

1 **Diversity and spatial patterns of foraminiferal assemblages in the eastern Clarion–**
2 **Clipperton Zone (abyssal eastern equatorial Pacific)**

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24 **Abstract**

25 Foraminifera are a major component of the abyssal meiofauna in parts of the eastern Pacific
26 Clarion-Clipperton Zone (CCZ) licensed by the International Seabed Authority for polymetallic
27 nodule exploration. We analysed the diversity and distribution of stained ('live') and unstained
28 (dead) assemblages (0-1 cm layer, >150- μ m sieve fraction) in megacorer samples from 11 sites
29 (water depths 4051 - 4235 m) within three 30 x 30 km 'strata' in the United Kingdom 1 (UK1
30 Strata A and B; 5 and 3 samples, respectively) and Ocean Minerals Singapore (3 samples)
31 license areas and separated by distances of up to 28 km within a stratum and 224 km between
32 strata. Foraminiferal assemblage density, diversity and composition at the higher
33 taxon/morphogroup level were largely consistent between samples. Stained assemblages were
34 dominated (>86%) by single-chambered monothalamids, mainly spheres, tubes, komokiaceans
35 and forms that are difficult to categorise morphologically. Hormosinaceans were the most
36 common multichambered group (~10%), while calcareous taxa (mainly rotaliids) represented
37 only ~3.5% of stained tests. Dead foraminifera were more evenly distributed between
38 monothalamids (56%) and multichambered taxa (44%). Almost all test fragments were
39 monothalamids, mainly tubes. Morphospecies were added regularly with each new sample and
40 totalled 580 (stained + dead, complete + fragments), of which 159 occurred in all three strata,
41 222 were shared between UK1 Strata A and B, 209 between UK1A and the OMS Stratum, and
42 193 between UK1B and the OMS Stratum. Individual strata yielded 310 – 411 and individual
43 samples 132 – 228 putative morphospecies. The majority (550) of the 580 species were
44 represented by intact tests of which 462 included at least some that were stained. Most of the
45 stained (~80%) and stained + dead (~75%) species were monothalamids, almost all of them
46 undescribed. Many species were rare; 146 of the 550 species with complete tests (stained +
47 dead) were singletons and 53 doubletons. MDS plots suggest that assemblage composition falls
48 within 95% confidence limits across the 11 samples, although with a weak grouping of UK1A
49 samples. A distance-decay plot revealed only a small degree of species turnover between the 3
50 strata. However, Morisita's index suggested that most individual species represented by ≥ 10
51 complete tests had aggregated distributions. We conclude that the foraminiferal assemblages at
52 our eastern CCZ sites are highly diverse, dominated by monothalamids, and display a fairly high
53 degree of uniformity across our study site, but a patchy distribution at the level of individual
54 morphospecies.

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56 **Keywords: Benthic foraminifera; monothalamids; seabed mining; polymetallic nodules;**
57 **abyssal biodiversity; biogeography**

59 1. Introduction

60
61 Foraminifera are a major component of benthic communities in many marine habitats, from
62 intertidal to hadal settings. Their rich fossil record, and importance as indicators of past ocean
63 environments, has led to a very extensive body of literature on these testate (shell-bearing)
64 protists, much of it directed towards practical applications in palaeoceanography, palaeoecology,
65 and biostratigraphy (Murray, 2006; Jorissen et al., 2007; Jones, 2014). As a result, many of the
66 formally described species have fairly robust, multichambered tests, usually composed of
67 secreted calcium carbonate and with a good fossilization potential (Jones, 1994; Murray, 2007;
68 Holbourn et al. 2013). At the same time, there has been an increasing awareness among
69 biologists that foraminifera play an important ecological role in marine ecosystems, including
70 deep-sea settings where they sometimes represent a large proportion of the meiofauna,
71 macrofauna and megafauna (Tendal and Hessler, 1977; Bernstein et al., 1978; Snider et al.,
72 1984; Gooday et al., 1992; Gooday, 2019; Alt et al., 2019). As the organic-matter supply to the
73 seafloor declines with increasing water depth, the proportion of calcareous foraminifera
74 decreases and forms with agglutinated tests become more important (e.g., Kurbjeweit et al.,
75 2000; Gooday, 2003; Cornelius and Gooday, 2004; Phipps et al., 2012). In abyssal settings,
76 agglutinated species predominate and below the carbonate compensation depth (CCD),
77 calcareous foraminifera largely (although not entirely) disappear (Saidova, 1966, 1981). In these
78 regions, the foraminiferal assemblages are often dominated by single-chambered taxa
79 (monothalamids). Many of these ‘primitive’ foraminifera have delicate agglutinated tests with
80 very little fossilization potential and, as a result, they are poorly known and largely undescribed
81 (e.g., Nozawa et al., 2006; Kamenskaya et al., 2012; Goineau and Gooday, 2017).

82 Monothalamids, or putative monothalamids, are a dominant component of the meiofauna
83 (Nozawa et al., 2006; Gooday and Goineau, 2019), macrofauna (Tendal and Hessler,
84 1977; Bernstein et al., 1978) and megafauna (Amon et al., 2016; Gooday et al., 2017). in the
85 Clarion Clipperton Zone (CCZ) and other areas of the abyssal Pacific. The CCZ, which occupies
86 much of the equatorial Pacific, hosts extensive sea-floor deposits of polymetallic (‘manganese’)
87 nodules that have considerable potential commercial value (Hein et al., 2013), although their
88 exploitation would involve risks to seabed-dwelling fauna, including foraminifera, requiring
89 detailed monitoring and protection strategies (Wedding et al., 2013, 2015; Levin et al., 2016;
90 Jones et al., 2017; Miller et al., 2018). This vast region lies outside national jurisdictions, and the
91 exploitation of resources within it are controlled by the International Seabed Authority (ISA), a
92 UN body that enters into contracts for exploration and prospecting in areas of ~75,000 sq km
93 with companies and other entities that are interested in the seabed mining of nodules and are
94 sponsored by states that are party to the Law of the Sea Convention (Lodge et al., 2014; Lodge
95 and Verlaan, 2018). We studied modern foraminifera in two such areas located in the eastern
96 part of the CCZ: the United Kingdom 1 area (contractor UK Seabed Resources Ltd; UKSRL),
97 and the Ocean Minerals Singapore area (OMS, contractor of the same name). This work formed
98 part of the ABYSSal baseLINE (ABYSSLINE) project, funded by UKSRL, the purpose of
99 which was to conduct a baseline survey of benthic faunas in these two areas, as required by the
100 ISA under the terms of the exploration contracts.

101 In an earlier paper (Goineau and Gooday 2017), we presented an overview of benthic
102 foraminiferal assemblages based on a morphological analysis of specimens picked from the 0-1
103 cm layer (>150 µm fraction) of five megacorer samples collected during the AB01 cruise in the
104 UK1 area. These samples were dominated by monothalamids, many of them with tubular or
105 spherical tests. A total of 416 morphospecies was recognized during this earlier study, the vast
106 majority of them undescribed. Here, we build on this previous work by analyzing 6 additional
107 samples, 3 from another part of the UK1 area and 3 from the OMS area. As in our earlier study,
108 we distinguish between complete and fragmented tests as well as between dead specimens and

109 those that were considered to have been alive at the time of collection. Our goals are to 1)
110 evaluate foraminiferal diversity across the three studied strata, and 2) determine the coherence of
111 assemblages within a single stratum and within a license area.

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114 **2. Material and methods**

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116 *2.1. Study area and environmental data*

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118 Two cruises conducted within the ABYSSLINE framework, AB01 (2013) and AB02 (2015),
119 sampled within 30 x 30 km areas (so-called 'strata', a term that refers here to areas of seafloor
120 and should not be confused with geological strata) in the UK1 (Stratum A and Stratum B) and
121 OMS areas (Fig. 1). A total of 11 sites was sampled, 5 in UK1 Stratum A (UK1A), 3 in UK1
122 Stratum B (UK1B), and 3 in the Ocean Minerals Singapore (OMS) Stratum (Fig. 1, Table 1;
123 Supplementary Fig. 1). Distances between pairs of sites within a particular stratum were as
124 follows: UK1A, 7.2 – 28.3 km (mean 15.8 km); UK1B, 7.9 – 19.9 km (mean 14.6 km); OMS,
125 9.8 – 19.9 km (mean 15.9 km). Distances between sites in different strata were as follows:
126 UK1A to UK1B, 131.2 – 199.7 km (mean 148.2 km); UK1A to OMS, 197.6 – 223.8 km (mean
127 207.6 km); UK1B to OMS, 72.5 – 89.6 km (mean 82.4 km).

128 Glover et al. (2016) provide a general account of the ABYSSLINE project and study
129 area, while Amon et al. (2016) and Goineau and Gooday (2017) summarise available
130 environmental information obtained for UK1A during the AB01 cruise. Polymetallic nodules
131 were common at all sites. For additional data on sediment granulometry, porosity and sorting,
132 total organic carbon and total nitrogen content from the Global Sea mineral Resources (GSR)
133 contract area, located to the west of the UK1 and OMS areas and in somewhat deeper water
134 (~4500 m), see Pape et al. (2017) and De Smet (2017).

135

136 *2.2. Sample collection and processing*

137

138 Our shipboard and laboratory methods closely followed those described by Goineau and Gooday
139 (2017). Samples were obtained using an OSNIL-type megacorer, equipped with 12 coring tubes
140 of 10 cm internal diameter. As soon as possible after collection cores were extruded and sliced
141 into 0.5-cm-thick layers down to 2 cm depth, and thereafter into 1-cm-thick layers down to 10
142 cm depth. Only the upper two layers (i.e., 0-1 cm) were analysed for the present study.

143 In the laboratory, each complete sediment slice (0-0.5 cm and 0.5-1.0 cm) was allowed to
144 settle for 2 days in a graduated cylinder in order to measure the volume of sediment (very little
145 further volume reduction occurred after this period) before being split into 1/8th fractions using a
146 wet splitter (Jensen 1982). After splitting, the volume of the splits to be sorted (either 3 or 4 of
147 the 8 splits) was measured in the same way. This procedure was introduced because the volume
148 of the intact slices varied between cores and between the upper and lower sediment layers, while
149 determining the volume of the splits allowed the accuracy of the splitting to be checked. Sample
150 splits were sieved on 300 and 150 µm screens and the sieves with their sediment residues
151 immersed in Rose Bengal solution overnight before being hand-sorted for foraminifera under a
152 stereo-microscope.

153

154 All stained ('live') as well as dead specimens, both complete and fragmentary, were
155 removed from the sample residues, usually with a pipette. Distinguishing between foraminifera
156 that were alive at the time of collection and dead (empty) shells is an essential requirement in
157 ecological studies of foraminiferal assemblages (Murray, 2000). Since the 1950s, the standard
158 method has been to stain samples with a solution of Rose Bengal (Walton 1955). This protein
stain colours cytoplasm red, making foraminiferal shells that contain a cell body stand out from

159 those that do not. When used with care, it yields accurate results (Murray and Bowser, 2000).
 160 We therefore stained the sieve residues by immersing them overnight in Rose Bengal solution,
 161 followed by gentle washing to remove excess stain. To avoid false positives, we also routinely
 162 placed stained specimens in glycerol (which renders the test more transparent) in a cavity slide
 163 and examined them at a high magnification under a compound microscope to confirm that the
 164 stained material was cytoplasm. In order to keep track of the multitude of species, all specimens
 165 were photographed and selected images of each species copied onto PowerPoint slides. These
 166 constituted a working catalogue that we constantly referred to and updated as an aid to
 167 organising specimens into putative morphospecies.

168

169 2.3. Statistical analyses and diversity estimation

170 Statistical analyses and diversity estimations were calculated using Excel and the open source
 171 software EstimateS (Version 9). Using complete specimens (either live or live plus dead
 172 combined), we calculated the Fisher alpha (α), Shannon (H' , using natural logarithm) and
 173 Evenness (E) indices, and generated *individual-based* rarefaction curves for each sample
 174 (Colwell et al., 2012). The curves did not reach an asymptote and therefore we extrapolated them
 175 up to 1,500 individuals (Colwell et al., 2012), and calculated the Chao1 to estimate the expected
 176 total number of species for each sample.

177 We produced *sample-based* rarefaction curves based on complete stained and dead
 178 specimens combined. This method estimates the expected number of species in t pooled samples
 179 (Colwell et al., 2012). Since the curve derived from the 11 samples had not reached an
 180 asymptote, we extrapolated it to 30 samples (Colwell et al., 2012). Diversity estimators based on
 181 the pooled data were then calculated in order to assess the expected total number of species.
 182 Because our 11 samples were of different sizes (3 complete samples, 8 split samples), we
 183 followed the recommendations of Hortal et al. (2006) and calculated the Chao1, Abundance
 184 Coverage-based Estimator (ACE), Jackknife 1 and Jackknife 2. The abundance-based estimators
 185 Chao1 and ACE were calculated using the number of complete specimens (stained and dead
 186 combined), while Jackknife 1 and 2, which are incidence-based estimators, were calculated based
 187 on complete specimens and fragments (stained and dead combined).

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190 3. Results

191

192 The raw data (species-level counts of stained and dead tests and test fragments) for this study are
 193 summarised in Supplementary Table S1 and the most abundant species in different categories in
 194 Supplementary Table S2). The more common morphospecies in our samples are briefly
 195 described and illustrated by Goineau and Gooday (2017; Figures 4, 5 and supplementary
 196 material therein) and in Fig. 2 and the supplementary material of the present paper (Taxonomic
 197 Appendix and Figs S9-S12).

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200 3.1. Abundance

201

202 The total numbers of complete stained foraminiferal tests picked from the 0–1 cm layer of 5
 203 samples from UK1A ranged from 514 to 966 (mean 676), compared with 302 to 588 (mean 467)
 204 in 3 samples from UK1B, and 222 to 877 (mean 516) in 3 samples from the Ocean Minerals
 205 Singapore (OMS) Stratum (Table 2). These numbers corresponded to densities of 71–146
 206 indiv.10 cm⁻² (UK1A), 68–165 indiv.10 cm⁻² (UK1B) and 30–171 indiv.10 cm⁻² (OMS
 207 Stratum). The numbers of stained fragments were variable but consistently lower than those of

208 complete stained individuals, ranging from 143 to 763 per sample in UK1A, compared with 103
 209 to 334 in UK1B, and 83 to 485 in the OMS Stratum (Table 2). The corresponding densities were
 210 22–97 frag.10 cm⁻² (UK1A), 29–76 frag.10 cm⁻² (UK1B) and 11–94 frag.10 cm⁻² (OMS
 211 Stratum).

212 The numbers and corresponding densities of complete dead tests were consistently lower,
 213 by a factor of 1.1 to 4.7 (usually between 2 and 4), compared to the stained tests (Table 2). With
 214 two exceptions (MC20, MC25), numbers and densities of dead fragments were also lower, in
 215 some cases much lower (MC02), than for the stained assemblage. However, the numbers varied
 216 considerably, particularly in the case of the OMS Stratum, where densities were 7, 46 and 69
 217 dead fragments per 10 cm² in the three samples.

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219 3.2. *Main taxa and morphological groups*

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221 The overall composition of the stained assemblage (complete tests) was similar at the higher
 222 taxon/group level in all eleven samples and across all 3 strata (Table 3). There are no statistically
 223 significant differences in their relative abundances in UK1A (5 samples) compared to UK1B
 224 plus OMS Strata combined (6 samples), except in the case of the *Nodellum*-like group and the
 225 saccamminids, both of which are significantly more abundant in UK1A in terms of absolute and
 226 percentage abundance ($p < 0.01$, t test). Monothalamids (89.1% of complete stained tests overall)
 227 were the main component with the most abundant groups in all samples being spheres (19.3%),
 228 tubular/spindle-like forms (19.1%), and monothalamids that are difficult to classify
 229 morphologically ('unclassified monothalamids' 22.7%). Komokiaceans (particularly
 230 baculellids, 6.8%) and komoki-like forms (4.5%) were also fairly common. Among the
 231 multichambered forms the agglutinated hormosinaceans (6.8%) were consistently ranked top
 232 with rotaliids (2.0%) being the most common calcareous taxon.

233 The dead assemblage (complete tests) showed no statistically significant differences in
 234 the relative abundances of the main groups between the UK1A and the UK1B plus OMS Strata
 235 combined. The distribution of complete dead tests was more even between the monothalamid
 236 (55.8%) and multichambered taxa (44.2%) than it was in the case of stained individuals (Table
 237 4). Also, in contrast to the stained assemblage, the multichambered hormosinaceans (19.9%)
 238 were the most abundant constituent in all strata, with 'other textulariids' (10.5%), rotaliids
 239 (5.54%) and trochamminids (4.49%) being more abundant, both absolutely and relatively, than
 240 in the stained assemblage.

241 Monothalamids represented almost all (96% in 3 strata combined) of the stained and
 242 dead fragments combined (Supplementary Tables S3, S4). The only exception was OMS sample
 243 MC20, where they accounted for less than three-quarters (73.8%) of fragments. Tubular
 244 foraminifera were particularly prone to fragmentation, making up almost half (47.8%) of stained
 245 + dead fragments in the combined dataset. The other groups common as fragments were the
 246 komokiacean families Baculellidae (14.3% overall) and Komokiidae (12.1%) and unclassified
 247 monothalamids (11.3%).

248

249 3.3 *Species richness, alpha species diversity and estimated species diversity*

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251 Putative morphospecies were added regularly with each new sample. The rate at which they
 252 were added declined progressively, although the upward trend in the cumulative number of
 253 species was maintained (Fig. 3). The grand total number of species was 580, of which 546 were
 254 represented by complete tests (stained, dead or both), including 10 gromiids (Table 5). Plots of
 255 species ranked by abundance reveal a relatively small number of abundant species and a long tail
 256 of rare species, a pattern evident in the case of stained, dead, and stained + dead specimens
 257 (Supplementary Figs S2A, S3A, S4A, respectively). More than a quarter (146 = 26.7%) of

258 species with complete tests (either stained or dead) were singletons and 53 (9.71%) doubletons
 259 (Table 6).

260 The total number of species present in particular strata was 411 in UK1A (5 samples),
 261 324 in UK1B (3 samples) and 310 in the OMS Stratum (3 samples) (Table 5), while the total
 262 number in individual samples ranged from 132 to 228 (Supplementary Figs S5). The majority of
 263 species (462 = 79.7%) included at least some complete stained individuals, although less than
 264 half (224 = 45.5%) of that number were confined to the stained assemblages. Fewer species (264
 265 = 45.5%) were represented by some dead tests and fewer still by stained (130 = 22.4%) and dead
 266 (113 = 19.5%) fragments, with the number confined to one of these categories being
 267 correspondingly lower (74, 12, 14, respectively). Individual samples yielded 76 - 186 stained
 268 species and 106 - 224 stained + dead species. The majority (79.4% overall) of the stained species
 269 and a somewhat lower proportion (74.6% overall) of the stained + dead species were
 270 monothalamids (Table 5). The most speciose multichambered taxon was the hormosinaceans
 271 (overall, 27.4% of multichambered species and 6.4% of all species); the most speciose
 272 monothalamids were the spheres, tubes and unclassified taxa (together, 58% of all monothalamid
 273 species and 43% of all species).

274 Values of rarefied species richness [$E(S_{100})$] and diversity metrics were generally similar
 275 across the three strata (Table 6). The UK1A samples tended to have slightly higher $E(S_{100})$
 276 values than samples from UK1B and the OMS Stratum. Similarly, diversity indices (H' and
 277 Fisher α) were somewhat higher overall in UK1A than the other two areas. None of the
 278 individual-based rarefaction curves based on stained and stained + dead tests reached an
 279 asymptote for any of our 11 samples (Supplementary Fig. S6). The extrapolated curves of
 280 species numbers were tending to level off for samples MC04, MC09, MC13 and MC20 at 750–
 281 1,500 individuals, but still increasing at >1,500 individuals for the 7 remaining samples. The
 282 sample-based rarefaction curve for all 11 samples extrapolated to 30 samples and based on the
 283 entire assemblage (i.e. complete live and dead specimens combined) showed signs of levelling
 284 off after about 20 samples (Supplementary Fig. S7), suggesting that 20 samples might have
 285 yielded ~90% of species. Estimates for the actual diversities, based on Chao 1, ranged from 111
 286 ± 16 (MC13, UK1B) to 257 ± 26 (MC07, UK1A) for the stained assemblage, and 68 ± 15 to 183
 287 ± 51 for the dead assemblage (Table 6). They followed the same patterns as $E(S_{100})$, H' and
 288 Fisher α , being generally highest in UK1A and lowest in the OMS Stratum. Abundance-based
 289 estimators ACE and Chao1 based on all samples from a single stratum combined (i.e. combined
 290 numbers of complete stained and dead specimens) estimated totals of, respectively, 483 and
 291 501 ± 28 species in UK1A, 489 and 516 ± 51 in UK1B, and 358 and 356 ± 21 in OMS (Fig. 4).
 292 The incidence-based estimators Jackknife 1 and 2, which are based on the occurrence of complete
 293 specimens and fragments (live and dead combined), estimated totals of, respectively, 638 and
 294 565 ± 20 species in UK1A, 521 and 463 ± 33 in UK1B, and 471 and 427 ± 17 species in OMS.
 295 Combined data from all 11 samples yielded estimates ranging from 680 (ACE) to 877 species
 296 (Jackknife 2) (Fig. 4).

297 298 3.4. Turnover and distribution of species

299
300 MDS plots based on the 'entire' assemblage (i.e., all species including monothalamids)
 301 represented by a) complete stained specimens, b) complete stained plus dead specimens, and c)
 302 all specimens (stained plus dead, complete plus fragments) reveal some tendency for the samples
 303 to be grouped according to strata (Fig. 5, left-hand column). In particular, the 5 samples from
 304 UK1A form a loose grouping, whereas those from UK1B and the OMS Stratum tend to be more
 305 or less intermingled. On the other hand, this pattern is not evident when only multichambered
 306 taxa are considered (Fig. 5, right-hand column). Nevertheless, irrespective of the category
 307 (stained, dead etc), all 11 samples fall within a space defined by the 95% confidence level,

308 indicating that the species composition is statistically identical. Similarly, a ‘decay-distance’ plot
 309 of Bray-Curtis Similarity against distance between samples reveals minimal differences between
 310 the species composition of samples separated by increasing distances (Fig. 6). There are no
 311 significant differences between the Bray-Curtis Similarity of samples within strata (distances =
 312 7.2- 28.3 km; unfilled symbols in Fig. 6) and values based on the UK1B vs OMS and UK1A vs
 313 UK1B comparisons (filled triangles and circles). The only significant difference ($p < 0.05$) is
 314 between samples within strata and the UK1A vs OMS comparison (distances = 198 – 224 km;
 315 filled squares), and this becomes non-significant if the two highest Bray-Curtis values are
 316 removed. This suggests that the foraminiferal fauna in the upper 1-cm layer of the sediment
 317 (>150- μ m fraction) is fairly uniform across the three sampled strata.

318 Of the 580 morphospecies identified in the 11 samples, 159 occurred in all three strata,
 319 222 were shared between UK1A and B, 209 between UK1A and the OMS Stratum, and 193
 320 between UK1B and the OMS Stratum (Fig. 7). The numbers of species confined to particular
 321 strata were 139 (UK1A), 68 (UK1B) and 67 (OMS). Within individual strata, the numbers of
 322 species shared between pairs of samples was 65–117 out of a total of 411 (UK1A, 5 samples),
 323 65–80 out of a total of 324 (UK1B, 3 samples) and 66–92 out of a total of 310 (OMS, 3
 324 samples).

325 Disregarding singletons (Table 6), which by definition are confined to one sample, the
 326 majority (303 = ~78%) of the 388 species represented by complete specimens (stained + dead)
 327 were found in 5 or fewer samples, while only 11 (3.35%) occurred in all 11 samples and 10
 328 (2.58%) in 10 samples (Fig. 8). The stained and dead assemblages followed a similar pattern,
 329 although the proportion of more widely distributed species was somewhat lower, particularly for
 330 dead species confined to a few samples (Supplementary Fig. S8). The maximum number of
 331 specimens assigned to species confined to only 1-2 samples was also much lower ($n = 17$) in the
 332 dead assemblage (Supplementary Figs. S3B) than in the stained and stained + dead assemblages
 333 ($n = 282$ and 296 , respectively; Supplementary Figs. S2B, S4B).

