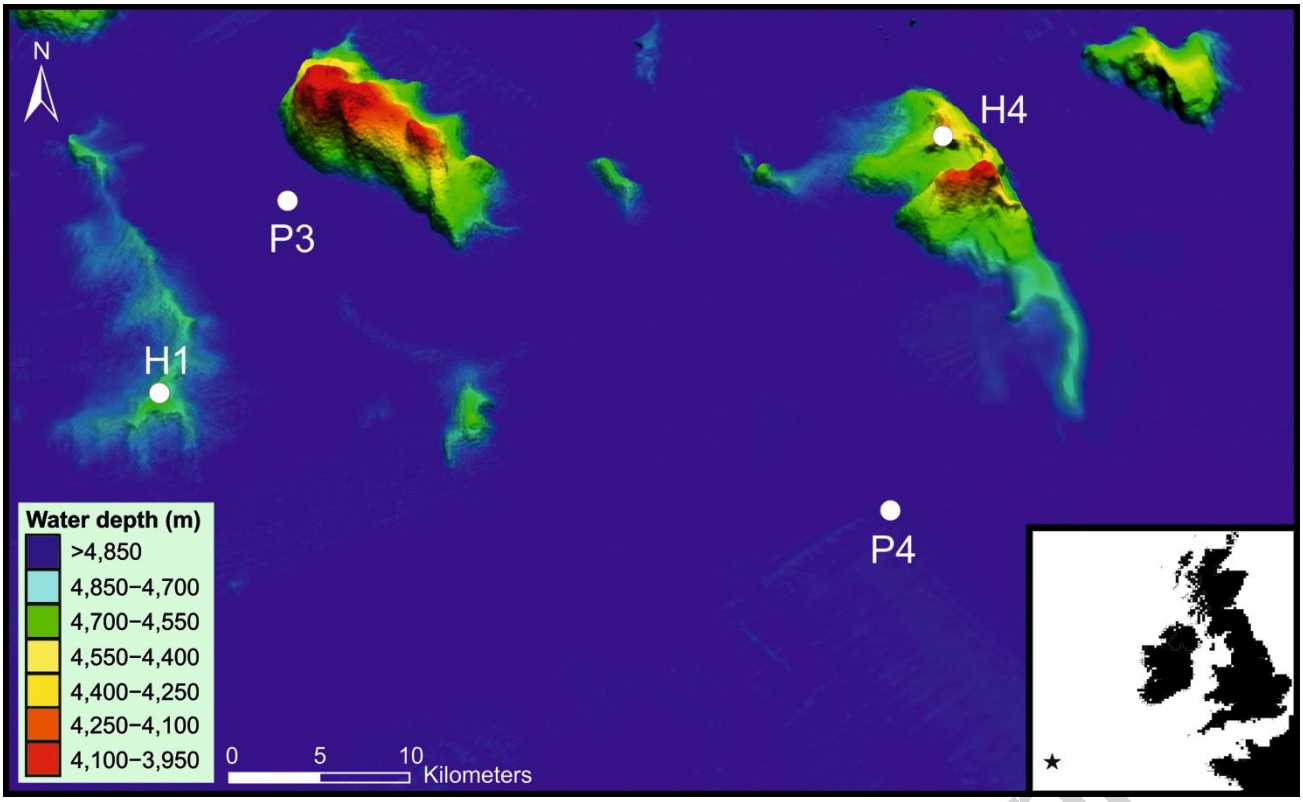

Fig. 1. 3D topographic representation of the PAP-SO area (48.79 to 49.21 °N, -16.03 to -16.93 °E) indicating the approximate location and bathymetry of the four study sites, H1 and H4 (abyssal hill sites) and P3 and P4 (abyssal plain sites). The inset shows the general location (star) of the Porcupine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

Table 1. Site and station information.

Site	Station	Topography	Water depth (m)	Latitude (°N)	Longitude (°E)	Date sampled
H1	JC062-053	Abyssal Hill	4679	48.977	-16.727	05.08.2011
H4	JC062-126	Abyssal Hill	4365	49.074	-16.264	22.08.2011
P3	JC062-101	Abyssal Plain	4851	49.083	-16.667	17.08.2011
P4	JC062-077	Abyssal Plain	4851	48.875	-16.293	11.08.2011

2.3 Sample processing

In the laboratory, the 0–0.5 cm and 0.5–1.0 cm slices of cores were gently washed through two sieves (300 µm and 150 µm) using filtered tap water. Residues >300 and 150–300 µm were stained with Rose Bengal (1 g dissolved in 1 L tap water) overnight (Murray and Bowser, 2000; Walton, 1952) and sorted for all 'live' (stained) and dead benthic foraminifera 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 recognizable morphotypes (*Psammosphaera* sp. 1 and 'white domes'; see taxonomic notes in Appendix B). These forms are not taken into account, as they are difficult to

separate into species and are poorly stained with Rose Bengal, making the distinction between live and dead specimens difficult. For the rest of the picked material, in order to ensure that the stained material was foraminiferal protoplasm, specimens were transferred to glass slides with glycerin and examined under a transmission light microscope. This enabled the distinction of 'fresh' cellular material from decayed cytoplasm, accumulations of bacteria, or other inhabiting organisms. Where 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. Thus, the 'fresh' (undegraded) appearance of stercomata was 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).

2.4 Light and scanning electron microscopy

Specimens were photographed using either a NIKON Coolpix 4500 camera mounted on an Olympus SZX10 compound microscope, or a Canon EOS 60D mounted on an Olympus SZX7 compound microscope, or a Canon EOS 350D mounted on 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.

2.5 Data processing

The taxonomic scheme we followed was a combination of those proposed by Loeblich and Tappan (1987) and Pawlowski et al. (2013). For the purposes of analysis we partitioned our data in three ways: (a) 'live' (Rose-Bengal-stained) versus 'dead' specimens; (b) 'entire' (fossilisable plus non-fossilisable taxa) versus 'potential fossil fauna', the latter consisting of calcareous taxa and agglutinates with a calcitic cement, such as *Eggerella* and *Karreriella* (Harloff and Mackensen, 1997; Mackensen et al., 1990; Mackensen et al., 1995; Schmiedl et al., 1997); and (c) 'common' versus 'all' (i.e. common plus rare) species, the former consisting of species having a relative abundance >5% in the live or dead fraction of at least one sample. Rarefied alpha diversity indices (species richness, exponential Shannon index, inverse Simpson index, Chao 1; see e.g. Magurran, 2004) were assessed via individual-based rarefaction (e.g. Colwell et al., 2012) implemented using EstimateS (9.1.0, viceroy.eeb.uconn.edu/estimates), based on count data for complete specimens. Community composition was examined on the basis of faunal dissimilarity (Bray-Curtis), calculated following a range of transformations (none; log [x+1]; square-root; fourth-root; presence-absence) on the count data for complete specimens, visualised with non-metric

multi-dimensional scaling ordination (MDS), and assessed using analysis of similarities (ANOSIM) (PRIMER 6, Clarke and Gorley, 2006). Multivariate dispersion (MVDISP), a measure of community heterogeneity, was also estimated in PRIMER.