334 In general, the abundant species were fairly widely distributed. Of the 20 species in the
 335 stained assemblage found across 9-11 sites (Supplementary Fig.S2C), 14 were ranked among the
 336 top 20 species in terms of abundance. However, species restricted to 1 or 2 samples also
 337 included a few that were abundant (Supplementary Fig. S2B). Notable among these was a
 338 distinctive radiolarian inhabitant (Fig. 2C,D) that was represented by 281 specimens in the
 339 MC25 sample and 1 specimen in the MC13 sample (both located in UK1B). Despite its
 340 restricted distribution, this was the second-ranked species overall. The pattern was similar for the
 341 dead (Supplementary Fig. S3C) and stained + dead (Supplementary Fig. S4C) assemblages,
 342 although the numbers of species found across 9-11 sites was lower (14) in the former and higher
 343 (34) in the latter compared to the 20 above-mentioned species in the stained assemblage.

344 At the species level, the Morisita index revealed that spatial patchiness was common
 345 among species represented by ≥ 10 complete tests (Table 7). With one exception, values of this
 346 metric for the 111 species represented by stained tests were between 1.2 and 11, corresponding
 347 to varying degrees of aggregation; the exceptional value was 0.9, indicating a regular
 348 distribution (McClain et al., 2011). In the stained + dead assemblage, 137 species yielded
 349 Morisita Index values ≥ 1.1 (aggregated), one had a value of 0.8 (regular) and four a value of 1.0,
 350 indicating a random distribution. In both cases, the majority of the species included in the
 351 analysis (70% of stained and 77% of stained + dead) fell within the range 1.1-3.9. The highest
 352 values were associated with species that were more or less confined to one sample.

353

354

355 4. Discussion

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357 4.1. Limitations of study

358
 359 The analysis of deep-sea foraminiferal assemblages, particularly the monothalamid component,
 360 poses problems that are less evident when analysing metazoan meiofauna and macrofauna.
 361 Notable among these are the criteria for regarding specimens as having been alive when
 362 collected and the fragmentation of delicate tests (Fig. 2E-G). We discuss these issues elsewhere
 363 (Goineau and Gooday, 2017; Supplementary Material in Gooday and Goineau, 2019). Further
 364 challenges are created by the high levels of diversity. During the present study we recognised
 365 well over 500 putative morphospecies, the majority of them undescribed monothalamids.
 366 Keeping track of this collection of largely unknown species, discriminating between them, and
 367 ensuring that they were identified as consistently as possible between samples proved a major
 368 task. Some species were easy to recognise but certain groups, notably the tubular and spindle-
 369 shaped stercomata-bearing forms, exhibited considerable morphological variability. Every
 370 specimen picked from the samples was photographed and photographs of all morphotypes were
 371 assembled on PowerPoint slides for easy comparison. In all cases of doubt, specimens were
 372 compared directly by placing them side by side in glycerol in open cavity slides and examining
 373 them under both a stereo- and a compound microscope. Where a specimen or fragment was too
 374 indistinct to be placed in a species or to be recognised as a previously unseen ('new') species, it
 375 was classified as indeterminate. The morphological variability displayed by some of the
 376 monothalamids is another likely source of error. Notable examples of morphologically variable
 377 morphospecies include Tube sp. 48 and Tube sp. 54, illustrated in Figures 4a-c and 4g-i,
 378 respectively, of Goineau and Gooday (2017). This problem meant that particular caution was
 379 used when recognising single specimens (singletons) as distinct species. Despite these
 380 precautions, the above-mentioned issues mean that it was impossible to exclude all errors.
 381 Nevertheless, we are confident that the large size of our dataset (Supplementary Table S1)
 382 ensures that the overall taxonomic composition of the assemblage, and the patterns of diversity
 383 and distribution revealed by this study, are robust.

384 There are some discrepancies between data presented for UK1A samples in Goineau and
 385 Gooday (2017, Tables 2-4) and those included in the present paper. These arose for several
 386 reasons. 1) The UK1A dataset used in the present study includes specimens >150 μm picked
 387 from an additional split of the MC11 sample as part of a study of finer sediment fractions
 388 (Gooday and Goineau, 2019). 2) The original UK1A dataset has been carefully revised in the
 389 light of new material obtained from the UK1B and OMS samples. For example, some forms that
 390 were originally regarded as separate species have been combined. 3) Some monothalamid
 391 species have been moved between major groupings. Overall, our new dataset is more
 392 conservative, as well as more extensive, than that of Goineau and Gooday (2017).

393

394 *4.2. Comparison with previous foraminiferal studies in the eastern Pacific*

395

396 Enge et al. (2011, Table 1 therein) reported 'live' foraminiferal densities ranging from 194 to
 397 364 (mean 279 ± 72) individuals 10 cm^{-2} in the 0-1 cm layer of 4 core samples from abyssal
 398 Station M on the Californian margin. These densities are substantially higher than those obtained
 399 from our samples (Table 2), a disparity partly attributable to the finer size fraction (>63- μm)
 400 analysed by Enge et al. (2011). The proportion of 'soft-shelled' monothalamids
 401 ('saccamminids') in this upper layer ranged from 39.6% to 53.0%, and reached higher values (up
 402 to 71%) in deeper sediment layers (2-3 cm). In a later study, Enge et al. (2012) analysed 6 core
 403 samples (including the 4 from their 2011 paper) collected at two sites in the region of Station M.
 404 They recorded a mean density of 365 stained individuals 10 cm^{-2} for the 0-1 cm layer at the new
 405 site (StnM09), where 29% and 30% of specimens (0-5 cm layer) were 'soft-shelled'
 406 monothalamids.

407 There are many similarities between the foraminiferal species in our samples and those

408 reported in several studies from nearby parts of the Clarion Clipperton Zone (CCZ).
 409 Kamenskaya et al. (2012) record a variety of macrofaunal-sized monothalamids from three
 410 samples (>500 and 250-500 μm fractions) collected at sites ($\sim 11^\circ 00' \text{N}$, $119^\circ 40' \text{W}$; 4,380-4,410
 411 m depth) in the Interoceanmetal Joint Organisation (IOM) license area in the eastern CCZ (Fig.
 412 1). Some of those illustrated in this paper (e.g., *Staphylion* sp.; some of the chain-like forms, and
 413 many of the tubes; Kamenskaya et al., 2012, Figures 2-4, therein) are present in our samples. In
 414 a preliminary survey of meiofaunal (>32 μm) foraminifera obtained at two other sites in the IOM
 415 area, Radziejewska et al. (2006) illustrated some common non-calcareous species, most of which
 416 are represented in the UK1 and Ocean Minerals Singapore (OMS) areas. A more extensive study
 417 of meiofaunal foraminifera was conducted by Nozawa et al. (2006) at the Kaplan East site
 418 ($\sim 15^\circ \text{N}$, 119°W , ~ 4100 m depth). Despite the different size fractions (>32 μm compared with
 419 >150 μm fraction in the present study), the general composition of the assemblages in the
 420 Kaplan East and ABYSSLINE samples was quite similar, with groups such as *Lagenammina*,
 421 *Nodellum*-like forms, saccamminids and psammosphaerids ('spheres') being common. Many of
 422 the individual species illustrated by Nozawa et al. (2006) are recognisable in our samples. These
 423 previous studies therefore suggest that there is a general uniformity of foraminiferal assemblages
 424 at similar water depths across the eastern CCZ.....

425

426 4.3. High foraminiferal diversity in the eastern Clarion Clipperton Zone

427

428 Individual samples from the UK1 and OMS areas yielded 132 to 228 putative morphospecies
 429 (Fig. 7; Supplementary Fig. S5), leading to a total number of 580 in all samples combined (Table
 430 5). Even allowing for, say, a 10% overestimate due to the likely sources of error mentioned
 431 above, these are very diverse assemblages, and the total does not include species confined to
 432 finer size fractions (Gooday and Goineau, 2019) or deeper sediment layers (Goineau and
 433 Gooday unpublished). Previous analyses of trends in foraminiferal species richness with water
 434 depth, based on stained + dead assemblages of hard-shelled species, have yielded inconsistent
 435 patterns; in some areas (e.g., NW Atlantic) diversity increases with depth onto abyssal plains,
 436 while in other areas (e.g., Gulf of Mexico, High Arctic) diversity decreases with depth (reviewed
 437 in Rex and Etter, 2010). Nevertheless, high levels of local foraminiferal species richness at
 438 abyssal depths are not unprecedented when monothalamids are included. The numbers of
 439 morphospecies in the top 1 cm layer of individual multicorer samples (>63 μm fraction) at sites
 440 on the Porcupine, Madeira and Cape Verde Abyssal Plains ranged from 135 to 146 (including
 441 phytodetrital layer), 100 to 149 and 117, respectively, while 217 species were recognised in a
 442 similar sample from the Arabian Sea. (Gooday et al., 1998). Other deep-sea meiofaunal taxa may
 443 also be highly specious. The huge number (682) of harpacticoid copepod species recorded by
 444 George et al. (2013) at two sites in the Angola Basin (SW Atlantic; 5389 m and 5448 m depth) is
 445 particularly notable. These sites yielded 172 and 600 species from 35 and 40 multicores,
 446 respectively; all but 5 were undescribed. Miljutina et al. (2010) recognised 325 nematode
 447 species from 2 box cores and 21 multicores in the central CCZ. Nematode generic richness in the
 448 CCZ may also be very high (reviewed in Radziejewska 2014).

449

450 In the present study, 42.2% of species represented by complete stained individuals and
 451 51.9% of those represented by complete dead individuals were singletons or doubletons (Table
 452 6). A predominance of rare species is a ubiquitous feature of diverse biological communities
 453 (Magurran 2004), including those from marine settings (Connolly et al., 2014). There is
 454 evidence from the NW Atlantic that deep-sea benthic communities have a more even distribution
 455 of individuals among species, and more rare species, than those in shelf environments (Rex and
 456 Etter, 2010). More than half (384) of the 682 harpacticoid species in the above-mentioned study
 457 of George et al. (2013) were singletons, and a further 111 doubletons. This is a common pattern
 among different taxa in the equatorial Pacific, including macrofaunal isopods and polychaetes

458 (Glover et al., 2002; Janssen et al., 2015; Wilson 2017) and meiofaunal nematode genera (Pape
 459 et al., 2017), as well as foraminifera from this and other oceans (Gooday 1986, 1996; Gooday et
 460 al., 2006; Buzas et al., 2013; Goineau and Gooday, 2017). As Paterson et al. (1998) remarks,
 461 where species richness is very high and rare species are common, it may never be possible to
 462 collect all species present in a particular area without analysing unrealistic numbers of samples.
 463 The sample-based rarefaction curve shown in Supplementary Fig. S7 suggests that it would be
 464 necessary to analysed at least 20 samples to find around 90% of the smaller foraminiferal species
 465 in our three study areas. Thus, chronic undersampling makes establishing whether or not species
 466 are endemic almost impossible, a conclusion reinforced by the modelling study of Tittensor et al.
 467 (2010).

468 What are the mechanisms that allow so many foraminiferal species to co-exist in
 469 relatively small volumes of sediment? Rex and Etter (2010, pp. 123-125) suggest that
 470 foraminiferal diversity may be particularly high in the abyssal NW Atlantic (as reported by
 471 Buzas and Gibson, 1969) because 1) the food supply is sufficient to maintain populations at a
 472 level that does not depress diversity, 2) low macrofaunal and megafaunal densities lead to less
 473 depletion of limited food supplies as well as reduced predation by animals on foraminifera, and
 474 3) the ability to reproduce asexually avoids the need that animals have to find mates. They
 475 further suggest that ‘dormancy’, asexual reproduction and efficient dispersal mechanisms may
 476 help immigrant foraminiferal species originating from distant sources to persist in abyssal
 477 settings (‘source-sink dynamics’). These arguments could apply equally in the eastern CCZ.
 478 Another factor may be that many monothalamids in our samples probably have a largely static
 479 life style that likely limits competition between species. This is suggested by test morphologies
 480 (e.g., tubular, branching or highly irregular) that would make movement on or through the
 481 sediment difficult, and by the frequent occupancy by foraminifera of cryptic microhabitats,
 482 particularly radiolarian tests in the case of the CCZ, from which they cannot escape (Goineau
 483 and Gooday, 2015). Attachment to small hard particles (e.g. micronodules) is also common.
 484 Jumars (1975a, 1975b) invoked ‘environmental grain structure’ to explain why largely sedentary
 485 (‘small ambit’) polychaete species were more diverse than more mobile species in the much
 486 shallower setting of the San Diego Trough (1230 m depth). In the CCZ, the scale of the
 487 ‘environmental grain structure’, created in particular by radiolarian tests as well as by the
 488 nodules themselves, may be highly relevant to at least some individual foraminifera and
 489 therefore well suited to enhancing foraminiferal diversity.

490

491 *4.4. Spatial patterns across the sampled area*

492

493 Our study revealed an overall uniformity in the relative abundance of the main foraminiferal
 494 taxa/groups, which showed no significant variations across the three strata (Table 3). In MDS
 495 plots based on ‘entire’ assemblages (i.e., including monothalamids), as well as those based on
 496 multichambered taxa alone, all samples lie within the 95% confidence envelope, indicating a
 497 large degree of uniformity (Fig. 5). However, particularly in the case of the complete stained
 498 tests, the five UK1A samples form a weak group that is somewhat separated from a second
 499 group comprising three of the UK1B and two of the OMS samples, with the third OMS sample
 500 (MC21) as an outlier. A loose clustering of the UK1A samples is also evident in plots based on
 501 the stained + dead tests and on presence/absence data for all specimens (stained and dead,
 502 complete and fragmentary) combined. This indication of a weak spatial structure within our
 503 species-level dataset is consistent the greater average distance between UK1A sampling sites and
 504 those in the other two strata (148 km for UK1B and 208 km for OMS) than between sites in the
 505 UK1B and OMS strata (82 km) (Supplementary Fig. S1). The distance-decay relationship
 506 (Fig.6) reveals a significant difference in assemblage composition only when the two most
 507 distant strata (UK1 Stratum A and OMS; mean sample spacing 208 km) are compared. At

508 similar spatial scales (60-270 km) within the Global Sea mineral Resources (GSR) contract area
 509 in the eastern CCZ, Pape et al. (2017) reported that metazoan meiofaunal assemblages were
 510 'largely comparable' in terms of abundance, composition and diversity at the higher taxon level
 511 and when considering nematode families and genera. Among higher taxa only minor groups that
 512 represented <1% of the assemblage showed any real spatial variation. Nematode families and
 513 genera fluctuated in abundance between samples and sites but in both cases the same taxa were
 514 dominant. De Smet et al. (2017) reported a similar degree of homogeneity in the abundance,
 515 diversity and assemblage composition of macrofauna at the same GSR sites.

516 Since the UK1A samples were taken in October 2013 and the UK1B and OMS samples
 517 in February and March 2015 (Table 1), it is possible that temporal variations could influence the
 518 weak spatial patterns observed in the MDS plot. Deep-sea foraminiferal populations can vary on
 519 both seasonal and inter-annual time scales (Gooday and Rathburn, 1999; Gooday et al., 2010;
 520 Glover et al., 2010), normally in response to fluctuating inputs to the seafloor of organic matter
 521 ('phytodetritus') derived from surface production (Gooday, 2002). Utilisation of this labile
 522 material leads to the development of enhanced populations of opportunistic species, typically
 523 rotaliids (Gooday, 2003). However, the lack of any clear difference in the relative abundance of
 524 stained rotaliids, or any other group, between the 2013 and 2015 samples (Table 3) suggests that
 525 temporal variation was not important. Surficial phytodetritus deposits were also never observed
 526 in any of our core samples.

527 Our samples revealed a greater degree of spatial structure in the dispersion patterns of
 528 individual species. Including singletons, almost half (252 = 43.4%) of all species were recorded
 529 from only one stratum with 211 (36.4%) restricted to a single core. This could indicate the
 530 existence of many species with narrow distributions. On the other hand, 238 (~95%) of the 251
 531 species confined to one stratum were represented by less than 10 specimens, and 187 (74.5%)
 532 were either singletons or doubletons (complete or fragmentary, stained or dead). Moreover, 181
 533 (85.8%) of the 211 species confined to a single core were represented by 1 or 2 specimens.
 534 Given the evidence for small-scale faunal patchiness in the deep sea (Grassle and Morse-
 535 Porteous, 1987; Snelgrove and Smith 2002; McClain et al., 2011; McClain and Schlacher, 2015),
 536 including among abyssal Pacific foraminifera (Bernstein et al., 1978; Bernstein and Meador,
 537 1979), and the small sediment area sampled by each of our cores (~78 cm²), these rare species
 538 are more likely to be undersampled, in which case little can be concluded regarding their
 539 distributions (Glover et al., 2002; McClain and Hardy, 2010). This point is underlined by the fact
 540 that some well-known, globally-distributed multichambered species (Gooday and Jorissen 2012)
 541 are rare in our samples; for example, *Cyclammina cancellata*, *Hoeglundina elegans* and
 542 *Laticarinata pauperata* are each represented by single specimens.

543 The Morisita index suggests that the majority of species represented by 10 or more
 544 complete tests had aggregated distributions (Table 7), with the highest values of this index being
 545 associated with species that were more or less confined to one sample. A particularly good
 546 example of the latter is a monothalamid, the second-ranked species in the stained assemblage
 547 with 282 specimens, that inhabits radiolarian tests and builds a short wide tube on the exterior
 548 (Fig. 2C, D). With the exception of a single example from sample MC13, all specimens
 549 (complete and stained) were found in sample MC25, yielding a Morisita index of 10.9. Bernstein
 550 et al. (1978) detected aggregation among foraminifera at scales from cms to kms in the abyssal
 551 North Pacific. This contrasts with the predominantly random dispersion patterns of macrofaunal
 552 (mainly polychaetes) and meiofaunal (harpacticoid copepods) taxa at scales from a few cms to
 553 100 km in studies at bathyal and abyssal sites in the Pacific and NE Atlantic Oceans (reviewed
 554 in Rex and Etter, 2010). However, these earlier results were based on variance-to-mean ratios,
 555 rather than the Morisita index recommended by McClain et al. (2011). Using this latter
 556 approach, McClain et al. (2011) detected aggregated distributions among polychaete species in
 557 samples collected across scales of between 1 and 350 m at a lower bathyal (3203 m depth) site in

558 the NE Pacific to the north of the CCZ. They concluded that some metazoan macrofaunal
 559 species (>300 µm) had aggregated distributions at small spatial scales in their nested samples,
 560 but that, despite a huge amount of species-level variation between samples, there was only weak
 561 spatial structure in assemblage composition across the entire sampling area. Although the spatial
 562 scale of their study is smaller, and the experimental design more rigorous, the results of McClain
 563 et al. (2011) are comparable to ours. In the aforementioned GSR area of the eastern CCZ, Pape
 564 et al. (2017) report that the abundance of 14 species of the nematode genus *Halalaimus* was
 565 highly variable between sites (and between the two sampling periods at B6SO2), with only 2
 566 species common to the three sites and half restricted to one site (Pape et al., 2017). However,
 567 *Halalaimus* abundance in individual samples was low (Table 3 in Pape et al., 2017), suggesting
 568 that undersampling may have been responsible for some of this variability.
 569

570 4.5. Distributions at larger scales

571
 572 Species turnover is generally higher with increasing water depth than it is in a horizontal sense,
 573 reflecting the greater degree of environmental change along bathymetric transects (Rex and
 574 Etter, 2010; McClain and Hardy, 2010; McClain and Rex 2015). There is also evidence for a
 575 greater degree of genetic differentiation along depth gradients on environmentally complex
 576 continental margins than horizontally across the more uniform abyssal plains (Taylor and
 577 Rotterman, 2017). At the same time, rates of β -diversity measured along bathymetric contours
 578 (i.e. horizontally) tend to decrease with depth among both macrofaunal metazoans (bivalves;
 579 McClain and Rex, 2015) and foraminifera (Buzas et al., 2013). These trends in β -diversity are
 580 consistent with the wide species ranges that appear to be common among some macrofaunal
 581 taxa, notably polychaetes, on Pacific and other abyssal plains (Glover et al., 2002; McClain and
 582 Hardy, 2010; Janssen et al., 2015; Wilson, 2017).

583 Our sample sites are situated at similar latitudes (116° 27.601' to 117° 22.284'W), and
 584 occupy a modest depth range (4051 – 4224 m) in an approximately N-S direction. They are
 585 therefore not exposed to any great extent to the east - west gradients of increasing depth and
 586 decreasing sea-surface productivity along the CCZ (Hannides and Smith, 2003; Smith and
 587 Demopoulos, 2003; Morgan, 2012). Organic-matter flux to the seafloor, which is directly related
 588 to surface productivity and water depth, is believed to strongly influence rates of β -diversity in
 589 the deep sea (reviewed in McClain and Rex, 2015), although the mechanisms involved are not
 590 well understood (McClain and Schlacher, 2015). Another factor may be sediment properties,
 591 which according to Leduc et al. (2012), explain about 25% of nematode species β -diversity on
 592 the continental slope west of New Zealand (350-3100 m depth). Nematode assemblages from
 593 nodule-free and nodule-bearing parts of the CCZ are significantly different in terms of diversity
 594 (higher where nodules are present) and the relative abundances of genera (Miljutina et al., 2010.
 595 Singh et al., 2016). Nodules are present at all our sites and the sediments are radiolarian oozes
 596 that appear to be uniform, although we lack detailed granulometric data. Given the relative
 597 consistency in environmental conditions (depth, surface productivity, sediment type) across our
 598 abyssal study areas, the overall faunal similarity is unsurprising. Nevertheless, the distance-
 599 decay relationship (Fig. 5) suggests that the spatial separation of samples across a maximum
 600 distance of 224 km (the maximum sample separation between UK1A and OMS Strata) could
 601 have some influence on the composition of species assemblages.

602 More widely, many of the foraminifera that can be identified belong to well-known
 603 multichambered deep-sea morphospecies that have been reported from different oceans (Table
 604 4) and are often regarded as having 'cosmopolitan' distributions (e.g. Gooday and Jorissen,
 605 2012; Holbourn et al. 2013). A number of monothalamids (e.g. *Lagenammia difflugiformis*) or
 606 presumed monothalamids (e.g. *Edgertonia floccula*, *Resigella moniliforme*) have similar

607 distributions. For a few calcareous species, notably *Epistominella exigua* (Pawłowski et al.,
608 2007; Lecroq et al., 2009) but also the top-ranked rotaliid in our samples *Nuttallides umbonatus*
609 (Pawłowski and Holtzmann unpublished), wide ranges in different ocean basins at lower bathyal
610 and abyssal depths are supported by genetic data. This is consistent with previous evidence for
611 wide ranges among many foraminiferal species across abyssal plains, perhaps reflecting the
612 apparent ease with which foraminiferal propagules can be transported over large distances (Alve
613 and Goldstein, 2003, 2010), combined with slower evolutionary rates in the deep sea (Buzas and
614 Culver, 1984). Wide morphospecies distributions are reported for other meiofaunal taxa at
615 abyssal depths across different ocean basins and oceans, for example, species of the harpacticoid
616 copepod genus *Mesocletodes* (Menzel et al., 2011). As mentioned above, foraminifera have the
617 added advantage of being able to reproduce asexually, which may allow rare species to maintain
618 low-density populations.

619

620 **Concluding remarks**

621

622 Foraminifera, and particularly monothalamids, are a major and ubiquitous component of deep-
623 sea benthic communities across all size classes. In the abyssal Pacific they dominate the
624 sediment-dwelling meiofauna (Snider et al., 1984; Nozawa et al., 2006), macrofauna (Tendal
625 and Hessler, 1977) and megafauna (Amon et al., 2016; Gooday et al., 2017; Simon-Lledo et al.,
626 2019), as well as the biota encrusting polymetallic nodules and other hard substrates
627 (Mullineaux, 1987; Veillette et al., 2007; Gooday et al., 2015). The present study underlines the
628 enormous diversity of these foraminiferal populations in the nodule-rich ecosystems of the
629 Clarion-Clipperton Zone. The analysis of further samples from other parts of the CCZ will
630 undoubtedly reveal more hitherto unknown species. Our results also suggest that, although
631 many species are found only in one stratum or one sample, rarity combined with undersampling
632 makes it impossible to establish whether any are endemic to these particular areas without
633 analyzing unrealistic numbers of samples.

634

635 In addition to their biodiversity, much remains to be learnt about the ecology of abyssal
636 foraminifera. For example, little is known about life spans, rates of growth, or the prevalence of
637 sexual vs asexual reproduction, while diets remain largely a matter of speculation (Gooday et al.,
638 2008). Nevertheless, field observations combined with experimental studies, together with their
639 shear abundance, suggest that foraminifera must play an important ecological role in the deep
640 sea (Gooday, 2003). It is clear that some calcareous species are important processers of pulsed
641 inputs of labile organic-matter, while foraminifera of all types are consumed, in turn, by
642 specialist predators and incidentally by deposit feeders, creating a link between lower and higher
643 levels of deep-sea food webs (Lipps and Valentine, 1970; Gooday et al., 1992). Evidence from
644 volcanic ash and turbidite deposits that foraminifera, including the megafaunal xenophyophores,
645 are among the early recolonisers of new sedimentary substrates led Gooday and Goineau (2019)
646 to speculate that opportunistic species may be quick to occupy areas that have been seriously
647 disturbed, directly or indirectly, by mining. Finally, large xenophyophore tests, which occur
648 everywhere across the CCZ, often in considerable numbers, are an important source of habitat
649 structure for metazoans and other foraminifera (Levin and Thomas, 1988; Hughes et al., 2004).

650 Biologists working in the deep sea are now more aware of foraminifera than they were in
651 the past. However, there is still a tendency to overlook them. Although they are not always an
652 easy group to study, we would argue that their abundance, diversity and potential ecological
653 significance make it important to include these ubiquitous and extremely successful protists in
654 studies of the seafloor communities in areas likely to be mined in the future.

654

655

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663

664 **Compliance with ethical standards**

665

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670 *Competing interests.* We declare that there are no competing interests

671

672 **Author contributions**

673

674 Both authors contributed equally to the paper. Six samples were analysed by AG, five by AJG
 675 and the authors together checked and collated the faunal data. AG analysed most of the data,
 676 prepared initial drafts of the figures (except Fig. 2) and the raw data spreadsheet (Table S1). AJG
 677 wrote most of the text, prepared the tables and much of the supplementary material.

678

679 **Additional information**

680

681 Supplementary material accompanies this paper.

682

683 **References**

684

685 Alt, C.H.S., Kremenetskaia (Rogacheva), A., Gebruk, A.V., Gooday, A.J., Jones, D.O.B., 2019.
 686 Bathyal benthic megafauna from the Mid-Atlantic Ridge in the region of the Charlie-
 687 Gibbs Fracture Zone fracture zone based on Remotely Operated Vehicle
 688 observations. *Deep-Sea Res. I.* <https://doi.org/10.1016/j.dsr.2018.12.006>.

689 Alve, E., Goldstein, S.T., 2002. Resting stage in benthic foraminiferal propagules: a key feature
 690 for dispersal? Evidence from two shallow water species. *J Micropalaeontol* 21, 95-96.

691 Alve, E., Goldstein, S.T., 2010. Dispersal, survival and delayed growth of benthic foraminiferal
 692 propagules. *J. Sea Res.* 63, 36-51.

693 Amon, D.J., Ziegler, A.F., Dahlgren, T.G., Glover, A.G., Goineau, A., Gooday, A.J., Wiklund,
 694 H., Smith, C.R., 2016. Insights into the abundance and diversity of abyssal megafauna in a
 695 polymetallic-nodule region in the eastern Clarion-Clipperton Zone. *Sci. Rep.* 6,
 696 <http://doi.10.1038/srep30492>.

697 Bernstein, B.B., Hessler, R.R., Smith, R., Jumars, P.A., 1978. Spatial dispersion of benthic
 698 foraminifera in the central North Pacific. *Limnol. Oceanogr.* 23, 401-416. Bernstein,
 699 B.B., Meador, J., 1979. Temporal persistence of biological patch structure in an abyssal
 700 benthic community. *Mar. Biol.* 51, 179-183.

701 Buzas, M.A., Culver, S.J., 1984. Species duration and evolution: benthic foraminifera on the
 702 Atlantic continental margin of North America. *Science* 225, 289-290.

703 Buzas, M.A., Gibson, T.G., 1969. Species diversity: benthonic foraminifera in western North
 704 Atlantic. *Science* 163, 72-75.

- 705 Buzas, M.A., Culver, S.J., 1984. Species duration and evolution: benthic foraminifera on the
706 Atlantic continental margin of North America. *Science* 225, 829-30.
- 707 Buzas, M.A., Hayek, L.-A.C., Culver, S.J., Hayward, B.W., Osterman, L.E., 2013. Ecological
708 and evolutionary consequences of benthic community stasis in the very deep sea (>1500
709 m). *Paleobiology* 40,102-112.
- 710 Brault, S., Stuart, C.T., Wagstaff, M.C., Rex, M.A., 2013. Geographic evidence for source-sink
711 dynamics in deep-sea neogastropods of the eastern North Atlantic: an approach using nested
712 analysis. *Glob. Ecol. Biogeogr.* 22, 433–39.
- 713 Colwell, R.K., Chao, A., Gotelli, N.J., Lin, S.Y., Mao, C.X., Chazdon, R.L., Longino, J.T.,
714 2012. Models and estimators linking individual-based and sample-based rarefaction,
715 extrapolation and comparison of assemblages. *J. Plant Ecol.* 5, 3–21.
- 716 Connolly, S.R., MacNeil, M.A., Caley, M.J., Knowlton, N., Cripps, E., Hisano, M., Thibaut,
717 L.M., Bhattacharya, B.D., Benedetti-Cecchi, L., Brainard, R.E., Brandt, A., Bulleri, F.,
718 Ellingsen, K.E., Kaiser, S., Kröncke, I., Linse, K., Maggi, E., O’Hara, T.D., Plaisance, L.,
719 Poore, G.C.B., Sarkare, S.K., Satpathy, K.K., Schückel, U., Williams, A., Wilson, R.S.,
720 2014. Commonness and rarity in the marine biosphere. *Proc. Natl. Acad. Sci.* 111, 8524-
721 8539.
- 722 Cornelius, N., Gooday, A.J., 2004. ‘Live’ (stained) deep-sea benthic foraminifera in the western
723 Weddell Sea: Trends in abundance, diversity and taxonomic composition in relation to
724 water depth *Deep-Sea Res. II* 51, 1571-1602.
- 725 De Smet, B., Pape, E., Riehl, T., Bonifacio, P., Colson, L., Vanreusel, A., 2017. The community
726 structure of deep-sea macrofauna associated with polymetallic nodules in the eastern part of
727 the Clarion-Clipperton Fracture Zone. *Front. Mar. Sci.* 4, 103.
728 <https://hdl.handle.net/10.3389/fmars.2017.00103>.
- 729 Enge, A.J., Kucera, M., Heinz, P., 2012. Diversity and microhabitats of living benthic
730 foraminifera in the abyssal Northeast Pacific. *Mar. Micropal.* 96–97, 84–104.
- 731 George, K.H., Veit-Köhler, G., Martinez Arbizu, P., Sifried, S., Rose, A., Willen, E., Bröhldick,
732 K., Corgosinho, P.H., Drewes, J., Menzel, L., Moura, G., Schminke, H.K., 2013.
733 Community structure and species diversity of Harpacticoida (Crustacea:Copepoda) at two
734 sites in the deep sea of the Angola Basin (Southeast Atlantic). *Org. Divers. Evol.* [http://doi.](http://doi.10.1007/s13127-013-0154-2)
735 [10.1007/s13127-013-0154-2](http://doi.10.1007/s13127-013-0154-2).
- 736 Glover, A.G., Smith, C.R., Paterson, G.L.J., Wilson, G.D.F., Hawkins, L., Shearer, M., 2002.
737 Polychaete species diversity in the central Pacific abyss: local and regional patterns, and
738 relationships with productivity. *Mar. Ecol. Prog. Ser.* 240, 157-170.
- 739 Glover, A.G., Gooday, A.J., Bailey, D.M., Billett, D.S.M., Chevaldonné, P., Colaço, A., Copley,
740 J., Cuvelier, D., Desbruyères, D., Kalogeropoulou, V., Klages, M., Lampadariou, N.,
741 Lejeune, C., Mestre, N.C., Paterson, G.L.J., Perez, T., Ruhl, H., Sarrazin, J., Soltwedel, T.,
742 Soto, E.H., Thatje, S., Tselepidis, A., Van Gaever, S., Vanreusel, A., 2010. Temporal
743 change in deep-sea benthic ecosystems: a review of the evidence from recent time-series
744 studies. *Adv. Mar. Biol.* 58, 1-95.
- 745 Glover, A.G., Dahlgren, T.G., Wiklund, H., Mohrbeck, I., Smith, C.R., 2016. An end-to-end
746 DNA taxonomy methodology for benthic biodiversity survey in the Clarion- Clipperton
747 Zone, central Pacific abyss. *J. Mar. Sci. Eng.* <http://dx.doi.org/10.3390/jmse4010002>.
- 748 Goineau, A., Gooday, A.J., 2017. Novel benthic foraminifera are abundant and diverse in an area
749 of the abyssal equatorial Pacific licensed for polymetallic nodule exploration. *Sci. Rep.* 7,
750 45288, <http://doi.10.1038/srep45288>.
- 751 Gooday, A.J., 1986. Meiofaunal foraminiferans from the bathyal Porcupine Seabight (northeast
752 Atlantic): size structure, standing stock, taxonomic composition, species diversity and
753 vertical distribution in the sediment. *Deep-Sea Res.* 33, 1345-1373.
- 754 Gooday, A.J., 1996. Epifaunal and shallow infaunal foraminiferal communities at three abyssal

- 755 NE Atlantic sites subject to differing phytodetritus input regimes. *Deep-Sea Res. I* 43,
756 1395-1421.
- 757 Gooday, A.J., 2002. Biological responses to seasonally varying fluxes of organic matter to the
758 ocean floor: a review. *J. Oceanogr.* 58, 305-332.
- 759 Gooday, A.J., 2003. Benthic foraminifera (Protista) as tools in deep-water palaeoceanography: a
760 review of environmental influences on faunal characteristics. *Adv. Mar. Biol.* 46, 1-90.
- 761 Gooday, A.J., 2019. Deep-sea benthic foraminifera, Chapter 09071 in: Cochran, J.K.,
762 Bokuniewicz, H., Yager, P. (Eds.), *Encyclopedia of Ocean Sciences*, 3rd Edition, Academic
763 Press. <https://doi.org/10.1016/B978-0-12-409548-9.09071-0>.
- 764 Gooday, A.J., Goineau, A., 2019. The Contribution of Fine Sieve Fractions (63–150 µm) to
765 Foraminiferal Abundance and Diversity in an Area of the Eastern Pacific Ocean Licensed
766 for Polymetallic Nodule Exploration. *Front. Mar. Sci.*
767 <http://doi:10.3389/fmars.2019.00114>
- 768 Gooday, A.J., Jorissen, F.J., 2012. Benthic foraminiferal biogeography: controls on global
769 distribution patterns in deep-water settings. *Ann. Rev. Mar. Sci.* 4, 237–62.
- 770 Gooday, A.J., Rathburn, A.E., 1999. Temporal variability in living deep-sea benthic
771 foraminifera: a review. *Earth-Sci. Rev.* 46, 187–212.
- 772 Gooday, A.J., Goineau, A., Voltski, I., 2015. Abyssal foraminifera attached to polymetallic
773 nodules from the eastern Clarion Clipperton Fracture Zone: a preliminary description and
774 comparison with North Atlantic dropstone assemblages. *Mar. Biodiv.* 45, 391-412.
775 <http://doi.10.1007/s12526-014-0301-9>
- 776 Gooday, A.J., Holzmann, M., Caille, C., Goineau, A., Kamenskaya, O.E., Weber, A.A.T.,
777 Pawlowski, J., 2017. Giant foraminifera (xenophyophores) are exceptionally diverse in
778 parts of the abyssal eastern Pacific where seabed mining is likely to occur. *Biol. Conserv.*
779 207, 106–116. <https://doi.org/10.1016/j.biocon.2017.01.006>.
- 780 Gooday, A.J., Levin, L.A., Linke, P., Heeger, T., 1992. The role of benthic foraminifera in deep-
781 sea food webs and carbon cycling, in: Rowe, G.T. Pariente, V. (Eds), *Deep-Sea Food*
782 *Chains and the Global Carbon Cycle*. Kluwer Academic Publishers, pp. 63-91.
- 783 Gooday, A.J., Nomaki, H., Kitazato, H., 2008. Modern deep-sea benthic foraminifera: a brief
784 review of their biodiversity and trophic diversity, in: Austin, W. E. N., James, R. H. (Eds)
785 *Biogeochemical Controls on Palaeoceanographic Environmental Proxies*. Geological
786 Society, London, Special Publications 303, 97–119. <http://doi:10.1144/SP303.8> 0305-
787 8719/08/
- 788 Gooday, A.J., Nozawa, F., Ohkawara, N., Kitazato, H., 2006. Foraminifera. ISA Technical
789 Study No. 3, 10-14.
- 790 Gooday, A.J., Malzone, M.G., Bett, B.J., Lamont, P.A., 2010. Decadal-scale changes in shallow-
791 infaunal foraminiferal assemblages at the Porcupine Abyssal Plain, NE Atlantic. *Deep-Sea*
792 *Res. II* 57, 1362–1382.
- 793 Hannides, A., Smith, C.R., 2003. The northeast abyssal Pacific plain, in: Black, K.B.,
794 Shimmield, G.B. (Eds.), *Biogeochemistry of Marine Systems*. Boca Raton, FL: CRC Press,
795 pp. 208-237.
- 796 Hein, J.R., Mizell, K., Koschinsky, A., Conrad, T.A., 2013. Deep-ocean mineral deposits as a
797 source of critical metals for high- and green-technology applications: comparisons with
798 land-based resources. *Ore Geol. Rev.* 51, 1-14.
- 799 Holbourn, A., Henderson, A., McLeod, N., 2013. *Atlas of Benthic Foraminifera*. Wiley-
800 Blackwell.
- 801 Hortal, J., Borges, P.A.V., Gaspar, C., 2006. Evaluating the performance of species richness
802 estimators: sensitivity to sample grain size. *J. Anim. Ecol.* 75, 274–287.
- 803 Hughes, J.A., Gooday, A.J., 2004. The influence of dead *Syringammina fragilissima*
804 (*Xenophyophorea*) tests on the distribution of benthic foraminifera in the Darwin

- 805 Mounds region (NE Atlantic). *Deep-Sea Res. I*, 51, 1741-1758.
- 806 Janssen, A., Kaiser, S., Meissner, K., Brenke, N., Menot, L., Martinez Arbizu, P., 2015. A
807 reverse taxonomic approach to assess macrofaunal distribution patterns in abyssal Pacific
808 polymetallic nodule fields. *PLoS One* 10 (2): e0117790.
- 809 Jensen, P., 1982. A new meiofaunal splitter. *Ann. Zool. Fennici* 19, 233-236.
- 810 Jones, D.O.B., Amon, D.J., Chapman, A.S.A., 2017. Mining deep-ocean deposits: what are the
811 ecological risks. *Elements* 14, 325-330.
- 812 Jones, R.W., 2014. *Foraminifera and their Applications*, Cambridge University Press,
813 Cambridge.
- 814 Jones, R.W., 1994. *The Challenger Foraminifera*, Oxford University Press Oxford.
- 815 Jorissen, F., Fontanier, C., and Thomas, E. 2007. Paleoceanographical proxies based on deep-sea
816 benthic foraminiferal assemblage characteristics, in: Hillaire-Marcel, C., de Vernal, A.:
817 Proxies in Late Cenozoic Paleoceanography, Elsevier, Amsterdam, Boston, Heidelberg,
818 London, New York, Oxford, Paris, San Diego, San Francisco, Singapore, Sydney, Tokyo,
819 pp. 263-325.
- 820 Jumars, P.A., 1975a. Methods for measurement of community structure in deep-sea
821 macrobenthos. *Mar. Biol.* 30, 245-252.
- 822 Jumars, P.A., 1975b. Environmental grain and polychaete species' diversity in a bathyal benthic
823 community *Mar. Biol.* 30, 253-266.
- 824 Kamenskaya, O.E., Gooday, A.J., Radziejewska, T., Wawrzyniak-Wydrowska, B., 2012. Large,
825 enigmatic foraminiferan-like protists in the eastern part of the Clarion-Clipperton Fracture
826 Zone (abyssal eastern equatorial Pacific): biodiversity and vertical distribution in the
827 sediment. *Mar. Biodiv.* 42, 311-327. DOI: 10.1007/s12526-012-0114-7.
- 828 Kurbjewit, F., Schmiedl, G., Schiebel, R., Hemleben, Ch., Pfannkuche, O., Wallmann, K.,
829 Schäfer, P., 2000. Distribution, biomass and diversity of benthic foraminifera in relation to
830 sediment geochemistry in the Arabian Sea. *Deep-Sea Res. II* 47, 2913-2955.
- 831 Lecroq, B., Gooday, A.J., Pawlowski, J., 2009. Global genetic homogeneity in the deep-sea
832 foraminiferan *Epistominella exigua* (Rotaliida: Pseudoparrellidae). *Zootaxa* 2096, 23–32
- 833 Leduc, D., Rowden, A.A., Probert, P. K., Pilditch, C.A., Nodder, S.D., Vanreusel, A., Duineveld,
834 G.C.A., Witbaard, R., 2012. Further evidence for the effect of particle-size diversity on
835 deep-sea benthic biodiversity. *Deep-Sea Res. I* 13, 164-169.
- 836 Levin, L.A., C.L. Thomas, 1988. The ecology of xenophyophores (Protista) on eastern Pacific
837 seamounts. *Deep-Sea Res.* 35, 2003-2027.
- 838 Levin, L.A., Mengerlink, K., Gjerde, K.M., Rowden, A.A., Van Dover, C.L., Clark, M.R.,
839 Ramirez-Llodra, Currie, B., B., Smith, C.R., Sato, K.N., Gallo, N., Sweetman, A.K.,
840 Lily, H., Armstrong, C.W., Bridler, J., 2016. Defining 'serious harm' to the marine
841 environment in the context of deep-seabed mining. *Mar. Policy.* 74, 245-259.
- 842 Lodge, M., Johnson, D., Le Gurun, G., Wengler, M., Weaver, P., Gunn, V., 2014. Seabed
843 mining: International Seabed Authority environmental management plan for the Clarion-
844 Clipperton Zone. *Mar. Policy* 49, 66-72.
- 845 Lodge, M., Verlaan, P.A., 2018. Deep-sea mining: international regulatory challenges and
846 responses. *Elements* 14, 331-336.
- 847 Magurran, A.E, 2004. *Measuring Biological Diversity*. Blackwell Science, Maldon, Oxford,
848 Carleton.
- 849 McClain, C.R, Nekola, J.C., Kuhnz, L., Barry, J.M., 2011. Local-scale faunal turnover on the
850 deep Pacific seafloor. *Mar. Ecol. Prog. Ser.* 422, 193–200.
- 851 McClain, C.R., Hardy, S.M., 2010. The dynamics of biogeographic ranges in the deep sea. *Proc.*
852 *R. Soc. B* 277, 3533–3546. doi:10.1098/rspb.2010.1057.
- 853 McClain, C.R., Rex, M.A., 2015. Toward a conceptual understanding of β -diversity in the deep-
854 sea benthos. *Annu. Rev. Ecol. Evol. Syst.* 46, 623–642.

- 855 McClain, C.R., Schlacher, T.A. 2015. On some hypotheses of animal life at great depths on the
856 sea floor. *Mar. Ecol.* 36, 849-872.
- 857 Menzel, L., George, K.H., Martinez Abizu, P., 2011. Submarine ridges do not prevent large-
858 scale dispersal of abyssal fauna: A case study of *Mesocletodes* (Crustacea, Copepoda,
859 Harpacticoida). *Deep-Sea Res. I* 58, 839–864.
- 860 Miljutina, M.A., Miljutin, D.M., Mahatma, R., Galéron, J., 2010. Deep-sea nematode
861 assemblages of the Clarion-Clipperton Nodule Province (Tropical North-Eastern Pacific).
862 *Mar. Biodiv.* 40, 1-15. Doi:10.1007/s12526-009-0029-0.
- 863 Miller, K.A., Thompson, K.F., Johnston, P., Santillo, D., 2018. An overview of seabed mining
864 including the current state of development, environmental impacts, and knowledge gaps.
865 *Front. Mar. Sci.* 4, 418. <http://doi:10.3389/fmars.2017.00418>.
- 866 Morgan, C., 2012. A geological model of polymetallic nodule deposits in the Clarion-Clipperton
867 fracture Zone. ISA Briefing Paper 1/12, International Seabed Authority, Kingston
868 Jamaica, 12p.
- 869 Mullineaux, L.S., 1987. Organisms living on manganese nodules and crusts: distribution and
870 abundance at three North Pacific sites. *Deep-Sea Res.* 34. 165-184.
- 871 Murray, J. W. 2000. The enigma of the continued use of total assemblages in ecological studies
872 of benthic foraminifera. *J. Foram. Res.* 30, 244–45.
- 873 Murray, J.W., 2006. Ecology and applications of benthic foraminifera, Cambridge University
874 Press Cambridge, New York, Melbourne, Madrid, Cape Town, Singapore, São Paulo.
- 875 Murray, J.W., 2007. Biodiversity of living benthic foraminifera: How many species are there?
876 *Mar. Micro.* 64, 163-176.
- 877 Murray, J.W., Bowser, S.S., 2000. Mortality, protoplasm decay rate, and reliability of staining
878 techniques to recognize ‘living’ foraminifera: a review. *Micropaleontology* 30, 66–77.
- 879 Nozawa, F., Kitazato, H., Tsuchiya, M., Gooday, A.J., 2006. ‘Live’ benthic foraminifera at an
880 abyssal site in the equatorial Pacific nodule province: abundance, diversity and
881 taxonomic composition. *Deep-Sea Res. I* 53, 1406–1422.
- 882 Pape, E., Bezerra, T.N., Hauquier, F., Vanreusel, A., 2017. Limited spatial and temporal
883 variability in meiofauna and nematode communities at distant but environmentally
884 similar sites in an area of interest for deep-sea mining. *Front. Mar. Sci.* 4, 205, [http://doi](http://doi.org/10.3389/fmars.2017.00205)
885 [.org/10.3389/fmars.2017.00205](http://doi.org/10.3389/fmars.2017.00205).
- 886 Paterson, G.L.J., Wilson, G.D.F., Cosson, N., Lamont, P.A., 1998. Hessler and Jumars (1974)
887 revisited: abyssal polychaete assemblages from the Atlantic and Pacific. *Deep-Sea Res.*
888 II 45, 225-251.
- 889 Pawlowski, J., Fahrni J., Lecroq B., Longet, D., Cornelius, N., Excoffier, L., Cedhagen T.,
890 Gooday A. J., 2007. Bipolar gene flow in deep-sea benthic foraminifera. *Mol. Ecol.* 16,
891 4089–4096.
- 892 Phipps, M., Jorissen, F., Pusceddu, A., Bianchelli, S., De Stigter, H., 2012. Live benthic
893 foraminiferal faunas along a bathymetrical transect (282–4987 m). on the Portuguese
894 margin (NE Atlantic). *J. Foramin. Res.* 42, 66-81.
- 895 Radziejewska, T., 2014. Meiobenthos in the sub-equatorial Pacific Abyss: a proxy in
896 anthropogenic impact evaluation. Springer, Heidelberg, New York, Dordrecht, London.
- 897 Radziejewska, T., Gooday, A.J., Koltan, M., Szyrwiel, E., 2006. Deep-sea non-calcareous
898 foraminifera: some examples from the Pacific abyssal nodule field. *Meiofauna Marina* 15,
899 3–10.
- 900 Rex, M.A., Etter, R.J., 2010. *Deep-Sea Biodiversity: Patterns and Scale*. Harvard University
901 Press, Cambridge, Massachusetts, London, England.
- 902 Rex, M.A., McClain, C.R., Johnson, N.A., Etter, R.J., Allen, J.A., Bouchet, P., Warén, A.. 2005.
903 A source–sink hypothesis for abyssal biodiversity. *Am. Nat.* 165,163–78.
- 904 Simon-Lledó, E., Bett, B.J., Huvenne, V.A.I., Schoening, T., Benoist, N.M.A., Jeffreys, R.M.,