We calculated live to dead ratios (L/D; Jorissen and Wittling, 1999) for all 'common' species in two ways: 1) using count (N) data (L_N/D_N), and 2) using relative abundance (%) data ($L_{\%}/D_{\%}$), the latter being less affected by the substantially higher numbers of tests in the dead fauna. Only the ratio based on relative abundance has been used for live-dead comparisons in previous studies (e.g. Jorissen and Wittling, 1999; Duros et al., 2014; Goineau et al., 2015). For the L/D ratios of potential fossil species, we first subtracted all non-fossilising agglutinated species (i.e. agglutinated species with an organic cement), and then calculated corrected relative abundances for all species in the living and dead assemblages.

3. Results

3.1 Density

A total of 512 obviously complete live foraminiferal specimens, 85–163 (mean 128 ± 33 standard deviation) individuals per sample, was picked from the four samples. The Hormosinacea (agglutinated) and the Rotaliida (calcareous), both multichambered groups, together represented about half of these specimens. In addition, we recorded 43 fragmented stained tests (12–28 per sample, mean 11 ± 12), the majority (77%) of them tubular monothalamids. The same samples yielded a total of 4686 obviously complete, dead foraminiferal specimens, 571–2122 per sample (mean 1172 ± 722). Almost two-thirds (63%) of these were rotaliids, with the next most abundant group being the multichambered textulariids (agglutinated) (~8% of the total dead assemblage). Fragments of dead tests ranged from 261 to 528 per sample (total 1527, mean 382 ± 110), of which more than two-thirds (72%) were tubular and almost all of the rest (~25%) were members of the Miliolida (calcareous; mostly *Pyrgo* spp. and *Quinqueloculina* spp.). Densities per major grouping for the live and dead assemblages are given in Appendix A.1.

3.2 Diversity

The majority (~88%) of all complete live tests could be assigned to morphospecies (either described or undescribed), the remainder being indeterminate. In total, 76 species were identified, with 29–46 (mean 37 ± 7 standard deviation) species being present in each sample. Most (~86%) of the live fragments could be assigned to 10 morphospecies, mainly tubular monothalamids, with 0–5 (mean 3 ± 2) species per sample. The total number of species with live tests (either complete or fragmentary) was 83. In the case of the dead assemblage, almost all (99%) of the specimens with complete tests could be assigned to a morphospecies. In total, 152 species were identified,

with 75–114 (mean 92 ± 17) per sample. Three quarters of the dead fragments could be assigned to 24 morphospecies (7–17 per sample, mean 11 ± 6), most of them tubular monothalamids. The total number of species with dead tests (either complete or fragmentary) was 163. The numbers of live and dead species in each major grouping are summarised in Appendix A.2. All species found in this study are briefly described and illustrated in Appendix B.

Rarefied alpha diversity indices (species richness, exponential Shannon index, inverse Simpson index, Chao 1) were comparable (ANOVA, $p<0.05$) between the live and dead assemblages, for both the entire and the potential fossil fauna. Interestingly, we found that the rarefied number of live species was always linearly correlated with that of the dead fraction for (i) individual samples, (ii) samples grouped by setting (hills, plain), and (iii) all samples combined (Fig. 2). This was especially true for the potential fossil fauna, where most of the samples were fairly close to the best-fit line.

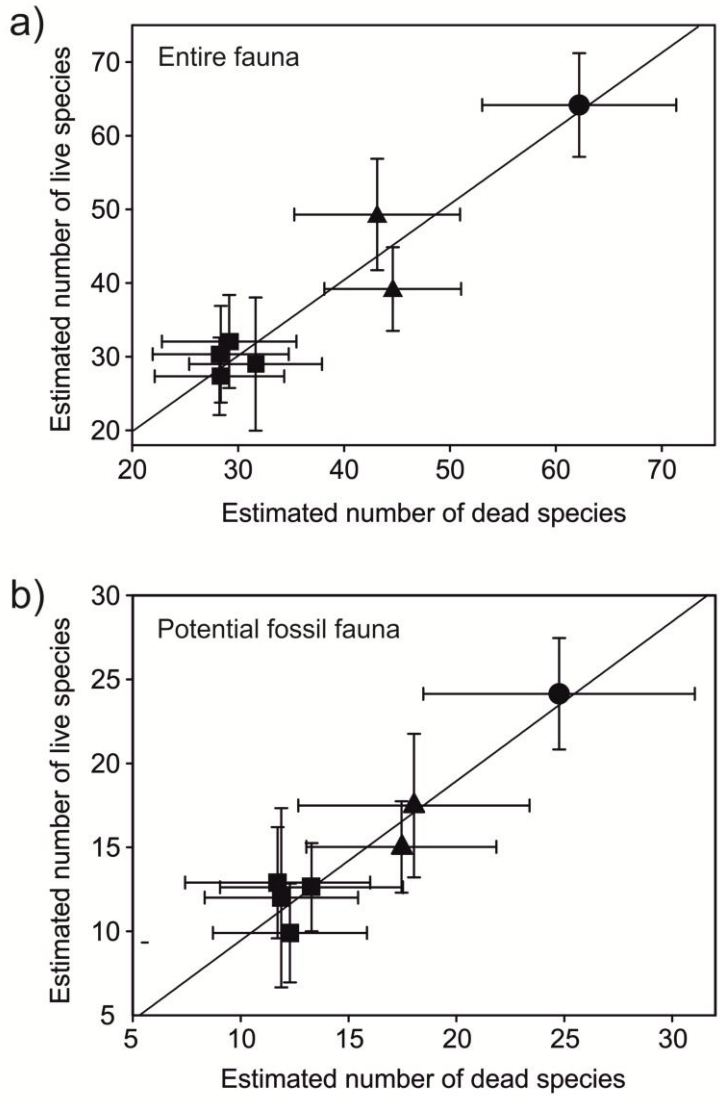

Fig. 2. Biplot of rarefied estimated number of live and dead species for each individual sample (square), samples grouped by topography (hills, plain; triangle) and all samples combined (circle), for the entire (a) and potential fossil fauna (b), respectively. (Data shown as mean and 95% confidence interval; line: linear least squares fit).

3.3 Comparison of living and dead assemblages

3.3.1 Species composition

Live and dead assemblages were highly distinct in terms of their species composition (Fig. 3). When the entire assemblage was considered, ANOSIM assessment indicated a significant ($p<0.05$) difference in the assemblages regardless of prior data transformation. When only the common species were considered, ANOSIM again indicated a significant ($p<0.05$) difference in the assemblages except in the case of simple presence absence assessment. Multivariate dispersion was always less in the dead than in the live assemblage ($MVDISP_{dead}<MVDISP_{live}$), indicating that the dead assemblages were more homogeneous in their composition. Identical results were obtained when only the potential fossil faunas were considered. The 2-d MDS plots suggested common ecological trends (e.g. plain to hill comparisons) in both the live and dead assemblages whether assessed in terms of the entire fauna (Fig. 3a) or only the fossilisable component (Fig. 3b), although that trend was always more pronounced in the live fauna. Similarly, the live to dead trend (e.g. live plain to dead plain) in species composition appeared to be consistent between both plains and hills, whether assessed in terms of the total fauna or only the fossilisable component.

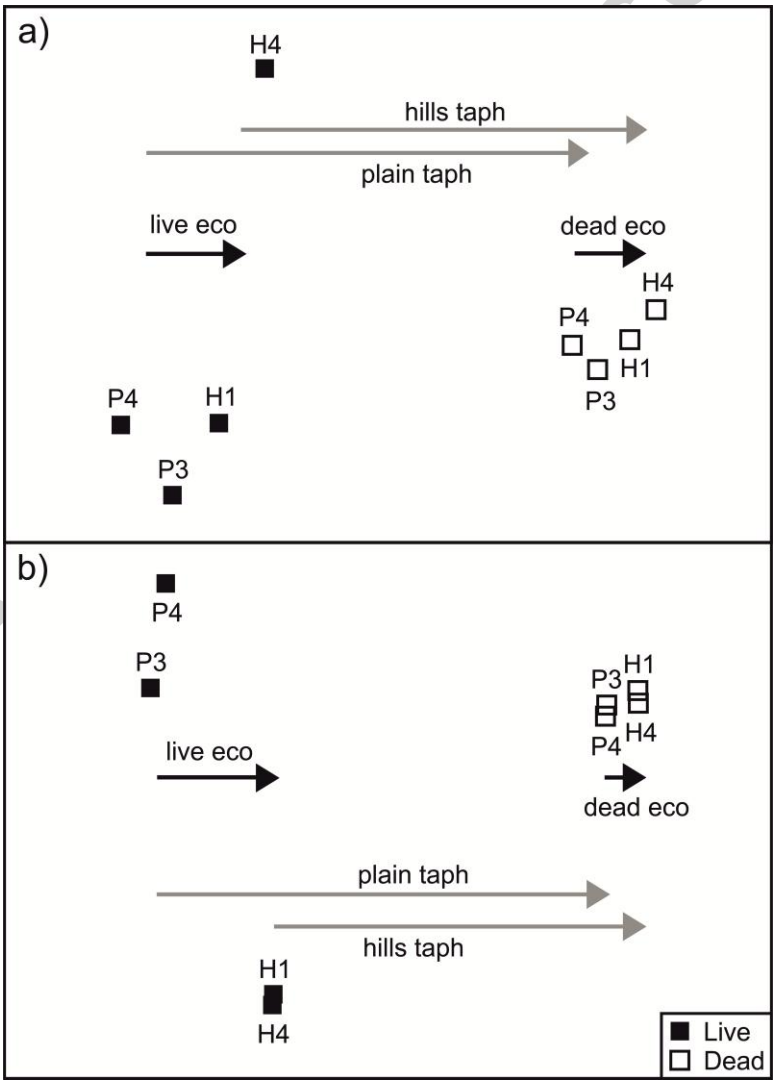

Fig. 3. 2-d Non-metric multi-dimensional scaling ordination plots of live (solid symbols) and dead (open symbols) foraminiferal assemblage composition from plain (P) and hill (H) sites on the PAP-SO area, based on Bray-Curtis dissimilarity of log (x+1) transformed data of all species (i.e. common plus rare). (a) Entire assemblage. (b) Potential fossil assemblage. Black arrows illustrate the degree of ecological variation (hills, plains) in assemblage composition within the living and dead fraction, while grey arrows indicate the amount of taphonomic change in assemblage composition per topographic setting.

Table 2. Top 20 'live' (Rose-Bengal-stained) species with complete tests per sample and in all samples combined (final column). N = total number of specimens. *A. glomerata* = *Adercotryma glomerata*, *A. shanonni* = *Ammoglobigerina shannoni*, *B.* aff. *earleandi* = *Bolivina earleandi*, *B. spathulata* = *Bolivina spathulata*, *C. wuellerstorfi* = *Cibicides wuellerstorfi*, *E. bradyi* = *Eggerella bradyi*, *E. exigua* = *Epistominella exigua*, *G. subglobosa* = *Globocassidulina subglobosa*, *L.* aff. *arenulata* = *Lagenammina* aff. *arenulata*, *N. dentaliniformis* = *Nodulina dentaliniformis*, *N. umboniferus* = *Nuttaliides umboniferus*, *O. globosa* = *Oolina globosa*, *O. tenerus*= *Oridorsalis tenerus*, *O. umbonatus* = *Oridorsalis umbonatus*, *P. aurantiaca* = *Placopsilinella aurantiaca*, *P. murrayi* = *Portatrochammina murrayi*, *P. murrhina* = *Pyro murrhina*, *R. agglutinatus* = *Reophax agglutinatus*, *R. bilocularis* = *Reophax bilocularis*, *Q. venusta* = *Quinqueloculina venusta*, *S. bulloides* = *Sphaeroidina bulloides*, *S. tenuis* = *Spirosigmoilina tenuis*, *T. albicans* = *Thurammina albicans*.

Rank	H1		Rank	H4		Rank	P3		Rank	P4		Rank	Total	
	Species	N		Species	N		Species	N		Species	N		Species	N
1	White domes	15	1	*A. glomerata*	24	1	*E. exigua*	16	1	*E. exigua*	13	1	*A. glomerata*	46
2	*L.* aff. *arenulata*	14	2	*Nodellum*-like sp.	9	2	*Reophax* sp. 28	14	2	*A. glomerata*	9	2	*E. exigua*	43
3	*A. glomerata*	11	3	*Reophax* sp. 21	8	3	*B. spathulata*	10	3	*R. bilocularis*	6	3	*Reophax* sp. 21	30
4	*Reophax* sp. 21	10	4	*E. exigua*	7	4	*N. dentaliniformis*	8	4	*L.* aff. *arenulata*	4	4	*L.* aff. *arenulata*	20
5	*E. exigua*	7	4	*S. bulloides*	7	4	*Reophax* sp. 21	8	4	*Reophax* sp. 9	4	5	*Reophax* sp. 28	20
6	*Reophax* sp. 19	6	6	*A. shannoni*	5	6	*G. subglobosa*	5	4	*Reophax* sp. 21	4	6	White domes	19
6	*T. albicans*	6	7	*Psammosphaera* sp. 1	4	6	*Reophax* sp. 19	5	7	*Lagenammina* sp. 89	3	7	*Reophax* sp. 19	14
8	*G. subglobosa*	5	7	*Reophax* sp. 9	4	8	White domes	4	7	*Reophax* sp. 19	3	8	*G. subglobosa*	13
8	*Lagenammina* sp. 19	5	7	*P. murrhina*	4	9	*C. wuellerstorfi*	3	7	*T. albicans*	3	8	*Nodellum*-like sp.	13
8	*O. umbonatus*	5	10	*P. murrayi*	3	9	*S. bulloides*	3	10	*M. barleeanus*	2	8	*N. dentaliniformis*	13
8	*P. murrhina*	5	10	*R. agglutinatus*	3	9	*T. albicans*	3	10	*P.murrhina*	2	8	*P. murrhina*	13
8	*Reophax* sp. 23	5	10	*R. bilocularis*	3	12	*A. glomerata*	2	20	**Multiple (18) spp.**	**1**	8	*Reophax* sp. 9	13
8	*Reophax* sp. 28	5	13	*C. wuellerstorfi*	2	12	*B.* aff. *earleandi*	2				13	*S. bulloides*	12
8	*Reophax* sp. 110/111	5	13	*E. bradyi*	2	12	*E. bradyi*	2				13	*T. albicans*	12
15	*Bathysiphon* sp. 1	4	13	*G. subglobosa*	2	12	*L.* aff. *arenulata*	2				15	*B. spathulata*	10
15	*Reophax* sp. 9	4	13	*N. umboniferus*	2	12	*Lagenammina* sp. 19	2				16	*C. wuellerstorfi*	8
17	*Nodellum*-like sp.	3	13	*O. tenerus*	2	12	*O. globosa*	2				16	*Lagenammina* sp. 19	8
17	*N. dentaliniformis*	3	13	*P. aurantiaca*	2	12	*P. murrhina*	2				16	*O. umbonatus*	8
17	*Q. venusta*	3	13	*S. tenuis*	2	12	*Reophax* sp. 27	2				16	*R. bilocularis*	8