- 905 Durden, J.M., Jones, D.O.B., 2019. Megafaunal variation in the abyssal landscape of the
 906 Clarion-Clipperton Zone. *Prog. Oceanogr.* 170, 119–133.
 907 <https://doi.org/10.1016/j.pocean.2018.11.003>
- 908 Singh, R., Mijulin, D.M., Vanreusel, A., Radziejewska, T., Miljutina, M.M., Tchesunov, A.,
 909 Bussau, C., Galtsova, V., Martinez Arbizu, P., 2016. Nematode communities inhabiting the
 910 soft deep-sea sediment in polymetallic nodule fields: do they differ from those in the
 911 nodule-free abyssal areas? *Mar. Biol. Res.* 12, 345-359.
 912 <http://doi:10.1080/17451000.2016.1148822>.
- 913 Smith, C.R., Demopoulos, A.W.J., 2003. The deep Pacific Ocean floor, in: Tyler, P.A. (Ed.),
 914 *Ecosystems of the Deep Oceans. Ecosystems of the World 28.* Elsevier, Amsterdam,
 915 Boston, London, New York, Oxford, Paris, San Diego, San Francisco, Singapore, Sydney,
 916 Tokyo, pp. 179-218.
- 917 Snelgrove, P.V.R., Smith, C.R., 2002. A riot of species in an environmental calm: the paradox of
 918 the species-rich deep-sea floor. *Oceanogr. Mar. Biol.* 40, 311-342.
- 919 Snider, L.J., Burnett, B.R., Hessler, R.R., 1984. The composition and distribution of meiofauna
 920 and nanobiota in a central North Pacific deep-sea area. *Deep-Sea Res.* 31, 1225-1249.
- 921 Taylor, M.L., Roterman, C.N., 2017. Invertebrate population genetics across the Earth's largest
 922 habitat: the deep-sea floor. *Mol. Ecol.* <http://doi:10.1111/mec.14237>.
- 923 Tendal, O.S., Hessler, R.R., 1977. An introduction to the biology and systematic of Komokiacea.
 924 *Galathea Rep.* 14, 165–194.
- 925 Tittensor, D.P., Schlacher, T., Smith, C.R., Susko, E., 2010. Endemism at low sampling effort:
 926 real or artefact? In: Svavarsson, J., Halldórsson, H.P., Þórðarson, S., dos Santos, E., 2010.
 927 12th International Deep-Sea Biology Symposium, Reykjavik, Iceland, 7-11 June, 2010.
 928 Symposium Program and Book of Abstracts, pp. 84-85.
- 929 Saidova, Kh. M., 1966. Benthic foraminiferal faunas of the Pacific. *Oceanology* 6, 222-227.
- 930 Saidova, Kh. M., 1981. Recent benthic foraminiferal communities of the Pacific abyssal plains.
 931 *Oceanology* 21, 259-262.
- 932 Veillette, J., Sarrazin, J., Gooday, A.J., Galéron, J., Caprais, J.-C., Vangriesheim, A., Étoubleau,
 933 J., Christian, J.R., Juniper, S.K., 2007. Ferromanganese nodule fauna in the Tropical North
 934 Pacific Ocean: species richness, faunal cover and spatial distribution. *Deep-Sea Res. I*, 54,
 935 1912-1935.
- 936 Walton W.R., 1955. Ecology of living benthonic foraminifera, Todos Santos Bay, Baja
 937 California. *J. Paleontol.* 29, 952-1018.
- 938 Wedding, L.M., Friedlander, A.M., Kittinger, J.N., Watling, L., Gaines, S.D., Bennett, M.,
 939 Hardy, S.M., Smith, C.R., 2013. From principles to practice: a spatial approach to
 940 systematic planning in the deep sea. *Proc. Roy. Soc. B* 280, 20131684.
 941 <http://dx.doi.org/10.1098/rspb.2013.1684>.
- 942 Wedding, L.M., Reiter, S.M., Smith, C.R., Gerde, K.M., Kittinger, J.N., Friedlander, A.M.,
 943 Gaines, S.D., Clark, M.R., Thurnherr, A.M., Hardy, S.M., Crowder, L.B., 2015.
 944 Managing mining of the deep seabed. *Science* 349, 144-145.
- 945 Wilson, G.D.F., 2017. Macrofauna abundance, species diversity and turnover at three sites in the
 946 Clipperton-Clarion Fracture Zone. *Mar. Biodiv.* 47, 323. [http://doi.org/10.1007/s12526-](http://doi.org/10.1007/s12526-016-0609-8)
 947 [016-0609-8](http://doi.org/10.1007/s12526-016-0609-8).

949 **Figure 1.** Sampling localities in the eastern equatorial Pacific investigated in the present study
 950 (UK1, OMS) and in earlier publications: Global Sea mineral Resources (GSR; Pape et al., 2017),
 951 Interoceanmetal Joint Organisation (IOM: Radziejewska et al., 2006); Kaplan East (KE =
 952 Kaplan East: Nozawa et al., 2006).

953
 954 **Figure 2:** Representative morphospecies. *Reophax* sp. 5 incorporating red mineral grains; UK1A
 955 Stratum, sample MC07 (A). *Deuterammia* aff. *grahami* Brönnimann and Whittaker 1988;
 956 UK1A Stratum, sample MC07 (B). Monothalamid sp. 85, radiolarian inhabitant with a tube, the
 957 second-ranked species overall but more or less confined to UK1B Stratum, sample MC25 (C,D).
 958 Tube sp. 73; UK1B Stratum, sample MC13 (E). *Rhizammina* aff. *algaeformis*; OMS Stratum,
 959 sample MC22 (F). *Rhizammina* sp. 5; UK1B Stratum, sample MC05 (G). *Baculella* aff. *hirsuta*;
 960 OMS Stratum, stratum MC22 (H). Tube sp.8/49; UK1B Stratum, sample MC05 (I).

961
 962 **Figure 3:** Number of ‘new’ species (i.e., those encountered for the first time) in each sample
 963 (dotted line), and cumulative number of species added with the addition of new samples (full
 964 line).

965
 966 **Figure 4:** Total numbers of species recognised in the 3 strata (S) and estimated number of
 967 species for the entire assemblage (ACE, Chao1, Jack 1, Jack 2). Abundance-based estimators
 968 ACE and Chao1 were calculated based on complete specimens, live and dead combined;
 969 incidence-based estimators Jackknife 1 and 2 (‘Jack 1’, ‘Jack 2’) were calculated based on
 970 complete specimens and fragments, live and dead combined.

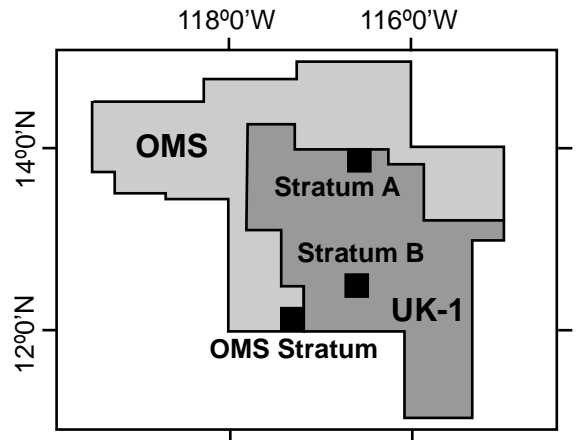
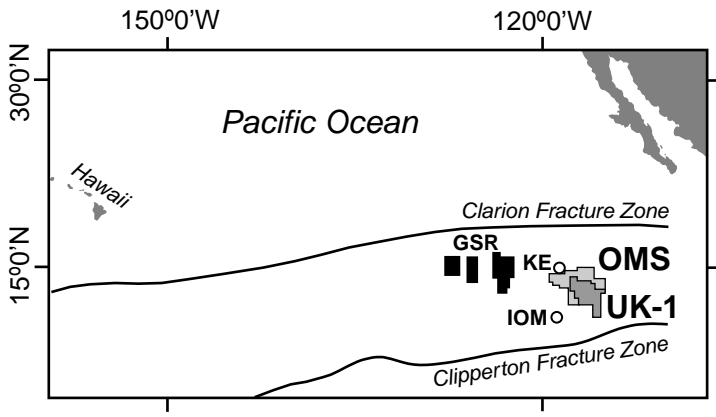
971
 972 **Figure 5:** Multidimensional scaling (MDS) plots of the eleven samples based on Bray-Curtis
 973 similarity indices computed with species presence-absence data and species relative abundances,
 974 for the entire assemblage and for multichambered species only. Dotted ellipses are 95%
 975 confidence regions of the samples. Samples MC02, MC05, MC07 and MC11 are from UK1
 976 Stratum A, samples MC05, MC13 and MC25 are from UK1 Stratum B, and samples MC20,
 977 MC21 and MC22 are from the OMS Stratum.

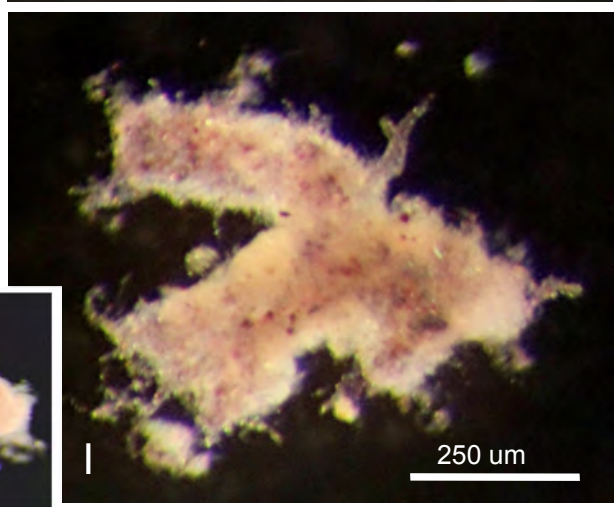
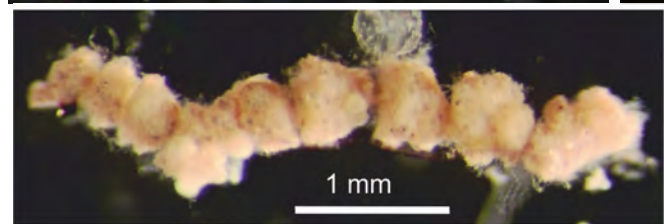
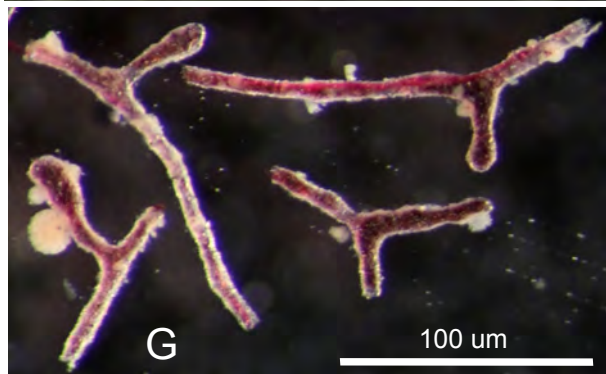
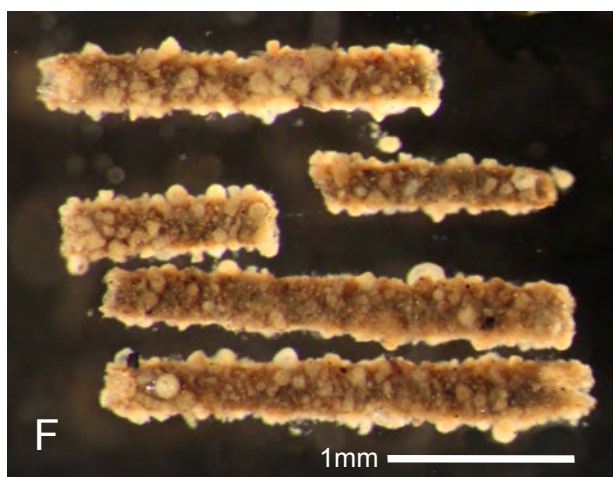
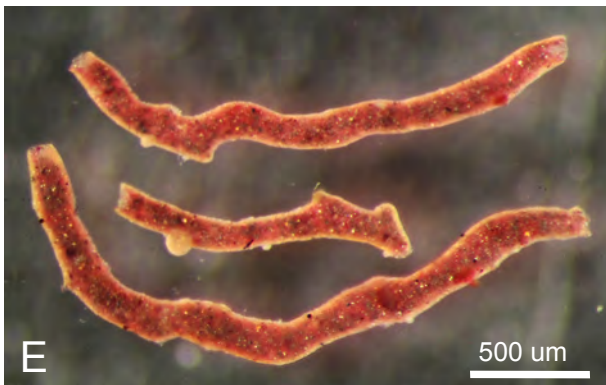
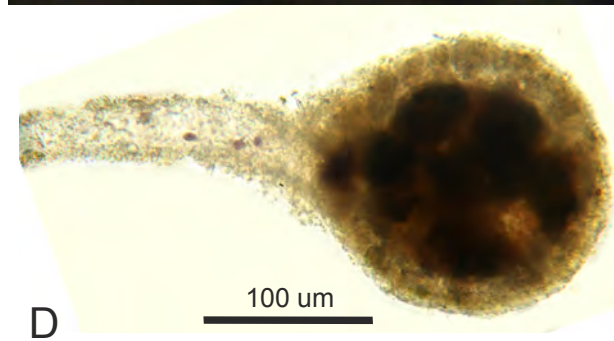
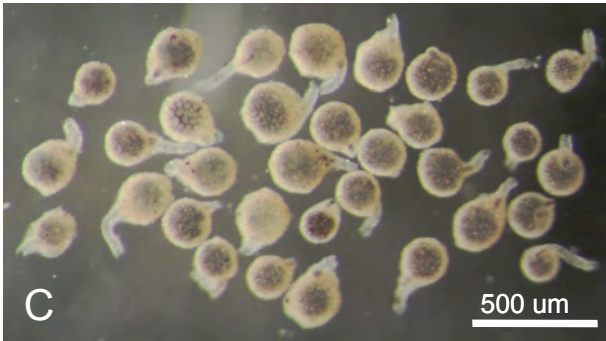
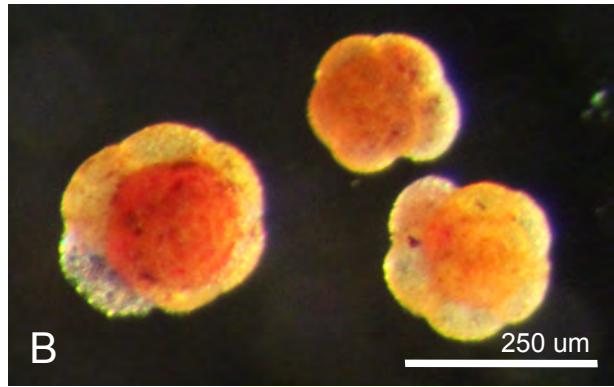
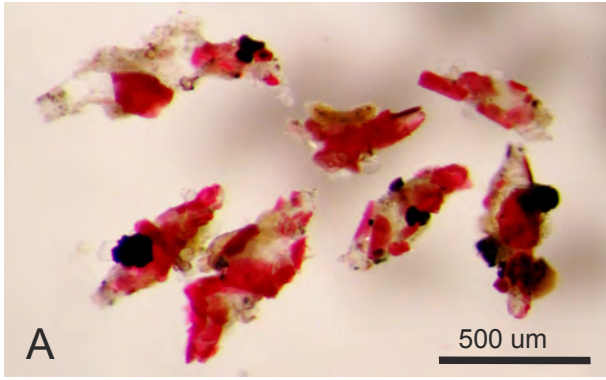
978
 979 **Figure 6:** Similarity between samples with increasing distance, based on Bray-Curtis similarity
 980 indices (\log_{10}) computed with species presence-absence data (live and dead complete
 981 specimens, live and dead fragments). The open symbols refer to comparisons of samples within
 982 a stratum, the filled symbols to comparisons of samples between strata. Within stratum and
 983 between stratum values are significantly ($p < 0.05$) different only in the case of the UK1A vs
 984 OMS comparison.

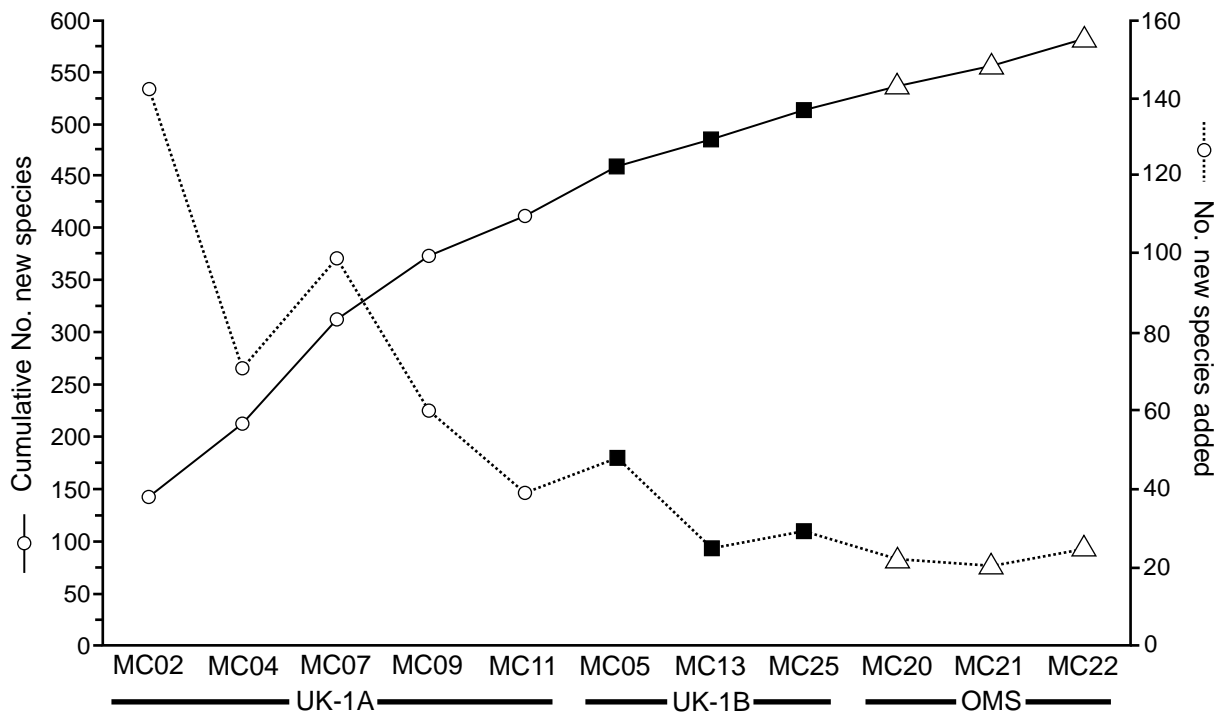
985
 986 **Figure 7:** Species shared between samples or strata and confined to one single sample or
 987 stratum. Five samples from UK1A Stratum (A). Three samples from UK1B Stratum (B). Three
 988 samples from OMS Stratum (C). The three strata (D). The filled circles represent samples (A-C)
 989 or strata (D). Bold values = total number of species recognised in the corresponding sample or
 990 stratum; central underlined values = number of species occurring in all samples within a stratum
 991 (A-C) or all strata (D); italicised values = number of species shared between samples or strata;
 992 values in brackets = number of species confined to the corresponding sample or stratum.

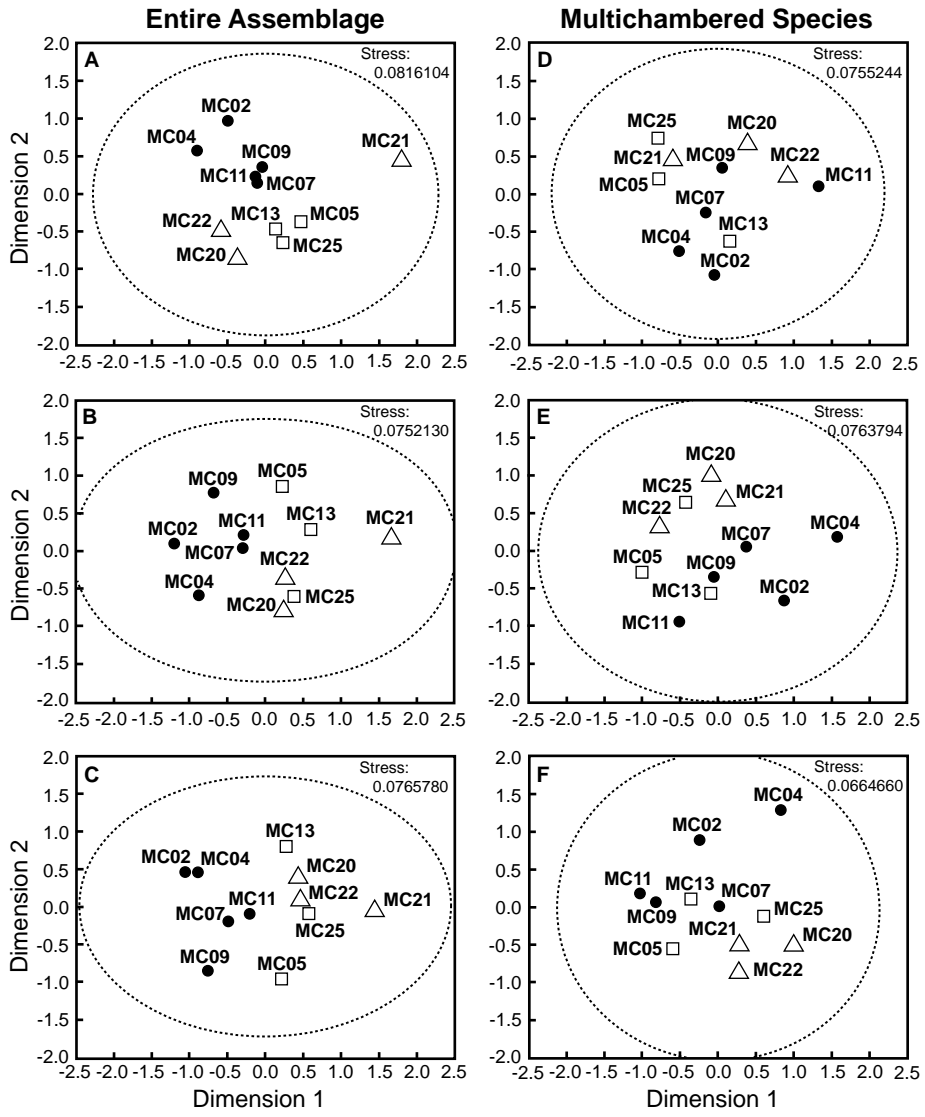
993
 994 **Figure 8.** Number of species (ignoring singletons) represented by stained + dead specimens,
 995 arranged by the number of samples in which they occur (from 1 to 11). A) Number of species. B)
 996 Percentage of species. See Supplementary Fig. S8 for a version of this figure that includes data
 997 for the stained and dead assemblages.