17	*Reophax* sp.8	3	20	**Multiple (21) spp.**	**1**	20	**Multiple (15) spp.**	**1**			20	*Reophax* sp. 23	7

Table 3. Top 20 dead species with complete tests per sample and in all samples combined (final column). N = total number of specimens. *A. glomerata* = *Adercotryma glomerata*, *C. wuellerstorfi* = *Cibicides wuellerstorfi*, *E. bradyi* = *Eggerella bradyi*, *E. exigua* = *Epistominella exigua*, *E. foliaceus* = *Eratidus foliaceus*, *G. subglobosa* = *Globocassidulina subglobosa*, *G. polia* = *Gyroidina polia*, *G.* aff. *soldanii* = *Gyroidina* aff. *soldanii*, *G. umbonata* = *Gyroidina umbonata*, *K. apicularis* = *Karrerulina apicularis*, M. *barleeanus* = *Melonis barleeanus*, *M. pombilioides* = *Melonis pombilioides*, *N. dentaliniformis* = *Nodulina dentaliniformis*, *N. umboniferus* = *Nuttaliides umboniferus*, *O. globosa* = *Oolina globosa*, *O. umbonatus* = *Oridorsalis umbonatus*, *P. aurantiaca* = *Placopsilinella aurantiaca*, *P. murrayi* = *Portatrochammina murrayi*, *P. murrhina* = *Pyro murrhina*, *Q. venusta* = *Quinqueloculina venusta*, *S. bulloides* = *Sphaeroidina bulloides.*

Rank	H1		Rank	H4		Rank	P3		Rank	P4		Rank	Total	
	Species	N		Species	N		Species	N		Species	N		Species	N
1	*E. exigua*	216	1	*S. bulloides*	564	1	*E. exigua*	146	1	*E. exigua*	129	1	*E. exigua*	669
2	*G. subglobosa*	112	2	*E. exigua*	178	2	*G. subglobosa*	34	2	*G. subglobosa*	57	2	*S. bulloides*	634
3	*E. bradyi*	87	3	*G. subglobosa*	86	2	*E. bradyi*	34	3	*A. glomerata*	27	3	*G. subglobosa*	289
4	*O. umbonatus*	79	4	*P. murrhina*	82	4	*N. umboniferus*	29	3	*M. barleeanus*	27	4	*P. murrhina*	199
5	*M. pompilioides*	69	5	*M. barleeanus*	80	5	*P. murrhina*	27	5	*P. murrhina*	26	5	*M. barleeanus*	191
6	*P. murrhina*	64	6	*C. wuellerstorfi*	76	6	*C. wuellerstorfi*	22	6	*E. bradyi*	24	6	*O.umbonatus*	186
7	*M. barleeanus*	63	7	*M. pompilioides*	74	6	*O. umbonatus*	22	6	*L.* aff. *arenulata*	24	7	*E. bradyi*	184
8	*C. wuellerstorfi*	46	8	*O. umbonatus*	70	8	*M. barleeanus*	21	8	*S. bulloides*	22	8	*M. pompilioides*	183
8	*L.* aff. *arenulata*	46	9	*N. umboniferus*	60	8	*M. pompilioides*	21	9	*M. pompilioides*	19	9	*C. wuellerstorfi*	159
10	*A. glomerata*	45	10	*G. polia*	45	10	*A. glomerata*	16	10	*C. wuellerstorfi*	15	10	*N. umboniferus*	130
11	*S. bulloides*	35	11	*Pullenia* sp. 1	44	11	*L.* aff. *arenulata*	14	10	*O. umbonatus*	15	11	*A. glomerata*	112
12	*N. dentaliniformis*	30	12	*E. bradyi*	39	12	*S. bulloides*	13	12	*N. umboniferus*	13	12	*L.* aff. *arenulata*	104
13	*N. umboniferus*	28	13	*P. aurantiaca*	30	13	*Gyroidina* sp. 1	12	13	*Hormosina* sp. 1	12	13	*G. polia*	80
14	*G. polia*	24	13	*Psammosphaera* sp. 1	30	14	*N. dentaliniformis*	9	14	*G.* aff. *soldanii*	10	14	*Gyroidina* sp. 1	60
14	*Gyroidinoina* sp. 1	24	15	*E. foliaceus*	25	14	*Oolina* sp. 4	9	14	*Oolina* sp. 4	10	15	*Pullenia* sp. 1	56
16	*Recurvoides* sp. 1	21	16	*A. glomerata*	24	14	*G.* aff. *soldanii*	9	14	*Parafissurina* sp. 3	10	16	*Recurvoides* sp. 1	53
17	*K. apicularis*	14	17	*P. murrayi*	23	17	*G. polia*	8	14	*Quinqueloculina* sp. 2	10	17	*N. dentaliniformis*	50
18	*O. globosa*	13	18	*Q.* venusta	21	18	*G. umbonata*	6	18	*Recurvoides* sp. 1	9	18	*Parafissurina* sp. 3	38
18	*Quinqueloculina* sp. 2	13	19	**Multiple (3) spp.**	**20**	19	**Multiple (5) spp.**	**5**	18	*Reophax* sp. 19	9	19	*G.* aff. *soldanii*	36
20	**Multiple (5) spp.**	**12**							20	*Lagenammina* sp. 19	8	19	*Quinqueloculina* sp. 2	36

3.3.2 Abundant species

The 20 top-ranked species from the entire assemblage, per sample and in all samples combined, are summarised in Table 2. The four most common species with consistently high rankings across all four samples were *Adercotryma glomerata* (ranked in the top three in three out of four samples), *Epistominella exigua* (ranked in the top five in all four samples), *Reophax* sp. 21 (ranked in the top four in all four samples) and *Lagenammina* aff. *arenulata* (ranked in the top four in two out of four samples). Other species had high rankings in one or two samples. For example, 'white domes' (distinctive form with a thick, white test made of finely agglutinated particles resembling the well-known agglutinated genus *Crithionina*) was ranked 1st and 8th in two samples but was entirely absent in others; *Reophax* sp. 28 was ranked in the top 8 twice; *Nodellum*-like sp. was ranked 2nd in one sample and 17th in another; *Sphaeroidina bulloides* was ranked 4th in one sample and 9th in another, and *Bolivina spathulata* was ranked 3rd in only one sample.

The top 20 species for the potential fossil fauna are summarised in Table 3. *Epistominella exigua* and *Globocassidulina subglobosa* were ranked 1st and 2nd in three out of four samples, and 2nd and 3rd in the fourth sample. Other species with consistently high rankings were *Pyrgo murrhina, Cibicides wuellerstorfi*, *Melonis barleeanus, M. pompilioides* and *Oridorsalis umbonatus*, all of which featured in the top 10 of all four samples. *Sphaeroidina bulloides* was usually a medium-ranked species in three out of four samples (mean rank 10, mean density 23 specimens per sample), but it achieved the highest abundance (564 specimens per sample) of any single species at site H4, which is located on top of a relatively large (~500 m high) abyssal hill (see Fig. 1). Only two species with poor fossilisation potential were amongst the top 20 species in the dead assemblage: *Adercotryma glomerata* (top 10 in three out of four samples) and *Lagenammina* aff. *arenulata* (top 8 in two out of four samples).