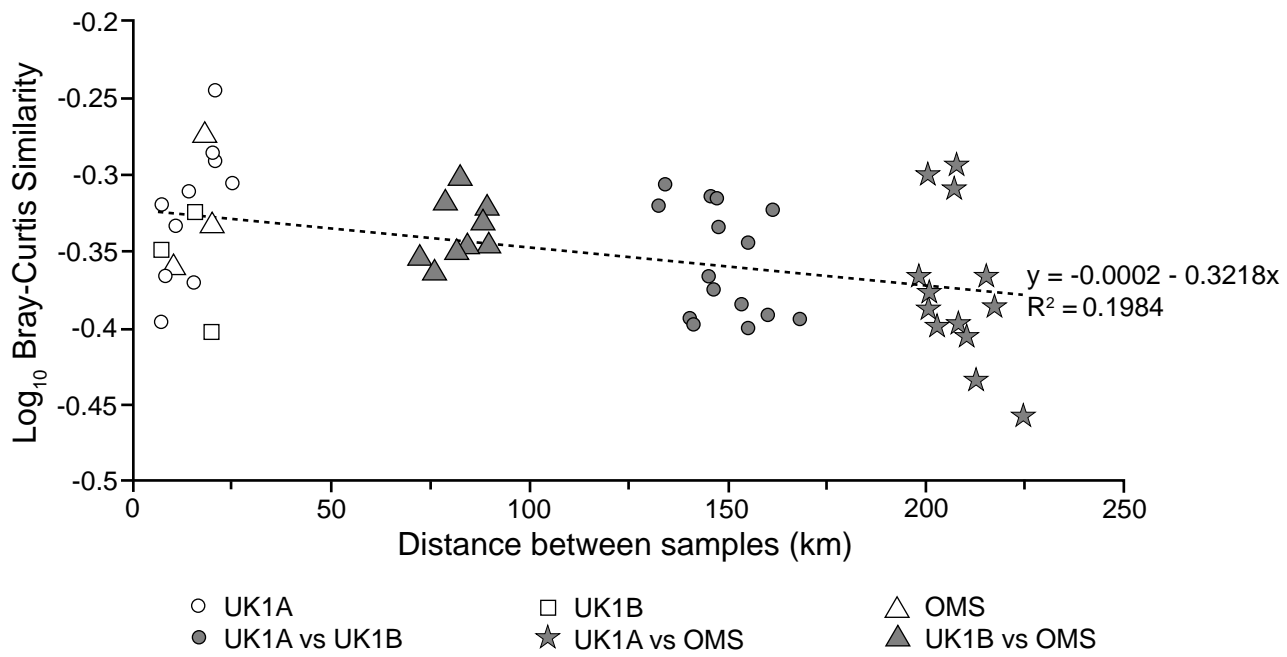
998

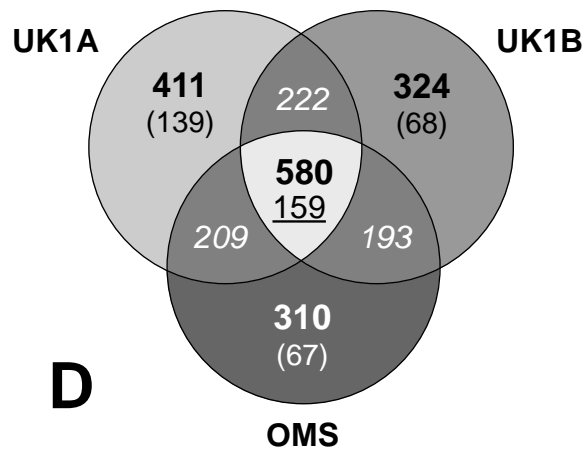
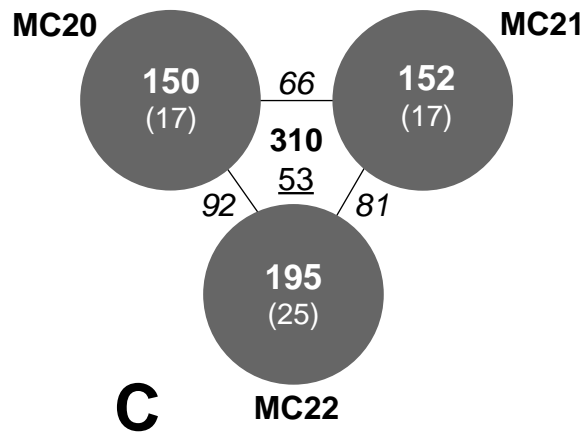
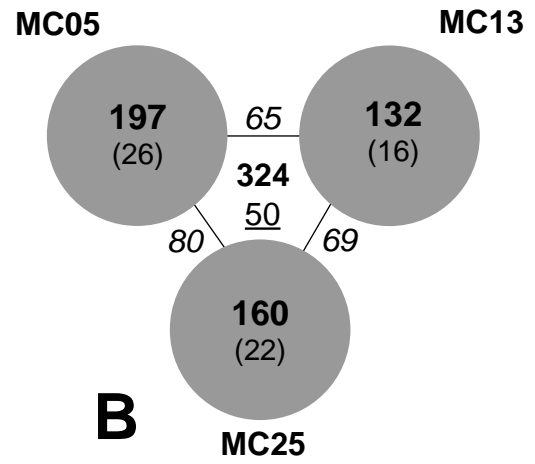
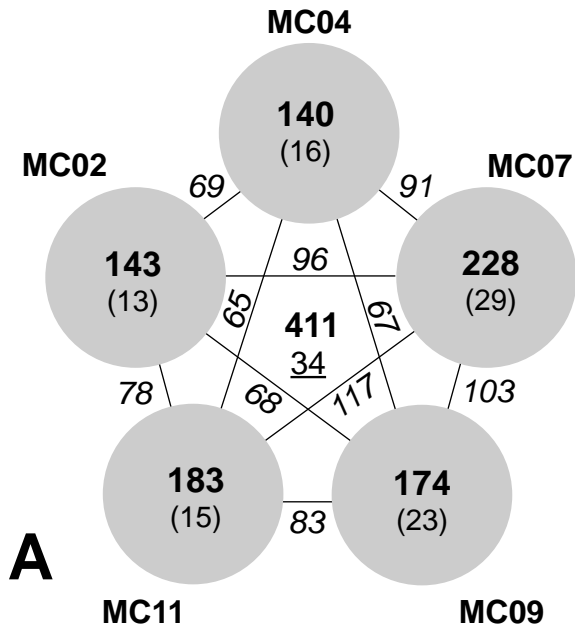


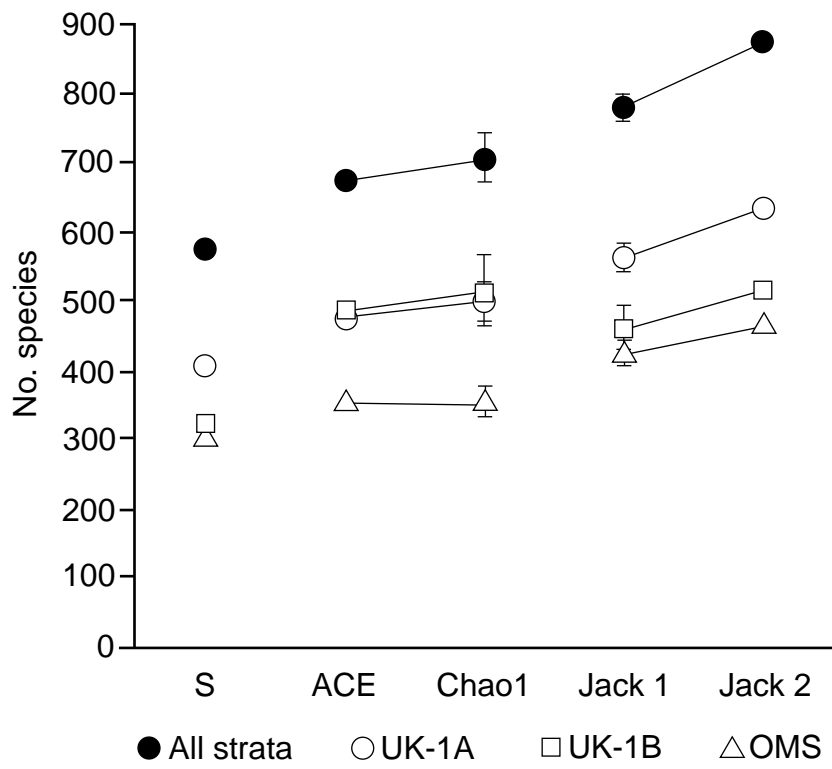


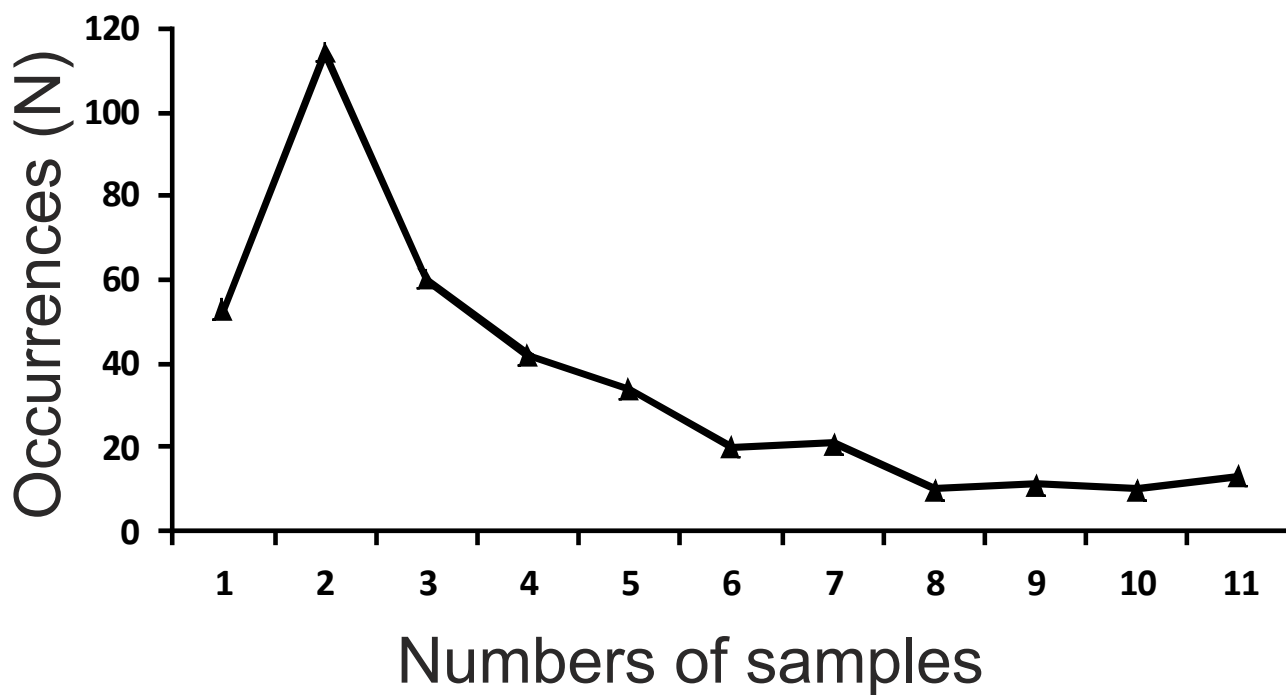
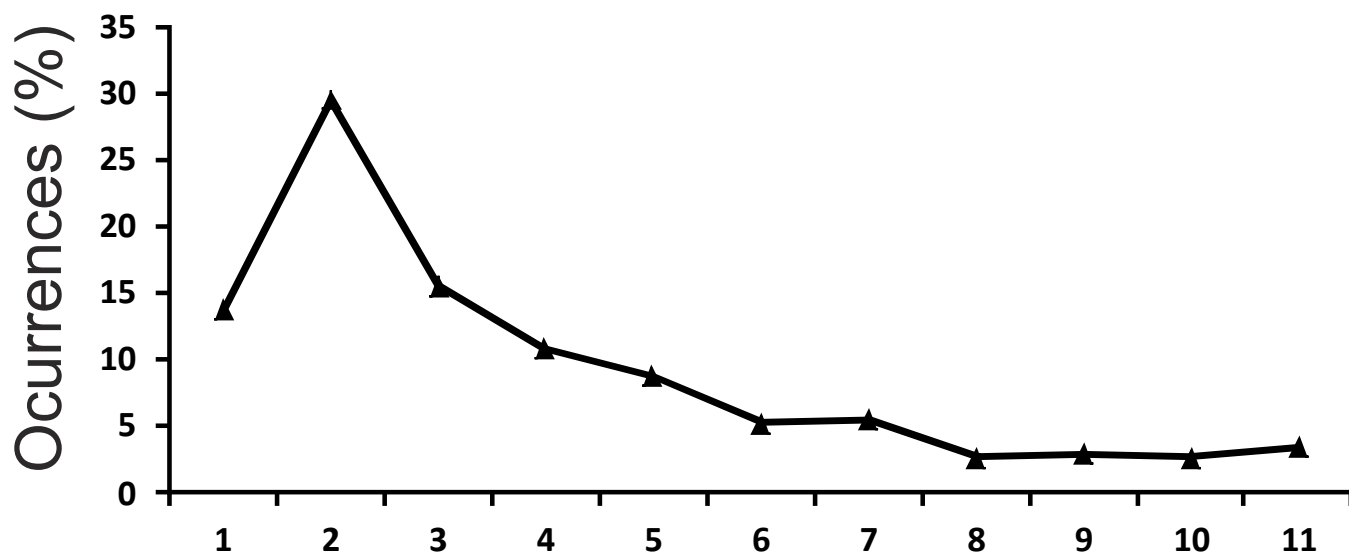












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4**Table 1.** Station data for the eleven investigated sampling sites in the UK1A, UK1B and OMS strata. MC = megacorer.

Strata	Sampling sites	Samples	Latitude (°N)	Longitude (°W)	Water depth (m)
UK1A	B	MC02	13°50.792'	116°37.59'	4079
	D	MC04	13°57.796'	116°34.093'	4084
	G	MC07	13°45.706'	116°27.601'	4111
	H	MC09	13°53.299'	116°41.399'	4150
	J	MC11	13°54.104'	116°35.401'	4166
UK1B	U04	MC05	12°34.738'	116°43.425'	4235
	U07	MC13	12°27.056'	116°35.669'	4129
	U15	MC25	12°34.953'	116°39.060'	4224
OMS	S07	MC20	12°8.160'	117°12.897'	4110
	S10	MC21	12°3.273'	117°15.097'	4051
	S08	MC22	12°11.409'	117°22.284'	4179

5

2 **Table 2.** Abundance and density of ‘live’ (stained) complete and fragmented foraminiferal
 3 specimens (without xenophyophores and gromiids) in the 0–1 cm layer (>150- μ m fraction) of
 4 individual samples and strata. Densities for individual strata and ‘Total’ are averaged values of
 5 samples within the corresponding stratum. ‘No.’ = actual number of individuals; ‘Dens.’ =
 6 number of individuals per 10 cm².

Sample	Splits	‘Live’ complete		‘Live’ fragments		Dead complete		Dead fragments	
		No.	Dens.	No.	Dens.	No.	Dens.	No.	Dens.
MC02	8/8	657	84	226	29	195	25	29	4
MC04	8/8	557	71	174	22	203	26	78	10
MC07	8/8	966	123	763	97	263	33	138	18
MC09	3/8	514	132	143	37	110	28	54	14
MC11	3/8	687	146	456	97	170	36	223	48
<i>UK1-A mean</i>		<i>676</i>	<i>111</i>	<i>352</i>	<i>56</i>	<i>188</i>	<i>30</i>	<i>104</i>	<i>19</i>
MC05	4/8	511	85	330	55	177	30	128	21
MC13	4/8	302	68	334	76	141	32	120	27
MC25	4/8	588	165	103	29	201	57	110	31
<i>UK1-B mean</i>		<i>467</i>	<i>106</i>	<i>256</i>	<i>53</i>	<i>173</i>	<i>40</i>	<i>119</i>	<i>26</i>
MC20	3/8	448	113	115	29	290	73	207	69
MC21	7/8	222	30	83	11	197	27	53	7
MC22	3/8	877	171	485	94	235	46	236	46
<i>OMS mean</i>		<i>516</i>	<i>105</i>	<i>228</i>	<i>45</i>	<i>241</i>	<i>49</i>	<i>165</i>	<i>41</i>
TOTAL mean		575	103	272	51	198	39	125	29

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9

1 **Table 3.** Absolute and relative abundances of stained (L = 'live') and stained + dead complete
 2 specimens of the major taxa/groups in the three Strata. Xenophyophore fragments and gromiids
 3 are excluded.
 4

Stratum	UKIA				UKIB				OMS				3 strata					
	L	%	L+D	%	L	%	L+D	%	L	%	L+D	%	L	%	L+D	%		
Multichambered																		
Robertinids	2	0.1	2	0.05	1	0.1	1	0.1	1	0.1	1	0.04	4	0.1	4	0.05		
Rotaliids	76	2.2	116	2.7	21	1.5	37	1.9	31	2.0	96	4.2	128	2.0	249	2.9		
Lagenids	5	0.1	9	0.2	0	0.0	1	0.1	1	0.1	2	0.1	6	0.1	12	0.1		
Miliolids	21	0.6	25	0.6	4	0.3	7	0.4	3	0.2	13	0.6	28	0.4	45	0.5		
Ammodiscids	4	0.1	36	0.8	4	0.3	15	0.8	4	0.3	20	0.9	12	0.2	71	0.8		
Hormosinids	201	5.9	402	9.3	101	7.2	203	10.6	128	8.3	259	11.4	430	6.8	864	10.2		
Trochamminids	14	0.4	66	1.5	3	0.2	23	1.2	11	0.7	37	1.6	28	0.4	126	1.5		
Other textulariids	32	0.9	148	3.4	11	0.8	63	3.3	12	0.8	73	3.2	55	0.9	284	3.3		
Total identified	339	10.0	761	17.6	143	10.2	334	17.2	181	11.7	473	20.8	663	10.5	1568	18.4		
Total indeterminate	16	0.5	43	1.0	2	0.1	16	0.8	10	0.6	28	1.2	28	0.4	87	1.0		
Total multichambered	355	10.5	804	18.6	145	10.3	350	18.0	191	12.3	501	22.0	691	10.9	1655	19.4		
Monothalamids																		
<i>Nodellum</i> -like	87	2.6	114	2.6	22	1.6	29	1.5	10	0.6	18	0.8	119	1.9	161	1.9		
Lagenamminids	69	2.0	135	3.1	16	1.1	52	2.7	48	3.1	116	5.1	133	2.1	303	3.6		
Flasks	158	4.7	248	5.7	84	6.0	158	8.2	81	5.2	168	7.4	323	5.1	574	6.7		
Saccamminids	64	1.9	73	1.7	15	1.1	18	0.9	6	0.4	16	0.7	85	1.3	107	1.3		
Droplet chambers	4	0.1	4	0.1	0	0.0	0	0.0	1	0.1	2	0.1	5	0.1	6	0.1		
Spheres	696	20.6	732	16.9	204	14.6	231	12.1	322	20.8	366	16.1	1222	19.3	1329	15.6		
Organic-walled	67	2.0	67	1.6	23	1.6	23	1.2	34	2.2	34	1.5	124	2.0	124	1.5		
Hyperamminids	7	0.2	17	0.4	2	0.1	18	0.9	1	0.1	3	0.1	10	0.2	38	0.4		
Tubes and spindles	690	20.4	822	19.0	200	14.3	252	13.1	320	20.7	391	17.2	1210	19.1	1465	17.2		
Chain-like	59	1.7	70	1.6	51	3.6	70	3.7	54	3.5	70	3.1	164	2.6	210	2.5		
Unclassified	697	20.6	761	17.6	474	33.9	519	27.1	263	17.0	314	13.8	1434	22.7	1594	18.7		
Komokiacean-like	169	5.0	192	4.4	54	3.9	73	3.8	63	4.07	76	3.3	286	4.5	341	4.0		
Komokiaceans																		
Baculellidae	207	6.1	219	5.1	86	6.2	94	4.9	136	8.8	169	7.4	429	6.8	482	5.7		
Komokiidae	52	1.5	64	1.5	22	1.6	30	1.6	17	1.1	25	1.1	91	1.4	119	1.4		
Total identified	2313	68.4	2751	63.7	1089	77.9	1363	71.1	1053	68.1	1401	61.7	4455	70.4	5515	64.8		
Total indeterminate	713	21.1	767	17.7	164	11.7	204	10.6	303	19.6	367	16.2	1180	18.7	1338	15.7		
Total monothalamids	3026	89.5	3518	81.4	253	89.6	1567	81.7	1356	87.7	1768	77.9	5635	89.1	6853	80.5		
															L		L+D	
Grand Total identified	2652	78.4	3512	81.3	1232	88.1	1697	88.5	1234	79.8	1874	82.6	5118	80.9	7083	83.3		
Grand Total indeterminate	729	21.6	810	18.7	166	11.9	220	11.5	313	20.2	395	17.4	1208	19.1	1425	16.7		
Grand Total	3381	-	4322	-	1398	-	1917	-	1547	-	2269	-	6326	-	8508	-		

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1 **Table 4.** Absolute and relative abundance of dead complete specimens of major taxa/groups in
 2 the three Strata. Xenophyophore fragments and gromiids are excluded.
 3

Morphological groupings	UK1A		UK1B		OMS		3 strata	
	N	%	N	%	N	%	N	%
Multichambered								
Robertinids	0	0	0	0	0	0	0	0
Rotaliids	40	4.25	16	3.08	65	9.00	121	5.54
Lagenids	4	0.43	1	0.19	1	0.14	6	0.27
Miliolids	4	0.43	3	0.58	10	1.39	17	0.78
Ammodiscids	32	3.40	11	2.12	16	2.22	59	2.70
Hormosinids	201	21.4	102	19.7	131	18.1	434	19.9
Trochamminids	52	5.53	20	3.85	26	3.60	98	4.49
Other textulariids	116	12.3	52	10.0	61	8.45	229	10.5
Total identified	422	44.8	191	36.8	292	40.4	905	41.5
Total indeterminate	27	2.87	14	2.68	18	2.49	59	2.70
Total multichambered	449	47.7	205	39.5	310	42.9	964	44.2
Monothalamids								
<i>Nodellum</i> -like	27	2.87	7	1.35	8	1.11	42	1.92
Lagenamminids	66	7.01	36	6.94	68	9.42	170	7.79
Flasks	90	9.56	74	14.3	87	12.0	251	11.5
Saccamminids	9	0.96	3	0.58	10	1.39	22	1.01
Droplet chambers	0	0	0	0	1	0.14	1	0.05
Spheres	36	3.83	27	5.20	44	6.09	107	4.90
Organic-walled	0	0	0	0	0	0	0	0
Hyperamminids	10	1.06	16	3.08	2	0.28	28	1.28
Tubes	132	14.0	52	10.0	71	9.83	255	11.7
Chain-like	11	1.17	19	3.66	16	2.22	46	2.11
Unclassified	64	6.80	45	8.67	51	7.06	160	7.33
Komokiacean-like	23	2.44	19	3.66	13	1.80	55	2.52
Komokiaceans								
Baculellidae	12	1.28	8	1.54	33	4.57	53	2.43
Komokiidae	12	1.28	8	1.54	8	1.11	28	1.28
Total identified	438	46.5	274	52.8	348	48.2	1060	48.6
Total indeterminate	54	5.73	40	7.71	64	8.86	158	7.24
Total monothalamids	492	52.3	314	60.5	412	57.1	1218	55.8
Total identified	860	91.4	465	89.6	640	88.6	1965	90.1
Total indeterminate	81	8.60	54	10.4	82	11.4	217	9.94
Total	941		519		722		2182	