3.3.3 L/D ratios

Considering the entire assemblage, a total of 17 species had a relative abundance >5% in the living and/or dead fauna (see Appendix A.4). Both count and relative abundance data were subsequently used for estimating the L/D ratios of these species (L_N/D_N and $L_{\%}/D_{\%}$, respectively; Table 4). Nine species had finely agglutinated walls and were inferred to have poor fossilisation potential. Four of these, *Nodellum*-like sp., 'white domes', *Reophax* sp. 9 and *Reophax* sp. 21, were consistently more common in the live than in the dead assemblage, in terms of both counts and relative abundances (Table 4). Another four

species (*Lagenammina* aff. *arenulata*, *Nodulina dentaliniformis*, *Reophax* sp. 28, *Aderctotryma glomerata*) were more common in the dead assemblage ($L_N/D_N<1$), although their relative abundance was usually greater in the live assemblage ($L_{\%}/D_{\%}>1$). *Reophax bilocularis* had mixed patterns. All of the 8 species with good fossilisation potential, except for *Bolivina spathulata,* were always more abundant in the dead that in the live assemblage (L_N/D_N and $L_{\%}/D_{\%}$ <1, Table 5). *B. spathulata* had by far the highest L_N/D_N ratio, even in comparison with the easily-degradable species (Table 4).

Table 4 Live/dead (L/D) ratios for all major species (i.e. relative abundance >5% in at least one sample), considering the 'entire' (fossilisable plus non-fossilisable) assemblage. L/D ratios are calculated based on counts (N; L_N/D_N) and relative abundance (%; $L_{\%}/D_{\%}$). L_{only} = only live (Rose-Bengal-stained) specimens found, D_{only} = only dead specimens found, A = absent from both live and dead fraction. Lag = *Lagenammina*, Nod = *Nodellum*-like group, Sph = Spheres (no aperture), Hor = Hormosinacea, Rot = Rotaliida, Tex = Textulariida, Tro = Trochamminacea.

		H1		**H4**		**P3**		**P4**	
Group	**Species**	L_N/D_N	$L_{\%}/D_{\%}$	L_N/D_N	$L_{\%}/D_{\%}$	L_N/D_N	$L_{\%}/D_{\%}$	L_N/D_N	$L_{\%}/D_{\%}$
	Poor fossilisation potential								
Lag	*Lagenammina* aff. *arenulata*	0.30	2.56	D_{only}	D_{only}	0.14	0.74	0.17	1.48
Nod	*Nodellum*-like sp.	L_{only}	L_{only}	9	156.18	L_{only}	L_{only}	D_{only}	D_{only}
Sph	White domes	3	25.22	A	A	L_{only}	L_{only}	A	A
Hor	*Nodulina dentaliniformis*	0.10	0.84	0.14	2.48	0.89	4.59	0.25	2.22
Hor	*Reophax bilocularis*	D_{only}	D_{only}	3	52.06	D_{only}	D_{only}	1.67	14.79
Hor	*Reophax* sp. 9	4	33.63	0.29	4.96	L_{only}	L_{only}	2	17.74
Hor	*Reophax* sp. 21	5	42.04	0.89	15.43	L_{only}	L_{only}	4	35.49
Hor	*Reophax* sp. 28	0.83	7.01	D_{only}	D_{only}	4.67	24.10	0.33	2.96
Tro	*Adercotryma glomerata*	0.24	2.06	1	17.35	0.13	0.65	0.33	2.96
	High fossilisation potential								
Rot	*Bolivina spathulata*	A	A	A	A	10	51.64	A	A
Rot	*Epistominella exigua*	0.03	0.27	0.04	0.68	0.11	0.57	0.10	0.89
Rot	*Globocassidulina subglobosa*	0.04	0.38	0.02	0.40	0.15	0.76	0.02	0.16
Rot	*Melonis pompilioides*	D_{only}	D_{only}	Donly	D_{only}	0.05	0.25	0.05	0.47
Rot	*Nuttallides umboniferus*	0.04	0.30	0.03	0.58	0.03	0.18	0.08	0.68
Rot	*Oridorsalis umbonatus*	0.06	0.53	0.01	0.25	0.05	0.23	0.07	0.59
Rot	*Sphaeroidina bulloides*	0.06	0.48	0.01	0.22	0.23	1.19	D_{only}	D_{only}
Tex	*Eggerella bradyi*	D_{only}	D_{only}	0.05	0.89	0.06	0.30	D_{only}	D_{only}

When considering only the potential fossil foraminifera, a total of 17 species had a relative abundance >5% in the living and/or dead fauna (see Appendix A.5). Except for *B. spathulata,* L_N/D_N ratios were all <1, reflecting a greater abundance in the dead than in the live assemblage (Table 5). However, $L_{\%}/D_{\%}$ indicated that in addition to *B. spathulata,* a

further 5 species (*Pyrgo murrhina*, *Cibicides wuellerstorfi*, *Epistominella exigua*, *Globocassidulina subglobosa*, *Oridorsalis tenerus*), were relatively more abundant in the live than in the dead assemblages ($L_{\%}/D_{\%}>1$; Table 5). The remaining species had mixed patterns.

Table 5 Live/dead (L/D) ratios for all major species (i.e. relative abundance >5% in at least one sample), considering potential fossil species only. L/D ratios are calculated based on counts (N; L_N/D_N) and relative abundance (%; $L_{\%}/D_{\%}$). L_{only} = only live (Rose-Bengal-stained) specimens found, D_{only} = only dead specimens found, A = absent from both live and dead fractions. Mil = Milioliida, Rot = Rotaliida, Tex = Textulariida.

		H1		H4		P3		P4	
Group	**Species**	L_N/D_N	$L_{\%}/D_{\%}$	L_N/D_N	$L_{\%}/D_{\%}$	L_N/D_N	$L_{\%}/D_{\%}$	L_N/D_N	$L_{\%}/D_{\%}$
Mil	*Pyrgo murrhina*	0.08	2.06	0.05	2.17	0.07	0.69	0.08	1.30
Mil	*Quinqueloculina venusta*	0.33	8.79	0.05	2.12	D_{only}	D_{only}	D_{only}	D_{only}
Mil	*Quinqueloculina* sp. 2	0.15	4.06	D_{only}	D_{only}	D_{only}	D_{only}	D_{only}	D_{only}
Rot	*Spirosigmoilina tenuis*	0.08	2.20	0.67	29.62	D_{only}	D_{only}	D_{only}	D_{only}
Rot	*Alabaminella weddellensis*	0.29	7.54	D_{only}	D_{only}	D_{only}	D_{only}	A	A
Rot	*Bolivina spathulata*	A	A	A	A	10	93.6	A	A
Rot	*Cibicides wuellerstorfi*	0.04	1.15	0.03	1.17	0.14	1.28	0.07	1.13
Rot	*Epistominella exigua*	0.03	0.85	0.04	1.75	0.11	1.03	0.10	1.70
Rot	*Globocassidulina subglobosa*	0.04	1.18	0.02	1.03	0.15	1.38	0.02	0.30
Rot	*Gyroidina* sp. 1	0.08	2.20	0.05	2.34	D_{only}	D_{only}	D_{only}	D_{only}
Rot	*Melonis barleeanus*	D_{only}	D_{only}	D_{only}	D_{only}	D_{only}	D_{only}	0.07	1.25
Rot	*Melonis pompilioides*	D_{only}	D_{only}	D_{only}	D_{only}	0.05	0.45	0.05	0.89
Rot	*Nuttallides umboniferus*	0.04	0.94	0.03	1.48	0.03	0.32	0.08	1.30
Rot	*Oridorsalis tenerus*	D_{only}	D_{only}	0.5	22.22	A	A	0.2	3.38
Rot	*Oridorsalis umbonatus*	0.06	1.67	0.01	0.63	0.05	0.43	0.07	1.13
Rot	*Sphaeroidina bulloides*	0.06	1.51	0.01	0.55	0.23	2.16	D_{only}	D_{only}
Tex	*Eggerella bradyi*	D_{only}	D_{only}	0.05	2.28	0.06	0.55	D_{only}	D_{only}

4. Discussion

4.1 Limitations

Our study was limited to foraminiferal tests retained on a 150-µm mesh sieve. Analysing the 63–150-µm fraction of abyssal samples is extremely time consuming, especially when taking into account dead foraminifera, and could not be accomplished during the time frame of this study. These finer size fractions often include some abundant, opportunistic species that are absent or under-represented in the >150-µm fraction (Gooday, 1988; 1993; Sun et al., 2006). Nevertheless, many small species that appear among the top 20 in Gooday et al's (2010) time-series data at the PAP central site (e.g. *Alabaminella weddellensis* and

Epistominella exigua, although not the most abundant species *Trochammina* sp. 126), are represented in the residues retained on coarser-meshed sieves (125 or 150 μm). We also note that coarser sieves are commonly used in paleoceanographic (Gooday, 2003) and modern deep-sea research (Murray, 2007, 2015), and size-fractioned data from the NE Atlantic (>150 and >63 μm) resulted in similar correlations between diversity measures and benthic foraminiferal densities (Gooday et al., 2012).

4.2 To what extent are dead benthic foraminiferal assemblages representative of the original live fauna?

Previous comparisons of live and dead foraminiferal faunas demonstrated varying degrees of correspondence between the two assemblages. Most of the discrepancies were attributed to taphonomic destruction of agglutinated species (de Stigter et al., 1999; Mackensen et al., 1990), calcite dissolution of calcareous species (Murray and Alve, 1999; Murray and Pudsey, 2004), transport of dead tests (Douglas et al., 1980; Duros et al., 2012), population dynamics (Gooday and Hughes, 2002), microhabitat occupancy (Loubere and Rayray, 2016) or an interplay between multiple factors (Duros et al., 2014; Mackensen and Douglas, 1989).

Our results revealed a significant change between the 'entire' live and the dead assemblages in the surface 0–1 cm at each station (Fig. 3a). This trend persisted even when we restricted our comparisons to potential fossil species (Fig. 3b). A mixture of taphonomic processes and biological factors (population dynamics) (see sections 4.3–4.4) is likely responsible for these differences in composition. Similarities in species composition between samples were greater for the dead compared to the live assemblages, even when we did not consider delicate agglutinated taxa ($MVDISP_{dead}$<$MVDISP_{live}$ in both entire and fossilisable cases). This likely reflects the fact that dead assemblages provide a time averaged record integrating different seasonal conditions and possibly changing environmental conditions over longer time scales (Glover et al., 2010). In the present case the dead assemblage in the 0–1 cm layer consists of a mixture of specimens that could be anywhere from 300 to 3100 years old, given sedimentation rates of 3.5 cm ky^{-1} and the depth (11 cm) of the sediment mixed layer (Billett and Rice, 2001; Smith and Rabouille, 2002). Integration over time also potentially explains the greater number of species in the dead compared to the live assemblage (163 versus 83). Nevertheless, rarefied alpha diversity (species richness, exponential Shannon index, inverse Simpson index, Chao 1) was always similar. In fact, the rarefied number of species in the live assemblage was

linearly correlated with that of both the entire and the potential fossil dead assemblage (Fig. 2). Thus, for the PAP-SO area, the number of live species is a good indicator of the number of dead species and vice versa.

4.3 Taphonomic processes affecting the composition of dead assemblages

The main taphonomic processes that can modify dead foraminiferal faunas in the area of PAP-SO are i) post-mortem physicochemical destruction of tests, ii) transportation of tests and iii) predation.

4.3.1 Post-mortem physicochemical destruction of tests

Selective destruction of organic-walled tests and agglutinated tests with organic cement may result in the poor representation or absence of certain taxa in the dead assemblage (Denne and Sen Gupta, 1989; Douglas et al., 1980; Schröder, 1988). In the present study fragile species, including *Lagenammina* spp., *Nodellum*-like sp., *Saccammina* spp. and *Reophax* spp., as well as species with more robust tests (e.g. *A. glomerata*), all of which have organic cement, were found mainly in the living fauna (Tables 2, 4), suggesting that significant post-mortem destruction took place. These taxa are known from previous studies to be substantial and persistent components of the 'live' PAP foraminiferal fauna (Gooday, 1996; Gooday et al., 2010), making it very unlikely that the live vs dead differences reflect recently established populations. Their abundance in the live assemblage contrasts with agglutinated species with calcitic cement, notably *Eggerella bradyi*, which were mainly found in the dead assemblages (Table 3). This is consistent with previous evidence that the use of calcitic cement by agglutinating foraminifera enhances the preservation potential of their tests (Bender, 1989; de Stigter et al., 1999; Harloff and Mackensen, 1997).

Since the PAP-SO area is located above the CCD but close to or within the lysocline (Biscaye et al., 1976; Rutgers van der Loeff and Lavaleye, 1986), dissolution could have affected some calcareous tests (Berger, 1968, 1970), including those of miliolids, a group that is particularly sensitive to dissolution (Douglas, 1983; Jorissen and Wittling, 1999). Typical visual indicators of carbonate dissolution are etching of the wall surface, test breakage, and the translucent or opaque appearance of hyaline test walls that are normally transparent (Murray, 1967; Murray and Wright, 1970). Corliss and Honjo (1981) found a good statistical correlation between the proportion of broken benthic foraminiferal tests and bottom-water carbonate undersaturation. Our samples yielded numerous miliolid fragments (constituting 32% of all picked fragments; Appendix A.1), mostly belonging to the genera

Pyrgo and *Quinqueloculina,* which may have resulted from dissolution. Gooday and Alve (2001) considered carbonate dissolution a potentially important environmental factor in this area. However, the consistently low L/D ratios of most major calcareous species (Table 5) as well as the transparent walls of most hyaline species, indicates that this process is unlikely to have been particularly important in the present case.

4.3.2 Transport of tests

The transport of dead foraminifera tests in the deep sea can be caused by bottom currents (bed- and suspended load), turbidity currents and submarine slides (Murray, 1976; Murray, 2006). Living foraminifera are less likely to be transported, at least by bottom currents, since they can utilise their reticulopodial network to anchor among sediment particles (Goldstein, 1999).