4
5

Stratum	UK1-A							UK1-B							OMS							3 strata combined						
	L	L _{frag}	D	D _{frag}	L+D	Tot	%	L	L _{frag}	D	D _{frag}	L+D	Tot.	%	L	L _{frag}	D	D _{frag}	L+D	Tot.	%	L	L _{frag}	D	D _{frag}	L+D	Tot.	%
<u>Multichambered</u>																												
Robertinids	2	0	0	0	2	2	0.5	1	0	0	0	1	1	0.3	1	0	0	0	1	1	0.3	2	0	0	0	2	2	0.3
Rotaliids	14	0	11	0	18	18	4.4	9	0	4	0	10	10	3.1	10	0	12	0	17	17	5.5	21	0	17	0	27	27	4.7
Lagenids	1	0	4	0	5	5	1.2	0	0	1	0	1	1	0.3	1	0	1	0	2	2	0.6	2	0	6	0	8	8	1.4
Miliolids	5	0	1	0	5	5	1.2	2	0	2	0	3	3	0.9	2	0	3	0	3	3	1.0	5	0	3	0	6	6	1.0
Ammodiscids	2	0	3	0	3	3	0.7	2	0	3	0	3	3	0.9	3	0	3	0	3	3	1.0	3	0	3	0	3	3	0.5
Hormosinids	27	3	21	8	29	29	7.1	21	1	19	8	25	27	8.3	22	3	18	13	24	26	8.4	34	6	29	16	37	37	6.4
Trochamminids	10	0	10	0	14	14	3.4	2	0	8	1	9	9	2.8	5	0	7	1	10	10	3.2	12	0	15	1	18	18	3.1
Other textulariids	9	0	19	0	20	20	4.9	6	0	17	1	21	21	6.5	6	0	20	1	22	22	7.1	14	0	31	2	34	34	5.9
Total Multichambered	70	3	69	8	96	96	23.4	43	1	54	10	73	75	23.1	50	3	64	15	82	84	27.1	93	6	104	19	135	135	23.3
<u>Monothalamids</u>																												
<i>Nodellum</i> -like	11	1	4	2	11	11	2.7	5	0	5	1	6	6	1.9	5	1	4	2	5	5	1.6	11	2	7	2	12	12	2.1
Lagenamminids	8	0	7	0	9	9	2.2	5	0	8	1	11	11	3.4	5	0	6	0	7	7	2.3	9	0	11	1	13	13	2.2
Flasks	4	0	4	0	4	4	1.0	4	0	4	0	5	5	1.5	3	0	3	0	3	3	1.0	5	0	6	0	6	6	1.0
Saccamminids	17	0	5	0	19	19	4.6	11	0	2	0	12	12	3.7	5	0	4	0	8	8	2.6	24	0	8	0	27	27	4.7
Droplet chambers	2	0	0	0	2	2	0.5	0	0	0	0	0	0	0.0	1	0	1	0	1	1	0.3	2	0	1	0	2	2	0.3
Spheres	56	0	10	0	58	58	14.1	32	0	13	1	41	41	12.7	34	0	9	0	38	38	12.3	76	0	22	1	85	85	14.7
Organic-walled	15	1	0	0	15	15	3.6	10	2	0	0	10	10	3.1	11	1	0	0	11	11	3.5	22	2	0	0	22	22	3.8
Hyperamminids	3	0	2	1	4	5	1.2	1	1	4	2	5	5	1.5	1	1	2	3	3	4	1.3	3	2	6	4	6	6	1.0
Tubes	49	39	14	24	49	66	16.1	32	27	19	21	41	56	17.3	33	26	20	29	39	53	17.1	68	56	33	45	74	96	16.6
Chain-like	10	7	5	4	12	15	3.6	10	4	6	2	11	12	3.7	6	2	4	1	6	7	2.3	14	8	10	4	16	20	3.4
Unclassified	41	10	14	5	47	47	11.4	30	4	12	1	36	37	11.4	27	4	14	2	34	36	11.6	60	15	25	5	68	68	11.7
Komokiacean-like	18	6	4	3	18	19	4.6	10	3	5	1	14	15	4.6	8	4	8	3	10	12	3.9	20	10	11	6	21	22	3.8
<u>Komokiaceans</u>																												
Baculellidae	18	13	4	6	19	22	5.4	16	5	2	8	16	19	5.9	14	11	5	5	15	17	5.5	25	17	7	13	26	28	4.8
Komokiidae	16	7	5	5	18	20	4.9	11	8	4	3	13	16	4.9	7	5	4	5	9	13	4.2	20	11	10	8	23	25	4.3
Total Monothalamids	268	84	78	50	285	312	75.9	177	54	84	41	221	245	75.6	160	55	84	50	189	215	69.4	359	123	157	89	401	432	74.5
<u>Xenophyophores</u>	0	0	0	0	0	0	0.0	0	0	0	0	0	0	0.0	0	1	0	2	0	3	1.0	0	1	0	2	0	3	0.5
<u>Gromiids</u>	2	0	2	0	3	3	0.7	4	0	0	0	4	4	1.2	8	0	1	0	8	8	2.6	10	0	3	0	10	10	1.7
Total No. Species	340	87	149	58	384	411	-	224	55	138	51	298	324	-	218	59	149	67	279	310	-	462	130	264	110	546	580	-

Table 5. Number and proportion of species assigned to major foraminiferal groupings in the three Strata separately and combined. L = stained ('live') complete; L_{frag} = stained fragment; D = dead; D_{frag} = dead fragment; Tot = all four categories combined.

Table 6: Diversity indices based on stained ('live') complete specimens, and on dead complete specimens, computed for each sample based on the entire assemblage (including gromiids and xenophyophores). S = no. species; %S_{Tot} = proportion of species recognised in individual samples relatively to the total number of species in the 11 combined samples; Singl. = no. singletons; Doubl. = no. doubletons; E(S₁₀₀) = estimated number of species for 100 individuals; H = Shannon index; α = Fisher alpha; E = Evenness index; RID = Rank 1 Dominance; Chao1 = estimated total number of species.

'Live'	Complete										Fragments	
	S	%S _{Tot}	Singl.*	Doubl.*	E(S ₁₀₀)	H'	α	E	R1D	Chao 1	S	%S _{Tot}
MC02	103	17.8	39	13	45.64	3.82	39.7	0.44	11.5	161 ± 24	13	2.2
MC04	103	17.8	35	14	53.07	4.09	49.1	0.58	6.1	155 ± 20	23	4.0
MC07	175	30.2	51	22	56.02	4.39	67.3	0.46	8.6	257 ± 26	47	8.1
MC09	135	23.3	59	19	57.78	4.33	70.9	0.56	5.6	230 ± 31	23	4.0
MC11	135	23.3	43	15	55.37	4.3	55.9	0.55	6.1	192 ± 20	37	6.4
<i>UK1A total</i>	340	58.6	<i>151</i>	<i>35</i>	–	<i>4.85</i>	<i>103.6</i>	–	<i>5.7</i>	<i>449 ± 27</i>	87	15.0
MC05	137	23.6	59	17	56.59	4.31	71.4	0.54	5.9	246 ± 34	23	4.0
MC13	74	12.8	30	11	42.11	3.52	34.6	0.46	11.3	111 ± 16	25	4.3
MC25	101	17.4	38	10	35.84	2.77	35.9	0.16	47.8	159 ± 22	24	4.1
<i>UK1B total</i>	224	38.6	<i>114</i>	<i>17</i>	–	<i>4.12</i>	<i>80.0</i>	–	<i>20.1</i>	<i>370 ± 39</i>	55	9.5
MC20	88	15.2	29	5	49	3.86	41.4	0.54	9.1	156 ± 30	22	3.8
MC21	78	13.4	29	9	52.68	3.92	48.7	0.65	9.3	145 ± 28	17	2.9
MC22	141	24.3	41	12	51.01	4.19	51.4	0.47	6.5	237 ± 33	39	6.7
<i>OMS total</i>	218	37.6	<i>85</i>	<i>19</i>	–	<i>4.61</i>	<i>76.5</i>	–	<i>4.6</i>	<i>339 ± 35</i>	59	10.2
TOTAL	462	79.7	96	43	–	4.99	123.0	–	4.8	583 ± 27	130	22.4

Dead	Complete										Fragments	
	S	%S _{Tot}	Singl.	Doubl.	E(S ₁₀₀)	H \square	α	E	R1-D	Chao 1	S	%S _{Tot}
MC02	44	7.6	16	2	35	3.29	19.8	0.61	5.6	68 ± 15	7	1.2
MC04	49	8.4	15	4	35	3.13	21.0	0.47	9.2	74 ± 14	17	2.9
MC07	71	12.2	18	3	45	3.78	32.1	0.62	3.3	105 ± 17	17	2.9
MC09	49	8.4	16	7	48	3.56	36.6	0.72	4.1	86 ± 18	12	2.1
MC11	54	9.3	10	5	46	3.63	32.0	0.70	3.8	72 ± 10	38	6.6
<i>UK1A total</i>	149	25.7	<i>30</i>	<i>5</i>	–	<i>4.23</i>	<i>51.9</i>	–	<i>7.9</i>	<i>213 ± 23</i>	58	10.0
MC05	69	11.9	30	4	51	3.77	46.7	0.63	3.8	183 ± 51	30	5.2
MC13	62	10.7	26	6	54	3.87	46.9	0.78	2.7	105 ± 20	19	3.3
MC25	71	12.2	28	4	50	3.80	43.7	0.63	3.7	166 ± 43	18	3.1
<i>UK1B total</i>	138	23.8	<i>47</i>	<i>8</i>	–	<i>4.34</i>	<i>66.3</i>	–	<i>5.7</i>	<i>221 ± 27</i>	51	8.8
MC20	76	13.1	23	7	48	3.82	39.2	0.60	3.5	133 ± 25	30	5.2
MC21	71	12.2	25	7	50	3.75	40.9	0.60	4.3	108 ± 17	23	4.0
MC22	79	13.6	20	6	52	3.97	44.7	0.67	2.7	122 ± 19	37	6.4
<i>OMS total</i>	149	25.7	<i>25</i>	<i>12</i>	–	<i>4.34</i>	<i>61.0</i>	–	<i>5.8</i>	<i>224 ± 25</i>	67	11.6
TOTAL	264	45.5	50	10	–	4.61	82.0	–	6.3	388 ± 34	110	19.0

*The numbers of singletons and doubletons refer to numbers in individual samples, strata (italics) and the combined dataset (bold). These terms mean that there are only 1 or 2 specimens of any type (stained, dead or fragments) in a sample, stratum or combined dataset; i.e., a single stained specimen is not counted as a singleton if it is accompanied by one or more dead specimens or fragments.

1 **Table 7.** Morisita Index of spatial dispersion: distribution of species represented by ≥ 10
 2 complete tests in different ranges. Values < 1 = regular distribution; 1 = random distribution; > 1
 3 = clumped distribution. 'Live' = stained.

4

Morisita Index	Number of species	
	'Live'	'Live' + Dead
<1	1	1
1	0	4
1.1-1.9	31	51
2-2.9	30	30
3-3.9	17	28
4-4.9	7	5
5-5.9	6	8
6-6.9	5	4
7-7.9	5	4
8-8.9	0	1
9-9.9	3	1
10-11	6	5
Total species	111	142

5

See Excel spreadsheet for Supplementary Tables S1, S2

Supplementary Table S3: Absolute abundance of stained ('L' = 'live'), dead (D) and stained +dead (L+D) fragments of major groupings in the 3 strata. For the 3 strata combined, percentage abundances are also given. Xenophyophores and gromiids omitted.

Main group	UK1-A			UK1-B			OMS			3 Strata		
	L _{Frag}	D _{Frag}	L+D _{frags}	L _{Frag}	D _{Frag}	L+D _{frags}	L _{Frag}	D _{Frag}	L+D _{frags}	L _{Frag}	D _{Frag}	L+D _{frags}
<u>Multichambered</u>												
Robertinids	0	0	0	0	0	0	0	0	0	0	0	0
Rotaliids	0	0	0	0	0	0	0	0	0	0	0	0
Lagenids	0	0	0	0	0	0	0	0	0	0	0	0
Miliolids	0	0	0	0	0	0	0	0	0	0	0	0
Ammodiscids	0	0	0	0	1	1	0	0	0	0	1	1
Hormosinids	15	35	50	3	32	35	16	62	78	34	129	163
Trochamminids	0	1	1	0	3	3	0	8	8	0	12	12
Other textulariids	0	3	3	0	1	1	0	5	5	0	9	9
Total identified	12	26	38	1	16	17	15	45	60	28	87	115
Total indeterminate	3	13	16	2	21	23	1	30	31	6	64	70
Total multichambered	15	39	54	3	37	40	16	75	91	34	151	185
<u>Monothalamids</u>												
<i>Nodellum</i> -like	2	9	11	0	1	1	1	3	4	3	13	16
Lagenamminids	0	0	0	0	2	2	0	0	0	0	2	2
Flasks	0	0	0	0	0	0	0	23	23	0	23	23
Saccamminids	0	0	0	0	0	0	0	0	0	0	0	0
Droplet chambers	0	0	0	0	0	0	0	0	0	0	0	0
Spheres	0	0	0	0	1	1	0	0	0	0	1	1
Organic-walled	2	0	0	6	0	6	4	0	4	12	0	12
Hyperamminids	0	1	1	4	5	9	1	13	14	5	19	24
Tubes	676	276	952	412	259	571	313	256	569	1401	791	2192
Chain-like	188	41	229	17	9	26	21	19	40	226	69	295
Unclassified	417	50	467	11	2	13	32	5	37	460	57	517
Komokiacean-like	39	12	51	18	3	21	24	13	37	81	28	109
<u>Komokiaceans</u>												
Baculellidae	253	37	290	68	16	84	224	59	283	545	112	657
Komokiidae	170	57	227	228	23	251	47	30	77	445	110	555
Total monothalamids identified	1610	438	2048	743	264	1007	580	358	938	2933	1060	3993
Total monothalamids indet.	137	45	182	21	57	78	87	63	150	245	165	410
Total monothalamids	1747	483	2230	764	321	1085	667	421	1088	3178	1225	4403
Grand Total identified	1622	464	2087	744	280	1024	595	403	998	2961	1147	4108
Grand Total indeterminate	140	58	198	23	78	101	88	93	181	251	229	480
Grand Total	1762	522	2284	767	358	1125	683	496	1179	3212	1376	4588

Supplementary Table S4: Relative abundance of stained ('L' = 'live') and dead (D) fragments of major groupings in the 3 strata. Xenophyophores and gromiids omitted

Main group	UK1-A			UK1-B			OMS			3 Strata		
	%L _{Frag}	%D _{Frag}	%L+D _{frags}	%L _{Frag}	D _{Frag}	%L+D _{frags}	%L _{Frag}	%D _{Frag}	%L+D _{frags}	%L _{Frag}	%D _{Frag}	%L+D _{frags}
<u>Multichambered</u>												
Robertinids	0	0	0	0	0	0	0	0	0	0	0	0
Rotaliids	0	0	0	0	0	0	0	0	0	0	0	0
Lagenids	0	0	0	0	0	0	0	0	0	0	0	0
Miliolids	0	0	0	0	0	0	0	0	0	0	0	0
Ammodiscids	0	0	0	0	0.28	0.09	0	0	0	0	0.07	0.02
Hormosinids	0.85	6.70	2.19	0.39	8.94	3.11	2.34	12.5	6.62	1.06	9.37	3.55
Trochamminids	0	0.19	0.04	0	0.84	0.27	0	1.61	0.67	0	0.87	0.26
Other textulariids	0	0.57	0.13	0	0.28	0.09	0	1.01	0.42	0	0.65	0.20
Total identified	0.68	4.98	1.66	0.13	4.47	1.51	2.20	9.07	5.09	0.87	6.32	2.50
Total indeterminate	0.17	2.49	0.70	0.26	5.87	2.04	0.15	6.05	2.63	0.19	4.65	1.53
Total multichambered	0.85	7.47	2.36	0.39	10.3	3.55	2.34	15.1	7.72	1.06	11.0	4.03
<u>Monothalamids</u>												
<i>Nodellum</i> -like	0.11	1.72	0.48	0	0.28	0.09	0.15	0.60	0.34	0.09	0.94	0.35
Lagenamminids	0	0	0	0	0.56	1.18	0	0	0	0	0.15	0.04
Flasks	0	0	0	0	0	0	0	4.64	1.95	0	1.67	0.50
Saccamminids	0	0	0	0	0	0	0	0	0	0	0	0
Droplet chambers	0	0	0	0	0	0	0	0	0	0	0	0
Spheres	0	0	0	0	0.28	0.09	0	0	0	0	0.07	0.02
Organic-walled	0.11	0	0	0.78	0	0.53	0.59	0	0.34	0.37	0	0.26
Hyperamminids	0	0.19	0.04	0.52	1.40	0.80	0.15	2.62	1.19	0.16	1.38	0.52
Tubes	38.4	52.9	41.68	53.7	72.3	50.7	45.8	51.6	48.3	43.6	57.5	47.8
Chain-like	10.7	7.85	10.0	2.22	2.51	2.31	3.07	3.83	3.39	7.04	5.01	6.43
Unclassified	23.7	9.58	20.4	1.43	0.56	1.16	4.69	1.01	3.14	14.3	4.14	11.3
Komokiacean-like	2.21	2.30	2.23	2.35	0.84	1.87	3.51	2.62	3.14	2.52	2.03	2.38
<u>Komokiaceans</u>												
Baculellidae	14.4	7.09	12.7	8.87	4.47	7.47	32.8	11.9	24.0	17.0	8.14	14.3
Komokiidae	9.65	10.9	9.94	29.7	6.42	22.3	6.88	6.05	6.53	13.9	7.99	12.1
Total monothalamids identified	91.4	83.9	89.7	96.9	73.7	89.5	84.9	72.2	79.6	91.3	77.0	87.0
Total monothalamids indet.	7.78	8.62	7.97	2.74	15.9	6.93	12.7	12.7	12.7	7.63	12.0	8.94
Total monothalamids	99.1	92.5	97.6	99.6	89.7	96.4	97.7	84.9	92.3	98.9	89.0	96.0
<u>Grand Total</u>												
Grand Total identified	92.1	88.9	91.4	744	78.2	91.0	87.1	81.2	84.6	92.2	83.3	89.5
Grand Total indeterminate	7.94	11.1	8.67	23	21.8	8.98	12.9	18.7	15.3	7.81	16.6	10.5
Grand Total Numbers	1762	522	2284	767	358	1125	683	496	1179	3212	1376	4588

S1. TAXONOMIC APPENDIX: TOP 30 SPECIES IN ALL CATEGORIES

Description of the top-ranked species among complete specimens and fragments, live and dead combined. The names of formal taxa follow the higher-level classification of Pawlowski et al. (2013) and Kaminski (2014). The names of informal morphology-based groupings are given with inverted commas.

Multichambered taxa

Tubothalamea

Ammodiscidae

Glomospira gordialis (Jones & Parker 1860)

Trochammina squamata var. *gordialis* Jones & Parker, 1860, p. 304-305

Glomospira gordialis (Jones & Parker) Gooday and Goineau 2019; Supplementary Fig. S8F.

Gooday and Goineau (2019) provide the following information. ‘Our specimens of this widely distributed species typically measure around 200 µm (185-215 µm) in diameter. The test varies from being relatively flat to more three-dimensional and somewhat contorted, as in the illustrated specimen from Station M on the abyssal Californian margin assigned to this species by Enge et al. (2012, Pl. 1, fig. 11).’

Globothalamea

Rotaliida

Nuttallides umbonifera (Cushman 1933)

Pulvinulinella umbonifera Cushman, 1933, p. 90, Pl. 9, fig. 9

Nuttallides umbonifera (Cushman) Goineau and Gooday 2017, Supplementary Figure S2a.

A common species widely distributed in different oceans at abyssal depths and typically associated with carbonate-undersaturated bottom water masses below the lysocline (Mackensen et al., 1995).

Hormosinidae

Hormosinella distans (Brady, 1881)

Reophax distans Brady, 1881, p.50

Reophax distans (Brady). Brady, 1884, p. 296, Pl. 31, figs 18–22.

See Jones (1994, Pl. 31, figs 18,19) and Schröder et al. (1988, Plate 5, Fig. 7; as *Reophax distans*). This distinctive species has a test comprising a small number of relatively large, more or less equally-sized oval chambers joined by stolons.

Hormosinella guttifer (Brady 1881)

Reophax guttifer Brady, 1881, p. 49

Reophax guttifer (Brady). Brady, 1884, p. 295, Pl. 31, figs 10–15.

See Jones (1994 Pl. 31, Figs.10–15). Another distinctive species comprising a long, more or less straight series of droplet-shaped chambers, often decorated with large agglutinated particles.

Hormosinella sp. 3
Supplementary Figure S9A

A small, delicate species comprising a spherical proloculus (~55-65 μm diameter) followed by a series of chambers of increasing length (90-200 μm) and relatively uniform width (65-70 μm). The wall is thin, finely-agglutinated and translucent, but often decorated with larger particles, mainly radiolarian fragments.

Hormosinella sp. 4
Supplementary Figure S9D

Small, 2-chambered species in which the second chamber is larger than the first and is produced into a fairly long neck. One specimen measures 690 μm in length, with individual chambers 240 and 440 μm long. Another measures 960 μm with chambers 310 and 625 μm long.

Hormosinella sp. 5
Supplementary Figure S9C

Small, delicate test comprising a more or less linear series of oval chambers (78-100 μm long) joined by relatively long stolons, 50-90 μm long. The largest specimen, which is probably complete, has an overall length of 570 μm .

Reophax aff. *helenae* Rhumbler, 1931

Goineau and Gooday 2017; Supplementary Figure S2b,c.

Goineau and Gooday (2017) note that this species resembles *R. helenae* (Rhumbler, 1931) of Enge et al. (2012) from Station M in the NE Pacific and Schröder (1986) from the NW Atlantic but differs from the original description of Rhumbler (in Wiesner, 1931), based on material from >4,000 m in the Caribbean, which has a test composed of large planktonic foraminiferal shell fragments rather than mineral grains.

Reophax scorpiurus de Montfort, 1808

Reophax scorpiurus de Montfort, 1808, p. 551-552, Pl.83.

Reophax scorpiurus de Montfort, 1808. Brönnimann and Whittaker 1980, p. 261, Figs 1-7, 12, 17.

Reophax scorpiurus de Montfort, 1808. Goineau and Gooday 2017, Supplementary Figure S2d,e

Reophax scorpiurus de Montfort, 1808. Goineau and Gooday 2019, Fig. 2I

Goineau and Gooday (2017) provide the following comments. ‘Our specimens have the typical asymmetrical shape of this well-known and widely-distributed ‘species’, which was first described from beach sands in the Adriatic (Brönnimann and Whittaker, 1980). They resemble the specimen illustrated by Resig (1981; Pl. 9, Fig. 14). This ‘species’ is best considered a morphotype or species complex (Gooday and Jorissen, 2012).’

Reophax sp. 112/113

Reophax sp. 112/113. Gooday et al. 2010, Fig. 14A

Reophax sp. 9. Stefanoudis et al. 2016, Pl. 1, Figs. 11–12 (as *Reophax* sp. 9)

Reophax sp. 112/113. Gooday and Goineau 2019, Supplementary Fig. S3A,B.

A small delicate species, typically comprising 2-3 asymmetrical chambers of increasing size. In stained specimens the cytoplasm is confined to the final chamber. This species is well-known from the Porcupine Abyssal Plain (NW Atlantic).

Reophax sp. 1

Reophax sp. 1. Goineau and Gooday 2017, Supplementary Figure S2f–i.

Reophax sp. 1. Gooday and Goineau 2019, Fig. 2J.

Goineau and Gooday (2017) provide the following description of this species, which is the most common hormosinid in our samples.

‘Test composed of 3–5 rounded to ovate, clearly-defined chambers, arranged along a straight or curved axis. Test coarse-grained and consisting of mineral grains. Aperture at end of short neck. Length 550–1350 μm .’

Reophax sp. 2

Goineau and Gooday 2017; Supplementary Figure S2j–l.

Goineau and Gooday (2017) provide the following description. ‘Test composed of 2 to 3 rounded to slightly ovate chambers arranged along a more or less linear axis. Wall thin with a relatively smooth outer surface and often incorporating coloured mineral particles. Some specimens with a dusting of fine-grained particles that obscure parts of the test. The most characteristic feature is the development of a fairly long apertural neck, flared at the distal end. Length 300–800 μm .’

Reophax sp. 5 Figure 2A

Test somewhat fusiform in shape, comprising 3-5 chambers of increasing size along a straight to curved axis. Nine specimens from MC07 range from 420 to 910 μm in length. Wall coarse grained with uneven surface, composed of various mineral grains including characteristic red particles in addition to whitish or transparent particles and occasional micronodules.

Trochamminoidea

Adercotryma sp.

Adercotryma sp.. Gooday and Goineau 2019; Fig. 1G, H.

Gooday and Goineau (2019) provide the following information.

‘Brönnimann and Whittaker (1987) distinguished *Adercotryma glomeratum*, for which they established a lectotype from a 146-m-deep site in the Canadian Arctic, from a new species, *A. wrighti*. Among the criteria used to distinguish the two species was the presence of four chambers in the final whorl in *A. glomeratum* compared with only three in *A. wrighti*. Some of our small specimens of *Adercotryma* have three whereas larger species tend to have four such chambers. Given this variation, and the fact that our samples originate from abyssal depths, we prefer to leave our Pacific species unidentified. Nevertheless, it is probably the same as *Adercotryma glomeratum* (Brady, 1878), Kuhnt et al. (2000) and Gooday et al. (2010) from the deep Atlantic, Resig (1981 Pl. 10, fig. 11) from the SE Pacific, and Enge et al. (2012) from Station M in the NE Pacific. These authors recognised more elongate and less elongate forms, both of which are present in the CCZ material.’