Visual inspection of the sediment cores from which our samples were taken provides information on the sedimentary processes operating at each site (Ruhl, 2012; Durden et al., 2015, Appendix C.1). The P3 core, which was collected adjacent to a large, (~900 m high) steep hill, had a uniform light greyish colour, and was poorly consolidated for its full length (c. 40 cm) – common characteristics for cores collected in that area, but very distinct from other locations on the Porcupine Abyssal Plain (Appendix C.1; Ruhl, 2013). It is possible that run out of slope failures from the large, steep-sided hill could have transported some benthic foraminiferal tests to this site. In a more detailed comparison of live benthic foraminiferal assemblages from hill and plain sites in the PAP-SO area (Stefanoudis et al., 2016a), including the data used in this study, we found that site P3 was more similar to hill samples (especially H1) than site P4, which is located >10 km away from the nearest hill (Fig. 1). The core from P4, in common with most cores from the Porcupine Abyssal Plain, had a dark band ~25 cm below the sediment surface (Appendix C.1). This is interpreted as a turbidite deposit (Thomson et al., 1987) and/or chemical oxidation front (Wallace et al., 1988), potentially dating to the glacial/Holocene transition. Cores from the hills (H1, H4) were more variable (Appendix C.1); in general, they were light brown in colour with the lower quarter to a third being somewhat darker but with no evidence of a turbidite layer.

The abyssal hills in the PAP-SO area have coarser (greater proportion of particles >63 μm) sediments than the plain (Durden et al., 2015; Stefanoudis et al., 2016b; Turnewitsch et al., 2004, 2013, 2015), a winnowing effect of the stronger bottom currents above the hills that preferentially remove fine particles and redeposit them on the adjacent plain. It is possible that some dead tests could be transported in this way. This might

contribute to the enhanced homogeneity between dead foraminiferal faunas (Fig. 3), although current-induced transport is thought to mainly influence tests <150 µm (Jorissen and Wittling, 1999; Murray, 2006).

4.3.3 Predation

Etching and boring by fungi, protozoans and metazoan meiofauna and macrofauna can lead to the weakening or complete destruction of foraminiferal tests (Culver and Lipps, 2003; Hickman and Lipps, 1983; Lipps, 1983; Mageau and Walker, 1976). In our samples, a total of 60 dead tests (42 *Pyrgo*, 10 *Quinqueloculina*, 7 *Melonis*, 1 *Eggerella*) displayed rather irregular punctures, reminiscent of holes observed in other benthic foraminiferal tests that were suggested to be a result of nematode predation (Sliter, 1971; Douglas, 1983; Fig. 1 therein). However, some of the etching we observed could be the result of carbonate dissolution (see section 4.2.1). For example, Bé et al. (1975) and Hecht et al. (1975) illustrated similar-shaped holes in planktonic foraminiferal tests caused by carbonate undersaturation in a series of dissolution experiments. Freiwald (1995) has also reported etching on *C. lobatulus* tests, presumed to result from bacterially-induced carbonate degradation. In any case, borings and or signs of etching were rare, occurring in only ~0.01% of all dead specimens of the present study. We conclude that predation and dissolution were unlikely to have had a major influence on the composition of the observed dead assemblage.

4.4. The influence of population dynamics on the composition of dead assemblages

Living foraminiferal faunas vary throughout the year in response to inputs of organic matter (phytodetritus) from primary production that may trigger reproductive events (e.g. Gooday, 1988; Kitazato et al., 2000; Gooday and Hughes, 2002; Fontanier et al., 2003; Smart, 2008). After such events, certain species may show a sudden increase in population size (Gooday, 1993) or a change in their microhabitat occupancy (Jorissen et al., 1995; Ohga and Kitazato, 1997), leading to considerable differences between the living and time-averaged dead assemblages. Our samples were collected on 5–22 August 2011, after the spring phytoplankton bloom and the subsequent peak in particulate organic carbon flux that occurred in June 2011 (Frigstad et al., 2015). Phytodetritus was visible on the surface of some of our studied cores, mainly from P3 and less so from H4 (Appendix C.2–C.3).

Epistominella exigua, an opportunistic species that reproduces rapidly in response to pulsed fluxes of phytodetritus, was common in both the live and dead assemblages (Tables

2–3) with counts being substantially higher in the latter. However, considering only the potential fossil fauna, its relative abundance was consistently higher in the live assemblage ($L_{\%}/D_{\%}>1$, Table 5). This may indicate that we captured part of the reproductive period of this highly opportunistic species. The high abundance of *E. exigua* in the dead assemblage (Table 3), suggests that the 'phytodetrital signal' will also be expressed in the fossil fauna (Smart, 2008). *Alabaminella weddellensis,* another rotaliid species often associated with phytodetritus deposits in the PAP-SO area (Gooday, 1988, 1993; Smart and Gooday, 1997), was relatively scarce in our samples (Appendix A.3). *Epistominella exigua* and *A. weddellensis* appear to have distinct ecologies, the former being associated with regions of high seasonality, the latter with areas of high productivity (Fariduddin and Loubere, 1997; Hayward et al., 2002; Loubere, 1996; Sun et al., 2006). However, the relative scarcity of this small species probably also reflects the fact that we analysed the relatively coarse 150-µm fraction in which *A. weddellensis* is poorly represented because of its small size.

Like those of *E. exigua,* the $L_{\%}/D_{\%}$ ratios for *Cibicidoides wuellerstorfi* and *Globocassidulina subglobosa* were consistently >1. Jorissen and Wittling (1999) suggested that *C. wuellerstorfi* might be positively related to phytodetritus, and Gooday (1988) reports that this species inhabits phytodetrital aggregates, but a link with seasonal food input was not confirmed by other studies (Corliss et al., 2006; Smart, 2008). In the PAP area, *G. subglobosa* has also been found embedded within phytodetritus aggregates (Gooday, 1988, 1993, 1996), while in the Southern Ocean it has been shown to feed selectively on phytodetritus (Suhr et al., 2003; Suhr and Pond, 2006). However, Sun et al. (2006) again reported a negative correlation between *G. subglobosa* and seasonality in primary production. Our results provide some evidence that these two species (*C. wuellerstorfi*, *G. subglobosa*) behave in a manner similar to that of *E. exigua* by rapidly reproducing once food becomes available. However, the magnitude of their response is much less evident, at least for the size fraction >150 µm, as evidenced by their considerably lower contribution to the living and dead assemblages in comparison to *E. exigua* (Tables 2–3).

The case of *Sphaeroidina bulloides* also warrants attention. $L_{\%}/D_{\%}$ ratios showed that it was relatively more abundant in the live assemblages of two of the three samples in which it occurred, the exception being H4 (Table 5). The density of this species in the dead assemblage at site H4 was at least an order of magnitude higher than at other PAP-SO sites (Table 3). Topographic features, such as the abyssal hill on which H4 was located, are characterised by stronger currents, potentially enhanced organic matter supply, as well as by coarser sediments. These factors could influence the composition of modern

foraminiferal faunas (Stefanoudis et al., 2016a). Interestingly, small patches of phytodetritus were present on the surface of the sediment core from H4 (Appendix C.3). *Sphaeroidina bulloides* has been suggested to be positively associated with high organic carbon fluxes (Altenbach et al., 2003), which might explain its unusually high densities at H4. Linke and Lutze (1993) found that *S. bulloides* rapidly changed its habit from epifaunal to infaunal depending on food supply and environmental conditions. The infaunal tests were often enclosed within agglutinated mud coatings ('cysts'), a behaviour commonly observed among live specimens in our study area (Stefanoudis and Gooday, 2016), Additional information on the ecology of this species would be valuable in interpreting its relative abundance in the living and dead fractions in the PAP-SO area.