?*Paratrochammina challengerii* Brönniman & Whittaker, 1988 Supplementary Figure S9F-H

?*Paratrochammina challengerii* Brönniman & Whittaker 1988, p. 43-44, Figs. 16H-K

This species is close to *P. challengerii*, as illustrated by Brönnimann and Whittaker (1988). Two specimens from samples MC02 and MC07 measure 417 and 506 μm , respectively, and have 4 chambers in the final whorl.

Deuterammina aff. *grahami* Brönniman & Whittaker, 1988 Figure 2B

Our specimens resemble *Deuterammina grahmi*, as illustrated by Brönniman & Whittaker (1988, p. 104-107, Figs. 38A-J, 39A-C), in having 6 chambers, each with a rounded periphery, in the final test whorl. However, the agglutinated particles do not include barite (‘barytes’) grains, which are present in varying proportions in the holotype and paratypes. It is probably not the same species as *D. grahmi* as illustrated by Enge et al. (Pl. 2, figs 15-16), which has a smoother test outline and surface, in addition to being composed of barite particles. Five specimens from samples MC04 and

MC07 measure between 190 and 230 μm in maximum diameter and have 6 chambers in the outer whorl.

Other Textulariids

Cribrostomoides subglobosa (Cushman, 1910)

- Haplophragmium latidorsatum* Bornemann. Brady 1884, p. 307-308, Pl. 34, Figs. 8–10
Haplophragmoides subglobosum Cushman 1910, p. 105-106, Figs 162-164
Cribrostomoides subglobosum (M. Sars 1868). Thies, 1991, p. 23-24, Pl. 7, fig. 4a-c; Pl. 9, fig. 1-12; Pl. 10, fig 1-13.
Cribrostomoides subglobosus forma *subglobosus* (Cushman 1910). Jones et al., 1993, Fig. 1.1-3, 1.5; Pl. 1; Pl.2 figs 6a-8b; Pl. 3
Cribrostomoides subglobosus forma *bradyi* (Cushman 1910). Jones et al., 1993,
Cribrostomoides subglobosa (Cushman). Enge et al. (2012, Pl. 2, fig. 1)
Cribrostomoides subglobosa (Cushman). Holbourn et al. (2013, p. 220).

This well-known deep-sea species has been widely reported from different oceans, for example, by Thies (1991), Enge et al. (2012) and Holbourn et al. (2013). We have not attempted to distinguish between the two varieties of the species (forma *bradyi* and forma *subglobosus*) of the species recognised by Jones et al. (1993) in their detailed taxonomic revision of the genus.

Cyclammia trullissata (Brady, 1879)

- Trochammia trullissata* Brady 1879, p. 37-38, Pl. 5, figs 10a,b,11
Trochammia trullissata Brady 1879. Brady 1884, p. 342-343, Pl. 40, figs 13-16.
Cyclammia trullissata (Brady). Resig 1981, Pl.10, fig. 8
Cyclammia trullissata (Brady). Schröder 1986, p. 49-50, Pl. 18, fig. 9

Our specimens are smaller than those on Brady's type slide (see Jones 1994, Plate 40, Fig. 6), which originated from much a shallower site (390 fm = 714 m) in the Caribbean. They are more similar to the abyssal specimen from the SE Pacific illustrated by Resig (1981). This abyssal form may represent a distinct species.

?*Verneulinulla propinqua* (Brady, 1884)

- Verneuilina propinqua* Brady 1884, p. 387, Pl. 47, figs 8-12
 ?*Verneulinulla propinqua* (Brady). Goineau and Gooday 2017, Supplementary Figure S2m–o.

A large species that is common in ABYSSLINE epibenthic sledge samples. See Brady's original figure in Jones (1994, Plate. 47, Figs. 8–12).

'Monothalamids'

Monothalamids encompass a heterogeneous assortment of basically single-chambered foraminifera, which we divide into categories based mainly on morphological criteria. We include here species of the Komokiacea, a group of uncertain taxonomic affinity.

***Nodellum*-like forms**

Nodellum sp. 1

Nodellum sp. 1. Goineau and Gooday, 2017, Supplementary Figure S3g.

Goineau and Gooday (2017) provide the following brief description. ‘Test elongate, rigid, organic, yellowish. Slender, spindle-shaped proloculus with closed pointed proximal end. Main part of test tubular (~40–50 μ m maximum width), straight or gently arcuate. One or two internal partitions may be present. Aperture terminal, round, constricted, sometimes with delicate, tubular extension. Length ~1,100–1,800 μ m.’

This species is much smaller than *Nodellum aculeata* of Gooday et al. (2008) from the Challenger Deep (10,896 m).

Saccamminidae

Lagenammina difflugiformis (Brady, 1879)

Reophax difflugiformis Brady, 1879, p. 32-33, Pl. IV, figs 3a,b

Lagenammina difflugiformis (Brady) Goineau and Gooday, 2017; Supplementary Figure S6b,c.

Lagenammina difflugiformis (Brady) Gooday and Goineau, 2019; Supplementary Fig. S1C,D

Goineau and Gooday (2017) provide the following description. ‘Droplet-shaped chamber tapering to short apertural neck. Test wall often distinctly rusty-brown in colour, composed of fairly coarse-grained mineral particles. Length ~300–400 μ m.’ They comments that the ABYSSLINE specimens ‘are similar to some of those assigned by Brady (1884; Pl.30, Figs. 1–4) to this species. This is probably the same species as the ‘morphotype resembling *L. difflugiformis*’ from the abyssal NE Atlantic, illustrated by Gooday et al. (2010; Fig. 13C) and *Lagenammina* sp. of Gooday and Jorissen (2012; Fig.2e,f). It is one of the most common species in the ABYSSLINE material.’

Lagenammina tubulata (Rhumbler, 1931) Supplementary Figure S9B

Saccammina tubulatum Rhumbler, 1931, in Wiesner 1931, p. 82, Pl. 23, fig. 1.

Lagenammina tubulata (Rhumbler). Kuhnt et al., 2000, p. 279; Pl. 1, fig. 14; Pl. 10, fig. 2

Lagenammina tubulata (Rhumbler) Enge et al., 2012, Pl. 1, Fig. 8

Lagenammina tubulata (Rhumbler, 1931). Gooday and Goineau, 2019; Supplementary Fig. S1F

Gooday and Goineau (2019) comment as follows. ‘This distinctive species has a globular chamber followed by a long, straight neck. There is some confusion about the name. We refer to it here as *L. tubulata* (rather than *L. tabulata*), since this is the name more commonly used, including by Kuhnt et al. (2000) and Enge et al. (2012), who illustrate specimens from the Atlantic and Pacific, respectively, that resemble those found in our material.’

‘Flasks’

We include here several flask-like species that differ from *Lagenammina* that contain stercomata and have test walls that are composed, at least partly, of organic material.

Flask sp. 2 Supplementary Figure S9F-H

This curious form comprises a cluster of organic-walled flask-like chambers, each 220-310 μm long, with long necks. The flasks appear to lack any direct connection with each other but are pressed tightly together in an arc with the necks directed inwards. The wall typically gives rise to spiky processes around the bulbous proximal part. The interior often contains dark material, presumably the remains of stercomata.

Remarks. These clusters of flasks seem to be part of larger formations. Some specimens display komokiacean-like features, including long tubular filaments arising from tubercles.

Flask sp. 3

Goineau and Gooday 2017; Supplementary Figure S3d-f

Goineau and Gooday (2017) provide the following brief description.

‘Asymmetrical flask-shaped agglutinated chamber, ~150 μm in maximum width and 250 μm in length, including the long (~100–150 μm) tapered apertural neck. The interior is occupied by stercomata and stained material. The wall is composed of an organic layer overlain by a sparse agglutinated veneer comprising a mixture of mineral particles of different sizes, and in most cases with one or more radiolarian tests projecting from the outer surface.’

Flask sp. 4

Goineau and Gooday 2017; Figure 4: d-f.

Goineau and Gooday (2017) provide the following brief description.

‘Fairly coarsely-grained agglutinated chamber (~100–150 μm width), more or less spherical to somewhat angular. Two more or less straight open-ended tubes, often of different lengths (~50–100 μm and ~200–250 μm), extend from opposite sides of the chamber. Most specimens have dead radiolarian tests attached to the outer test surface. The cytoplasm appears dark brown in colour due to the presence of stercomata.’ Goineau and Gooday note that this species is distinguished from the genera *Astrammina* and *Armorella* by its much smaller size, the presence of stercomata, and the lack of an ‘allogromiid-like’ cell body of the type found in *Astrammina*.

‘Spheres’

Psammosphaerid sp. 19

Goineau and Gooday 2017, Figure 4j,k.

Goineau and Gooday (2017) provide the following brief description.

‘Spherical agglutinated test without visible aperture, and ranging from ~100 to ~300 μm . Wall finely granular and relatively thick, with variable numbers of radiolarian tests and mineral particles attached to the outer surface. Test interior with stained cytoplasm and stercomata.’

Psammosphaerid sp. 20

Goineau and Gooday, 2017; Supplementary Figure S3a

Goineau and Gooday (2017) provide the following brief description.

‘Tiny (<100 μm) agglutinated sphere without visible aperture. Wall fairly thick and finely granular with a rough surface. Interior with stercomata. Often attached to bigger mineral (micronodule) or biogenic (diatom frustule, radiolarian test) particle.’

Psammosphaerid with tubes sp. 5
Supplementary Figure S7E

The test is usually more or less oval and 180- 250 μm in maximum dimension. The wall is soft and translucent with a finely agglutinated surface and gives rise to 2-3 long delicate flexible tubes, up to 850 μm long. The interior is filled with stercomata.

Hyperamminidae

Hyperammina cylindrica Parr, 1950
Supplementary Figure S9K

Hyperammina cylindrica Parr, 1950

Hyperammina cylindrica Parr, 1950. Jones, 1994; Plate 23, Figs 4,7.

Hyperammina cylindrica Parr, 1950. Szerak, 2007, Pl. 1, Fig. 2.

Remarks. This species has a straight to slightly curved test. Two typical specimens from sample MC02 measure 2.3 and 2.5 mm long.

Hyperammina sp. 2
Supplementary Figure S10A,B

This distinctive species comprises a thin-walled organic tube originating from a clearly-developed proloculus and surrounded by a jumble of relatively large radiolarian shells, through which the organic tube is clearly visible. In ‘live’ specimens, the inner tube is filled with red-stained cytoplasm. A typical specimen measures ~1 mm long and 259-300 μm wide, including the radiolarians. The organic tube is 50-60 μm wide and the proloculus 250 μm long and 120 μm wide.

‘Tubes’

Bathysiphon sp. 2

Bathysiphon sp.2. Goineau and Gooday, 2017; Supplementary Figure S3h,i

Goineau and Gooday (2017) provide the following brief description.

‘Gently tapered tubular test, up to 2.3 mm long and ~30–40 µm wide, open at both ends and following a curved or sinuous course. Surface smooth, finely agglutinated, white with a reflective sheen.’

Rhizammina aff. *algaeformis*. Brady, 1879
Figure 2F

Rhizammina algaeformis Brady 1879. Kamenskaya et al., 2012, Fig. 5a

Test fragments are fairly stiff and relatively straight with occasional branches. The wall is finely but noticeably agglutinated from small transparent particles and fairly densely encrusted with whitish radiolarians shells, giving it a knobbly appearance. The width (without the radiolarians) typically ranges from about 200 to 270 µm. Grey masses of stercomata are clearly visible through the wall. In stained specimens a strand of cytoplasm runs alongside the stercomata mass, a typical feature of the genus.

Remarks This *Rhizammina* species is fairly similar to *R. algaeformis* of Brady (1884), although Brady’s type material in the Natural History Museum, London, is not densely encrusted with radiolarians. This species is probably the same as *Rhizammina algaeformis* of Kamenskaya et al. (2012) from the Interoceanmetal Joint Organization claim area of the eastern CCZ.

Rhizammina sp. 1
Supplementary Figure S10C,D

Goineau and Gooday 2017; Supplementary Figure S4g–i

The tubular test is to 1 mm or more in length and ~150–240 µm wide, straight or slightly bent, occasionally branching. The wall is thick (~50 µm) but delicate, comprising a mixture of fine, mostly transparent mineral grains, outwardly-directed sponge spicules and subordinate numbers of radiolarian tests forming an irregular bristling outer surface. Test interior with cytoplasm forming a narrow string (~20 µm width) extending along the entire length of the tube. A somewhat wider (~40 µm width) strand of stercomata enclosed within a very delicate organic membrane runs along the tube parallel to the cytoplasm. This internal organisation confirms the placement in *Rhizammina*.

Rhizammina sp. 5
Figure 2G; Supplementary Figure S10E,F

Tube fragments are narrow, generally 62 – 83 µm diameter, and follow a somewhat curved, sinuous or uneven course. Dichotomous branches are fairly common (although not all fragments branch) and branches occasionally end blindly. The tube interior contains a mass of stercomata and a thread of stained cytoplasm is occasionally seen running parallel to it, supporting the identification as a *Rhizammina* species.

Tube sp. 2
Supplementary Figure S10G-I

The test is an organic-walled tube with closed ends in complete specimens and a more or less circular cross section. The longest specimen (from sample MC02) is 1.1 mm long and 70-85 μm wide, with two short triangular side processes. Four specimens from the same sample are 260, 590, 725 and 895 μm long and relatively much wider (100-125 μm) than the longest specimen, while a fifth has a triradiate test with 3 short arms. These wider tests give rise to several conical processes that extend into long thin tubular filaments. All specimens contain dark stercomata mixed with red-stained material.

Remarks. It is possible that the slender (Fig. S10G,H) and wider forms (Fig. S10I) are distinct species.

Tube sp. 2E
Figure 2I

The test is fairly irregular, forming either a single tubular structure or a number of broad branches, typically more or less crooked and sometimes rather flattened. The wall is soft, finely agglutinated with somewhat fluffy surface. The test interior is densely dotted with small stercomata.

Tube sp. 9

Goineau and Gooday, 2017; Supplementary Figure S6a–c

The following description is amended from that of Goineau and Gooday (2017).

Basically tubular test, up to at least 3 mm long and of variable width (~100–150 μm), with short side branches and lateral swellings. There is no visible aperture. Wall thin, basically organic with a dusting of fine particles on the outer surface; conical tubercles giving rise to fine organic filaments and tubes are often developed. Test interior filled with a dense mixture of cytoplasm and stercomata.'

Tube sp. 10
Supplementary Figure S10K,L

Goineau and Gooday, 2017; Supplementary Figure S5a–c

Goineau and Gooday (2017) provide the following brief description.

'Narrow (~50 μm width), curved to slightly sinuous a gglutinated tube, up to 1 mm long. Most specimens are fragments but a closed end is present in some cases. Wall fairly thin, composed of coarse, angular grains, giving a rough 'sparkly' surface under the stereomicroscope. Cytoplasm with stercomata is visible through wall in transmitted light.'

Remarks. During the analysis of samples we referred to these informally as 'sparkly tubes'.

Tube sp. 19

Goineau and Gooday, 2017; Supplementary Figure S5l,m

Goineau and Gooday (2017) provide the following brief description.

‘Transparent, organic-walled tube, 0.6–1.0 mm long and ~50–80 µm wide; the wall is yellow, fairly thick, sometimes with a dusting of fine-grained particles. One end of the tube may be closed. Cytoplasm filled with dense stercomata.’

Tube sp. 23

Goineau and Gooday, 2017; Supplementary Figure S6: d–f

Goineau and Gooday (2017) provide the following brief description.

‘Delicate, branching, basically tubular test, ~50–80 µm wide and a few 100 µm in length. Wall composed of an organic layer covered by a thin dusting of fine-grained particles, and often incorporating radiolarian tests and large mineral grains. The organic layer gives rise to numerous short filaments extending from the organic part of the wall, giving a very fuzzy, ragged aspect. Cytoplasm contains large but relatively sparse stercomata.’

Tube sp. 25

Goineau and Gooday, 2017; Supplementary Figure S5f–i

Goineau and Gooday (2017) provide the following brief description.

‘Relatively short, more or less straight, slightly tapered tubular test, ~400–1,000 µm long and ~100 µm wide. One end is typically closed and the other end open. Wall noticeably granular under stereomicroscope, composed of small, angular particles and incorporating variable numbers of much larger radiolarian tests. Interior with stercomata embedded in red-stained material.’

Tube sp. 27

Goineau and Gooday, 2017; Supplementary Figure S5 j, k

Goineau and Gooday (2017) provide the following brief description.

Small, slender, spindle-shaped to tubular test, <500 µm long and ~40 µm maximum width. Wall with yellowish tinge and a variably developed, finely-agglutinated veneer overlying an organic base; a few scattered larger particles are sometimes present. Test contents finely granular, containing numerous tiny stercomata-like bodies.

Tube sp. 32

Goineau and Gooday, 2017; Supplementary Figure S3j–l

Goineau and Gooday (2017) provide the following brief description.

‘Basically tubular test, from a few 100 µm up to 2.6 mm long and ~150–250 µm wide, usually more or less straight or slightly crooked, sometimes with slight constrictions or swollen sections. One or both ends are closed in specimens that appear complete. Wall fairly thin but semi-opaque, finely agglutinated and typically with tiny scattered dark particles. A few larger biogenic particles and micronodules may be attached on the wall.’

Goineau and Gooday remark that smaller specimens of this species have an equidimensional shape that make it difficult to classify morphologically. It is rather similar to the xenophyophore

genus *Aschemonella* but lacks the internal features (stercomare and granellare) typical of xenophyophores.

Tube sp. 33/36

Goineau and Gooday, 2017; Supplementary Figure S6g–h

Goineau and Gooday (2017) provide the following brief description.

‘Delicate, fragmentary, tubular test, unbranched and either straight or gently curved; fragment are <500 μ m long and ~100 μ m wide. Wall with a distinct basal organic layer overlain by a very heterogeneous and coarse-grained mixture of angular quartz grains and biogenic particles, mainly radiolarian tests, that project to create a very un even outer surface. Cytoplasm filled with stercomata.’

Tube sp. 39

Supplementary Figure S10J

The test forms a basically tubular structure that follows a more or less irregular course and is constricted at regular intervals to form rather weakly-defined ‘pseudochambers’. The longest specimen is 3.75 mm in length (measured along the tube) and the ‘pseudochambers’ decrease in width from 290 μ m near the aperture to 125 μ m at the proximal end. A second specimen is smaller, measuring 1.43 mm along the length and tapering from 160 to 42 μ m. The wall is finely but noticeably agglutinated from mineral grains of different sizes. Fine hair-like filaments arise from the distal part of the structure. The largest specimen contains stained cytoplasm in the distal third end and stercomata in the proximal two thirds.

Tube sp. 40

Goineau and Gooday, 2017; Supplementary Figure S5d, e

Goineau and Gooday (2017) provide the following brief description.

‘Unbranched, tubular test, typically fragmented, 500 μ m or more long and of somewhat variable width (generally ~150–200 μ m), agglutinated with coarse, angular particles, with one closed end and an aperture at the opposite end. The tube follows a more or less straight or somewhat crooked course. Wall is noticeably granular under the stereomicroscope and composed of small quartz grains. It may give rise to fine, flexible filaments, although these are not always developed. Cytoplasm contains sparse stercomata.’

Tube sp. 41

Goineau and Gooday, 2017; Supplementary Figure S6i, j

Goineau and Gooday (2017) provide the following brief description.

‘Test forms a curved, sometimes slightly twisted, tapered tube, ranging in length from ~0.5 to 2.3 mm (measured along the length) and with a maximum width of ~150 μ m. Transverse constrictions are more or less well developed and the narrower (proximal) end is closed, forming a rounded proloculus (40–80 μ m diameter). The test interior is interrupted by occasional transverse septae. The entire tube is reddish in colour when stained. The wall is translucent and comprises a relatively

thick organic base overlain by a fine-grained agglutinated layer of variable thickness. Cytoplasm contains stercomata.’

Tube sp. 43

Goineau and Gooday, 2017; Figure 5n–p

Goineau and Gooday (2017) provide the following brief description.

‘Delicate, brownish tubular test that is occasionally branched. The longest pieces are 500–900 μm in length and $\sim 80\text{--}100\ \mu\text{m}$ wide. Specimens are often open-ended and appear to be fragments, but one closed end is sometimes observed. The tubes have a neat, finely agglutinated wall, $\sim 20\ \mu\text{m}$ thick, and at least one closed end. The test interior contains dark stercomata that appear, either singly or in clumps, as a series of dots along the length of the tube.’

Tube sp. 44

Goineau and Gooday, 2017; Supplementary Figure S7i, j

Goineau and Gooday (2017) provide the following brief description.

‘Delicate, narrow, branching tube, typically ~ 0.5 up to $1.5\ \text{mm}$ long and $< 50\ \mu\text{m}$ wide. The wall is thin and composed of fine particles. There is no obvious aperture, although the ends of the tubes are often broken. Cytoplasm contains numerous stercomata.’ Goineau and Gooday (2017) comments that this form ‘resembles Tube sp. 43 but is considerably narrower and more often branched.’

Tube sp. 45

Goineau and Gooday, 2017; Supplementary Figure S7a–f

Goineau and Gooday (2017) provide the following brief description.

‘Tubular test, $\sim 0.6\text{--}1.4\ \text{mm}$ long (complete specimens) and $\sim 100\text{--}150\ \mu\text{m}$ wide, either branched or unbranched, sometimes with short side lobes; ends are sometimes closed. Test wall soft and fine-grained and of relatively even thickness ($\sim 20\ \mu\text{m}$). Test interior with dense stercomata.’ They remark that Tube sp. 45 resembles Tube sp. 43 but is ‘distinctly wider’.

Tube sp. 46

Goineau and Gooday, 2017; Supplementary Figure S7g, h

Goineau and Gooday (2017) provide the following brief description.

‘Tubular test follows a more or less straight or somewhat crooked course; it is usually unbranched but sometimes has a short side lobe. Intact ends are closed, but all available specimens appear to be fragments with one or both ends broken. Most are $< 1\ \text{mm}$ but the longest reaches $\sim 3\ \text{mm}$ in length; the width varies from 230 to $350\ \mu\text{m}$. The wall is thick, finely agglutinated with a slightly fuzzy surface; the thickness is generally between 25 and $35\ \mu\text{m}$ but a thinner-walled variant also occurs. The test interior is densely packed with a mass of stercomata and red-stained material, the outline of which is visible through the wall when the tube is immersed in glycerol.’

Tube sp. 48

Goineau and Gooday, 2017; Figure 4a–c

Goineau and Gooday (2017) provide the following description.

‘Typical specimens are elongate and best described as approximately spindle-shaped, tapering towards both ends and sometimes with short triangular processes or tapering side branches. These typical spindles grade into more tubular tests. Most specimens are probably complete and measure from ~0.3 to 0.8 mm long and 60 to 220 μ m wide. Occasionally, two spindles are joined end to end. The wall is translucent with a very fine granularity visible when viewed under the stereomicroscope. Under high magnification in a compound microscope, the wall appears basically organic with a variably developed veneer of fine particles, normally 5–15 μ m thick but sometimes more. In some samples, a few radiolarians or other biogenic particles project from the test wall. Large, dark stercomata, sometimes densely packed, are a prominent feature of the test interior. Several variants are included within this form. In one type, the test has a smoother outline, is devoid of radiolarians, triangular processes and short side branches but sometimes bifurcates. Another variant has a rather irregular shape and a ‘fluffy’ surface with short filaments. All types contain dense stercomata.

Remarks. These spindle-shaped tubes are among the most common monothalamids in our samples. They exhibit considerable variability, however, and may possibly encompass more than one species. We regard individual spindles as individuals, although the occasional presence of two joined end to end suggests that at least some may be fragments of longer chain-like formations.

Tube sp. 54

Goineau and Gooday, 2017; Figure 4g–i

Goineau and Gooday (2017) provide the following description.