Miliolid species (*Pyrgo murrhina*, *Quinqueloculina auberiana*, *Quniqueloculina* sp. 2, *Spirosigmoilina tenuis*) had positive $L_{\%}/D_{\%}$ ratios at hill locations (H1, H4), but were absent from the living fauna in samples from the plain (Table 5). Moreover, their densities in the living and dead fractions were generally higher on the hills (Appendix A.3). A previous study at the PAP-SO central site found that an unnamed *Quinqueloculina* species, probably identical to *Quinqueloculina* sp. 2 of the present study, moved towards the sediment surface when food availability was high and retreated back into deeper layers once food resources had been exhausted (Gooday et al., 2010). As previously indicated, food supply is probably higher on the hills (e.g. Morris et al., 2016), which may help to explain the larger populations of *Quinqueloculina* spp. there in comparison to the plain.

Bolivina spathulata was absent from the living and dead fractions of all samples except for P3. Here, it was 10 times more abundant in absolute terms (i.e. L_N/D_N values) in the live than in the dead assemblage (Table 5), although the actual numbers of specimens (10 live and 1 dead) were fairly low (Appendix A.3). *Bolivina* species are generally considered to be indicative of low oxygen, high productivity environments (Altenbach et al., 1999; Jorissen et al., 1992; Schmiedl et al., 1997), typically at bathyal depths. In the southern Adriatic Sea, de Stigter et al. (1998) found *B. spathulata* penetrating deep into the sediment and efficiently exploiting the subsurface food resources available there, mainly degraded organic material. Nevertheless, in the PAP-SO area this species occurred in the upper sediment layer, suggesting that it is also able to exploit fresh organic material in well-oxygenated, abyssal settings. This is consistent with the fact that the surface of the core from the P3 site had a visible phytodetritus layer (Appendix C.2). It appears that *B. spathulata* was able to flourish in a local patch of fresh organic matter. The opportunistic species *Epistominella exigua* was also common in this sample (Table 2).

4.5. Concluding remarks

Our results from the PAP-SO area indicate that the transition from live to dead benthic foraminiferal assemblages involves a dramatic loss of delicate agglutinated and organic-walled tests (e.g. *Lagenammina*, *Nodellum*, *Reophax*), and to a lesser extent of some fragile calcareous tests (mostly miliolids), the latter possibly the result of dissolution. Other processes, such as hydrodynamically induced transport of tests and predation by metazoans, are unlikely to have significantly modified the dead assemblages. Relatively high live to dead ratios in some samples suggest that a few species (e.g. *Bolivina spathulata*, *Cibicidoides wuellerstorfi*, *Epistominella exigua*, *Globocassidulina subglobosa*) may have responded to recent food deposition with rapid reproduction.

In the PAP-SO area it seems that, for foraminifera in the >150 μm fraction of surficial sediments, taphonomic rather than life processes are largely responsible for the composition of dead assemblages. The magnitude of these processes is comparable between samples from the plain and the hills, suggesting that the preservation potential of benthic foraminifera is not markedly affected by local topography (Fig. 4). Particularly notable is the fact that the composition of the dead assemblages is quite similar between samples from the hills and the plain, despite the fact that live faunas are more distinct between these two settings, particularly between H4 and all other samples (Figs. 3–4; Stefanoudis et al., 2016a). This suggests that it may not be possible to differentiate between foraminiferal faunas originating from (modestly) topographically contrasting sites in the fossil record, despite potentially substantial differences in organic matter supply between such sites (Durden et al., 2015; Morris et al., 2016).

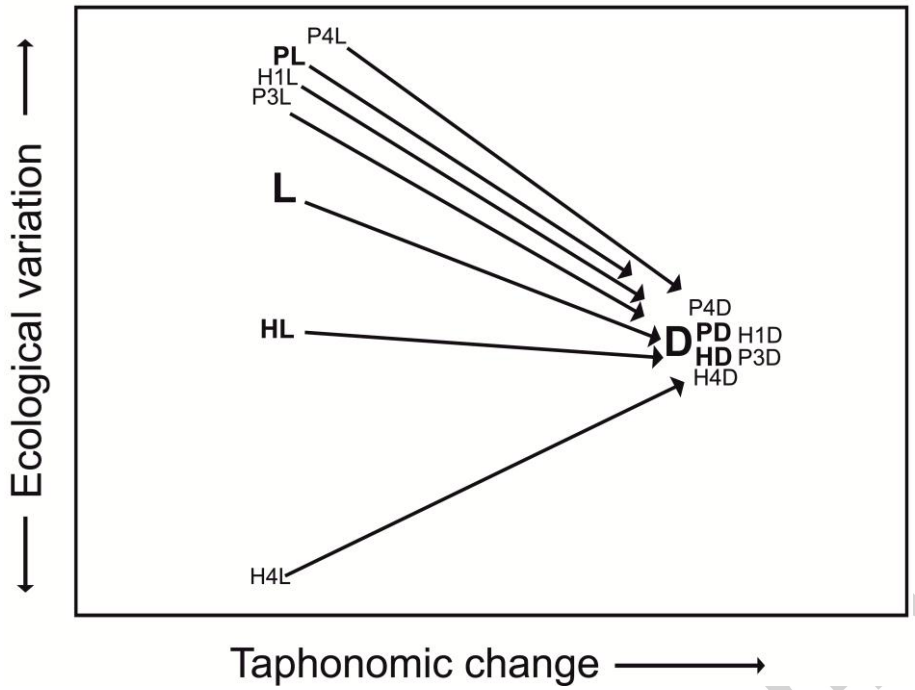

Fig. 4. 2-d Non-metric multi-dimensional scaling ordination plots of live (L) and dead (D) foraminiferal assemblage composition in samples from the PAP-SO area, based on Bray-Curtis dissimilarity of log (x+1) transformed relative abundance data (entire fauna; all species). Note compositional shift related to topographic setting (hills, H; plain, P), and striking difference between live and dead assemblages. (HL, hills live [H1L+H4L]; PL, plain live [P3L+P4L]), HD, hills dead [H1D+H4D]; PD, plain dead [P3D+P4D]; L, live [HL+PL]; D, dead [HD+PD]).

Copyright of interest of statement

The authors declare no actual or potential conflicts of interest.

Author contributions statement

Data collection was conducted by AJG and BJB. PVS analysed the sediment samples, identified and photographed the foraminifera described in this paper. AJG assisted with the identification and taxonomy of the foraminifera. PVS analysed the results. AJG and BJB provided advice on the data analysis and interpretation. PVS prepared the main manuscript text, tables and figures. All authors provided comments and reviewed the manuscript.

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Highlights

- We compared ‘live’ (stained) and dead benthic foraminiferal faunas in the NE Atlantic
- During transition from live to dead faunas there was a dramatic loss of delicate forms
- Other factors (e.g. dissolution, predation) had a minor impact on the composition of dead faunas

- L/D ratios indicated that some species responded to recent food input.
- Unlike ‘live’, composition of dead assemblages was not influenced by seafloor topography
- Differentiating fossil faunas from contrasting topographies might not be possible