‘Test basically tubular to spindle-shaped, 0.2–0.8 mm long and relatively wide (~50–150 μ m); some specimens bifurcate while others comprise two spindle-shaped elements, one of which buds off the side of the other. Wall fairly delicate and seems basically organic with variably developed surface layer of flat-lying, mainly siliceous particles resulting in a relatively smooth outer surface. Test contents very heterogeneous, including stercomata but also a variety of crumpled organic sheets and organic-walled cyst-like structures. A variant form includes tubular to spindle-shaped tests of similar size to typical specimens. Some intact tests have one end that is rounded and closed and the XII other end narrower and drawn out into a delicate organic filament. Compared to typical specimens, this form has a thicker wall that is more distinctly granular when observed in a compound microscope. The test interior is also dominated to a much greater extent by dark stercomata.’

Tube sp. 56

Goineau and Gooday, 2017; Supplementary Figure S4a–c

The tubular test occurs only as fragments, ranging in width from 90 to 155 μ m (typically 110–140 μ m). A few fragments have closed ends. The wall is finely agglutinated and largely devoid of larger particles. The interior contains dark stercomata mixed with stained particles.

Remarks These tubes superficially resemble *Rhizammina* but lack the typical internal organisation of this genus, i.e., a strand of cytoplasm running alongside a mass of stercomata. A few fragments also have closed ends, another feature that is not typical of *Rhizammina*.

Tube sp. 57

Goineau and Gooday, 2017; Supplementary Figure S4d–f

Goineau and Gooday (2017) provide the following brief description and remarks.

‘Unbranched or occasionally branched tubular test, up to 1 cm or more in length and 75–100 μm wide, open at both ends and following a curved, often somewhat crooked course. Wall finely granular with relatively smooth outer surface. Interior with dense stercomata and red-stained material.’

‘Remarks. Tube sp. 57 differs from Tube sp. 56 in being somewhat narrower and always open-ended rather than sometimes having a closed end. Although the agglutinated wall is fine-grained, the grains are noticeably larger than those that constitute the wall of Tube sp. 56 when observed under a compound microscope. Like Tube sp. 56, this species lacks internal features typical of *Rhizammina* a genus to which it was originally assigned.’

Tube sp. 73

Figure 2E

The tubes are relatively large, the longest fragment (from sample MC13) measuring 2.8 mm in length. The overall width ranges from 140 to 210 μm in 5 fragments from MC13. They follow a curved, somewhat sinuous or crooked course; one specimen branches and two others give rise to short, triangular projections, probably incipient side branches. The wall is fine-grained but dotted with a few larger particles, mainly radiolarian shells. It is fairly thick and almost opaque in reflected light. The test interior contains masses of stercomata in a red-stained matrix.

Tube sp. 92

Figure S9J

The largest tube fragment is 1.15 mm long. The tubes are relatively thick (160–215 μm) in relation to their overall size. They branch, in some cases several times, and where not broken, the branches are short and have rounded terminations. The wall is soft, very thick and uniformly fine-grained. The lumen contains stercomata, which form a dark core that is visible through the wall and occupies about a third of the width of the tube.

Tube sp. 122

Supplementary Figure S10M

The tubular test fragments are straight and usually unbranched; all have broken ends with no sign of closure. They range in width from 280 to 410 μm . The wall is thin, translucent, and noticeably granular under a stereo microscope. It is composed mainly of small transparent grains but also dotted with tiny dark particles.

‘Chains’

Although superficially appearing multichambered, we consider chains-like morphotypes to comprise a series of ‘pseudo-chambers’ or ‘segments’ rather than true chambers, and therefore include them with the monothalamids.

Chain sp. 13

Goineau and Gooday, 2017; Figure 5d–g

Goineau and Gooday (2017) provide the following brief description.

‘The elongate test is 0.5–1.5 mm long in specimens that are apparently complete (although most appear to be fragments) and ranges from <100 μ m to ~260 μ m in width, according to the thickness of the agglutinated layer. It occasionally branches but most specimens are unbranched. The wall is basically organic so that the entire test stains red. The organic layer is overlain by a layer of finely agglutinated material that varies in thickness from 90–100 μ m (in which case the test interior is largely obscured) to ~15 μ m, or in some cases is almost non-existent. Beneath this layer, the basically tubular organic part of the test is partitioned into a series of globular pseudo-chambers, each containing a clump of dark stercomata.’

‘Unclassified monothalamids’

Monothalamid sp. 19

Goineau and Gooday, 2017; Supplementary Figure S9d–f

Goineau and Gooday (2017) provide the following brief description.

‘Test rounded, generally ovate, sometimes more irregular in shape; small lobes may be developed, usually at one end of the test. Length ~0.20–0.45 m. Wall translucent to almost transparent, composed of an organic inner layer covered by a very thin layer of fine-grained agglutinated material. There is no obvious aperture. Test content very heterogeneous, including stercomata together with sheet-like and cyst-like structures of probable biogenic origin.’ They remark that the heterogeneous test contents of this species closely resemble those of Tube sp. 54, although the test morphology is different.

Monothalamid sp. 27

Goineau and Gooday, 2017; Figure 5h–j

Goineau and Gooday (2017) provide the following brief description.

‘Agglutinated test typically resembling a triangle or an arrow head with three or four pointed ends. Wall neat, fine-grained, ~20–30 μ m thick, and sometimes slightly produced at the pointed ends where it becomes much thinner. One wider variant (Fig. 5i) divides into two short broad branches with lobate extremities tapering on the opposite side to a single aperture. Length ~200–450 μ m. Width of ‘pointed’ variant ~200–300 μ m, and width of ‘branched variant ~420–600 μ m.’

Monothalamid sp. 85

Figure 2C,D

This form inhabits a spherical radiolarian test. It accumulates a veneer of fine-grained sediment on the exterior of the host test to create a sphere between 160 and 258 μ m (generally 175–220 μ m) in diameter. This gives rise to a delicate translucent tube, up to 275 μ m (generally 160–210 μ m) long and 35–45 μ m in diameter, with a fine-grained agglutinated surface. The interior of the radiolarian host contains relatively large stercomata that are visible through the wall as a dark mass.

Remarks. This is the second most abundant species overall, despite being largely restricted to sample MC25.

Monothalamid sp. 98
Supplementary Figure S11D

Clusters of short, branched arms, often expanding in width where branching occurs close to the extremities. The largest specimen measures 725 μm maximum dimension, but most are half of that size. The wall is very soft, fine-grained, and the dark, stercomata-rich core is vlearly visible through it.

‘Komokiacean-like’

We reserve this grouping for forms with some komokiacean-like features, for example, the division of the test of Komokiacean-like sp. 20 into compartments that resemble those subdividing *Normanina* chambers, but that lack typical komokiacean characters, notable tubules.

Komokiacean-like sp. 20

Goineau and Gooday, 2017; Figure 4l,m

Goineau and Gooday (2017) provide the following brief description.

‘Variably shaped test, often subtriangular, spindle-shaped or more rounded and often with tubular extensions (~40–100 μm long). Komokiacean-like wall structure with a fine-grained agglutinated veneer overlying an organic layer. Test interior compartmentalised to resemble a honeycomb and filled with masses of stercomata. Maximum dimension ~150–180 μm (without tubular extensions).’

Komokiacean-like sp. 26
Supplementary Figure S11A-C

The test forms a complex segmented structure, sometimes branched, comprising more or less bulbous sections, which themselves may give rise to lateral swellings, and are separated by more or less distinct constrictions. The segments are subdivided internally into compartments by partitions. The wall is fairly thick, brownish and appears to be largely organic. The surface gives rise to fine fibres, in places in dense concentrations. The illustrated specimen measures ~90 μm in maximum dimension (not including the fibres).

Remarks. The appearance of the test is reminiscent of *Baculella*, a relationship that is strengthened by the development of fine fibres.

Komokiacea: Baculellidae

Baculella globofera Tendal & Hessler, 1977

Baculella globofera Tendal and Hessler, 1977; Pl. 15, Figs. A,B

Remarks. Our specimens resemble those illustrated by Tendal and Hessler (1977)

Baculellidae sp. 8
Supplementary Figure S11E

The test comprises clusters of tiny brown bead-like chambers and more elongate protuberances that arise from a basal tubule. A few specimens comprise two such clusters joined by a short stalk. thick branches with an overall dimension of 275-350 μm .

Baculella aff. *hirsuta*
Figure 2H

An elongate formation in which the test is largely obscured by fine-grained muddy sediment, the main visible structures being short outwardly-projecting tubules. The longest specimen is ~1.9 mm long and ~420 μm wide. Some pieces have more or less distinct 'segments' joined by a narrow neck. This may be a species of *Baculella*. The accumulation of fine-grained sediment around the test is reminiscent of, *B. hirsuta*.

'*Edgertonia*' *floccula* Shires, Gooday & Jones, 1994

Shires et al., 1994; Plate 1, Figs. 1–7.

Remarks. Mudballs with a flocculent surface in which small chambers 'float' in a tangle of very fine fibres, first described in the abyssal NE Atlantic, are widely distributed in the lower bathyal and abyssal deep sea.

Edgertonia sp. 4

Goineau and Gooday, 2017; Supplementary Figure S10a,b

Goineau and Gooday (2017) provide the following brief description.

'Clusters of short, finger-like branching tubules, typically ~50 μm wide, usually ending in slightly bulbous swellings or clusters of swellings. Tubes and swellings contain discrete clumps of stercomata, often separated by more or less distinct septae that subdivide the interior into compartments. Wall organic with finely granular outer surface.'

Edgertonia sp. 5

Goineau and Gooday, 2017; Supplementary Figure S10c,d

Goineau and Gooday (2017) provide the following brief description.

'Branching tubules (~50 μm wide) ending in 1–2 bulbous swellings, ~100 and ~200 μm maximum dimension. Wall composed of organic layer overlain by variably developed agglutinated veneer. Test interior with sparse stercomata and stained material.' They remark that it 'differs from *Edgertonia* sp. 4 in having larger and more pronounced terminal swellings, no septae, and a flimsier wall.'

Edgertonia sp. 7

Goineau and Gooday, 2017; Figure 5k-m

Goineau and Gooday (2017) provide the following brief description.

‘Irregularly-shaped cluster of globular chambers (each ~50 µm wide), loosely to fairly tightly packed within a variably-developed fine-grained matrix and sometimes surrounded by fine organic fibres. Individual clusters measure up to 750 µm (usually 250–500 µm) in maximum dimension.

Edgertonia sp. 8

Supplementary Figure S11F

Delicate spheres (110-140 µm diameter), somewhat droplet-shaped, connected together in a bunch by delicate, flexible extensions. The wall is relatively thin and fine-grained. These formations are probably the same as the ‘probable komokiacean chambers’ of Nozawa et al. (2006, Fig. 3H)

Edgertonia sp. 8A

Supplementary Figure S11G,H

Droplet-shaped spheres connected together by delicate threads and resembling *Edgertonia* sp. 8. The main differences are that the spheres are smaller (typically 50-55 µm, maximum 70 µm, in length) and the walls are coarser-grained with a distinctly granular appearance compared to *Edgertonia* sp. 8.

Komokiacea: Komokiidae*Ipoa fragila* Tendal and Hessler, 1977

Supplementary Figure S12A,B

A single complete specimen (Fig. S12A) of this distinctive komokiacean was found in sample MC13 (0-0.5cm, >300, #3); other examples are fragments. They are easily identifiable by the wider basal tubule that divides into narrower branches (Fig. S10B)

Reticulum sp. 1

Goineau and Gooday, 2017; Supplementary Figure S11a,b

Goineau and Gooday (2017) provide the following brief description.

‘Test consists of branching and anastomosing tubules. Tubules non-septate, more or less parallel sided and following a somewhat irregular course between the branches. Distinct organic layer of wall overlain by variably developed fine-grained coating. The width of the inner organic tubule = 14–19 µm; width of the outer agglutinated layer = 5–6 µm; total tubule width = 22–30 µm.’

Reticulum sp. 4

Goineau and Gooday, 2017; Supplementary Figure S11c,d

Goineau and Gooday (2017) provide the following brief description.

‘Loose clump of narrow, branching, reticulated tubules (~10–15 µm width). Tubules non-septate, parallel-sided. Organic wall covered by a very thin fine-grained coating. Clumps, assumed to be fragments, are up to 1 mm or more in size. We place this species in the genus *Reticulum* because the tubules are fairly tightly meshed, more so than in the closely related genus *Lana*.’

Komokiidae sp. 10
Supplementary Figure S12C,D

Mudball structure packed with poorly-defined compartments (~90-100 µm across), each containing a single, or a cluster, of small stercomata. The specimens are probably either fragments or are damaged; the largest measures 1.34 mm maximum dimension.

Komokiidae sp. 13
Supplementary Figure S12E,F

The specimens, which are probably fragmentary, comprise a very fine tubule system, the details of which are very difficult to discern, embedded in a muddy matrix. The general appearance is that of a mudball densely speckled with tiny dark dots, corresponding to individual stercomata.

References

- Brady, H.B. 1881. Notes on some of the reticularian Rhizopoda of the Challenger Expedition. Part III. 1. Classification. 2. Further notes on new species. 3. Note on *Biloculina* mud. Q. J. Microsc. Sci., new series 21, 31–71.
- Brady, H.B., 1884. Report on the foraminifer dredged by H.M.S. Challenger during the years 1873–1876. Report of the scientific results of the voyage of H.M.S. Challenger, 1873–1876. Zoology 9, London, England.
- Brönnimann, P., Whittaker, J.E., 1980. A revision of *Reophax* and its type-species, with remarks on several other Recent hormosinid species (Protozoa: Foraminiferida) in the collections of the British Museum (Natural History). Bull. Br. Mus. Nat. Hist. (Zool.) 39, 259-272.
- Brönnimann, P., Whittaker, J.E., 1988. The Trochamminacea of the Discovery Reports. British Museum (Natural History). 152 pp.
- Cushman, J.A., 1933. Some new recent Foraminifera from the tropical Pacific. Contributions from the Cushman Laboratory for Foraminiferal Research 9, 77–95.
- Enge, A.J., Kucera, M., Heinz, P., 2012. Diversity and microhabitats of living benthic foraminifera in the abyssal Northeast Pacific. Mar. Micropaleontol 96, 84–104.
- Goineau, A., Gooday, A.J., 2017. Novel benthic foraminifera are abundant and diverse in an area of the abyssal equatorial Pacific licensed for polymetallic nodule exploration. Scientific Reports 7, 45288. doi:[10.1038/srep45288](https://doi.org/10.1038/srep45288)
- Gooday, A.J., Goineau, A., 2019. The contribution of fine sieve fractions (63-150 µm) to foraminiferal abundance and diversity in an area of the eastern Pacific Ocean licensed for polymetallic nodule exploration. Front. Mar. Sci. [http://doi:10.3389/fmars.2019.00114](https://doi.org/10.3389/fmars.2019.00114).
- Gooday, A.J., Malzone, M.G., Bett, B.J., Lamont, P.A., 2010. Decadal-scale changes in shallow infaunal foraminiferal assemblages at the Porcupine Abyssal Plain, NE Atlantic. Deep-Sea Res II 57, 1362–1382, doi:10.1016/j.dsr2.2010.01.012.
- Gooday, A.J., Todo, Y., Uematsu, K., Kitazato, H., 2008. New organic-walled Foraminifera (Protista) from the ocean’s deepest point, the Challenger Deep (western Pacific Ocean). Zool. J. Linn. Soc. 153, 399–423, doi:10.1111/j.1096-3642.2008.00393.x.
- Holbourn, A., Henderson, A.S., MacLeod, N., 2013. Atlas of benthic foraminifera. John Wiley & Sons.

- Jones, R.W. , Bender , H. , Charnock, M.A. , and Kaminski, M.A. , 1993. Emendation of the foraminiferal genus *Cribrostomoides* Cushman, 1910, and its taxonomic implications . J. Micropalaeontol. 12, 181 – 193.
- Jones, R.W., 1994. The Challenger foraminifera. Oxford University Press and The Natural History Museum, London.
- Jones, T.R.; Parker, W.K. (1860). On the rhizopodal fauna of the Mediterranean compared with that of the Italian and some other Tertiary deposits. *Q. J. Geol. Soc. London.* 16, 292-307
- Kamenskaya, O.E., Gooday, A.J., Radziejewska, T., Wawrzyniak-Wydrowska, B., 2012. Large, enigmatic foraminiferan-like protists in the eastern part of the Clarion-Clipperton. Marine Biodiversity fracture zone (abyssal eastern equatorial Pacific): biodiversity and vertical distribution in the sediment. *Mar Biodiv* 42, 311-327. DOI: 10.1007/s12526-012-0114-7.
- Kaminski, M., 2014. The year 2010 classification of the agglutinated foraminifera. *Micropaleontology* 60, 89-108.
- Kuhnt, W., Collins, E., Scott, D., 2000. Deep water agglutinated foraminiferal assemblages across the Gulf Stream: distribution patterns and taphonomy. In: Hart, M., Kaminski, M., Smart, C. (Eds.), *Proceedings of the Fifth International Workshop on Agglutinated Foraminifera.* Grzybowski Foundation Special Publication, 7, 261–298, pls 1-12.
- Mackensen, A., Schmiedl, G., Harloff, J. and Giese, M., 1995. Deep-sea foraminifera in the South Atlantic Ocean: Ecology and assemblage generation. *Micropaleontology* 41, 342-358.
- Nozawa, F., Kitazato, H. Tsuchiya, M. and Gooday, A.J., 2006, ‘Live’ benthic foraminifera at an abyssal site in the equatorial Pacific nodule province: abundance, diversity and taxonomic composition. *Deep-Sea Res* 51, 1406-1422.
- Pawlowski, J., Holzmann, M., Tyszka, J., 2013. New supraordinal classification of Foraminifera: Molecules meet morphology. *Mar. Micropaleontol.* 100, 1–10.
- Resig, J.M., 1981. Biogeography of benthic foraminifera of the northern Nazca plate and adjacent continental margin. *Geol. Soc. Am. Mem.* 154, 619–666, doi:10.1130/MEM154-p. 619.
- Schröder, C.J., Scott, D.B., Medioli, F.S., Bernstein, B.B., Hessler, R.R., 1988. Larger agglutinated foraminifera: comparison of assemblages from central Pacific and western North Atlantic (Nares Abyssal Plain). *J. Foramin Res* 18, 25-41.
- Shires, R., Gooday, A.J. , Jones, A.R., 1994. The morphology and ecology of an abundant new komokiacean mudball (komokiacea, Foraminiferida) from the bathyal and abysal N E Atlantic. *J. Foramin. Res* 24, 214-225.
- Stefanoudis, P.V., Schiebel, R., Mallet, R., Durden, J.M., Bett, B.J., Gooday, A.J., 2016. Agglutination of benthic foraminifera in relation to mesoscale bathymetric features in the abyssal NE Atlantic (Porcupine Abyssal Plain). *Mar Micropaleontol* 123, 15–28.
- Szarek, R., Nomaki,H., Kitazato, H. (2007). Living deep-sea benthic foraminifera from the warm and oxygen-depleted environment of the Sulu Sea. *Deep-Sea Res I* 54, 145-176.
- Schröder, C.J., 1986. Deep-water arenaceous foraminifera in the northwest Atlantic Ocean. *Can.Tech. Rep. Hydrogr. Ocean Sci.* 71, 1-191
- Thies, A. 1991. Die Benthos-Foraminiferen im Europäischen Nordmeer. *Ber. Sondersforschungsbereich* 313, Univ. Kiel 31, 1-97.
- Tendal, O.S., Hessler, R.R., 1977. An introduction to the biology and systematics of Komokiacea: *Galathea Rep* 14, 165-194, pls 9-26.
- Wiesner, H., 1931. Die Foraminiferen der Deutschen Südpolar-Expedition. In: von Drygalski, E. (Ed.), *Deutsche Südpolar-Expedition, 1901-1903*, 20:49-169

S2. Supplementary Figure captions

Figure S1. Location of sampling sites in the three Strata; from north to south UK-1A, UK-1B, and OMS.

Figure S2. ‘Live’ complete data (ignoring singletons). A) Species ranked by abundance. B) Species recorded from 1-2 samples, ranked by abundance. C) Species recorded from 9-11 samples, ranked by abundance; red = 11 samples; blue = 10 samples; yellow = 9 samples.

Figure S3. Dead complete data (ignoring singletons). A) Species ranked by abundance. B) Species recorded from 1-2 samples, ranked by abundance. C) Species recorded from 9-11 samples, ranked by abundance; red = 11 samples; blue = 10 samples; yellow = 9 samples.

Figure S4. ‘Live’ + dead complete data (ignoring singletons). A) Species ranked by abundance. B) Species recorded from 1-2 samples, ranked by abundance. C) Species recorded from 9-11 samples, ranked by abundance; red = 11 samples; blue = 10 samples;

Figure S5. Total number of species recognised in individual samples (MC02, MC04 etc), individual strata (UK1-A, UK1-B, OMS) and all strata combined.

Figure S6. Rarefaction curves based on complete live (A) and complete live and dead (B) specimens. Solid lines are based on actual data; dashed lines are extrapolated curves up to 1,500 specimens for each sample.

Figure S7. Sample-based rarefaction curves based on number of complete (stained + dead) specimens from individual strata and the 11 samples (solid lines) and extrapolated up to 15 or 30 samples (dotted lines), respectively (A). Corresponding number of new species added for each additional sample, based on the extrapolated sample-based rarefaction curves (B). For each sample, vertical bars indicate the 95% confidence interval.

Figure S8. Number of species (ignoring singletons) represented by live + dead specimens, arranged by the number of samples in which they occur (from 1 to 11). Data are given separately for ‘live’ (stained), dead, and ‘live’ + dead assemblages. For some data points the ‘live’ and/or dead occurrences exceed the ‘live + dead occurrences’. This is because species occurring in a particular number of samples in the ‘live’ assemblage will drop out of that datapoint if represented by dead specimens in other samples. A) Number of species. B) Percentage of species.

Figure S9. A) *Hormosinella* sp. 3; MC02, 0-0.5 cm, 150-300 µm. B) *Lagenammia tubulata*; MC02, 0-0.5 cm, 150-300 µm. C) *Hormosinella* sp. 5; MC02, 0-0.5 cm, 150-300 µm. D) *Hormosinella* sp. 4; MC09, 0-0.5 cm, >300 µm. E) Psammosphaerid with tubes sp. 5; MC04, 0.5-1.0 cm, 150-300 µm. F-H) *Paratrochammia challengerii*? I) Flask sp. 2; MC07, 0.5-1.0 cm, >300 µm (possibly a komokiacean). J) Tube sp. 92; MC25, 0.5-1.0 cm, >300 µm. K) *Hyperammia cylindrica*; MC02, 0.5-1.0 cm, >300 µm.

Figure S10. A,B) *Hyperammia* sp. 2; MC09, 0.5-1.0 cm, >300 µm. C,D) *Rhizammina* sp. 1; MC11, 0-0.5 cm, >300 µm (note the strand of stained cytoplasm alongside the stercomata). E,F) *Rhizammina* sp. 5; MC22, 0-0.5 cm, >300 µm. G,H) Tube sp. 2; MC02, 0-0.5 cm, 150-300 µm. I) Tube sp. 2; MC02, 0.5-1.0 cm, 150-300 µm. J) Tube sp. 39 (segmented); MC07, 0.5-1.0 cm, >300 µm. K,L) Tube sp. 10; MC02, 0-0.5-1.0 cm, 150-300 µm. M) Tube sp. 122; MC25, 0.5-1.0 cm, 150-300 µm.

Figure S11. **A-C)** Komokiacean-like sp. 26; MC13, 0.5-1.0 cm, >300 μm . **D)** Monothalamid sp. 98; MC22, 0-0.5 cm, 150-300 μm . **E)** Baculellidae sp. 8; MC04, 0.5-1.0 cm, 150-300 μm . **F)** *Edgertonia* sp. 8; MC05, 0.5-1.0 cm, 150-300 μm . **G,H)** *Edgertonia* sp. 8A; MC22, 0-0.5 cm, >300 μm .

Figure S12. **A)** *Ipoa fragila*; MC13, 0-0.5 cm, >300 μm . **B)** Possible fragment of *Ipoa*; MC22, 0.5-1.0 cm, >300 μm . **C)** Komokiidae sp. 10; MC09, 0.5-1.0 cm, 150-300 μm . **D)** Komokiidae sp. 10; MC13, 0-0.5 cm. **E,F)** Komokiidae sp. 13; MC04, 0.5-1.0 cm, >300 μm .

Supplementary Fig. S1

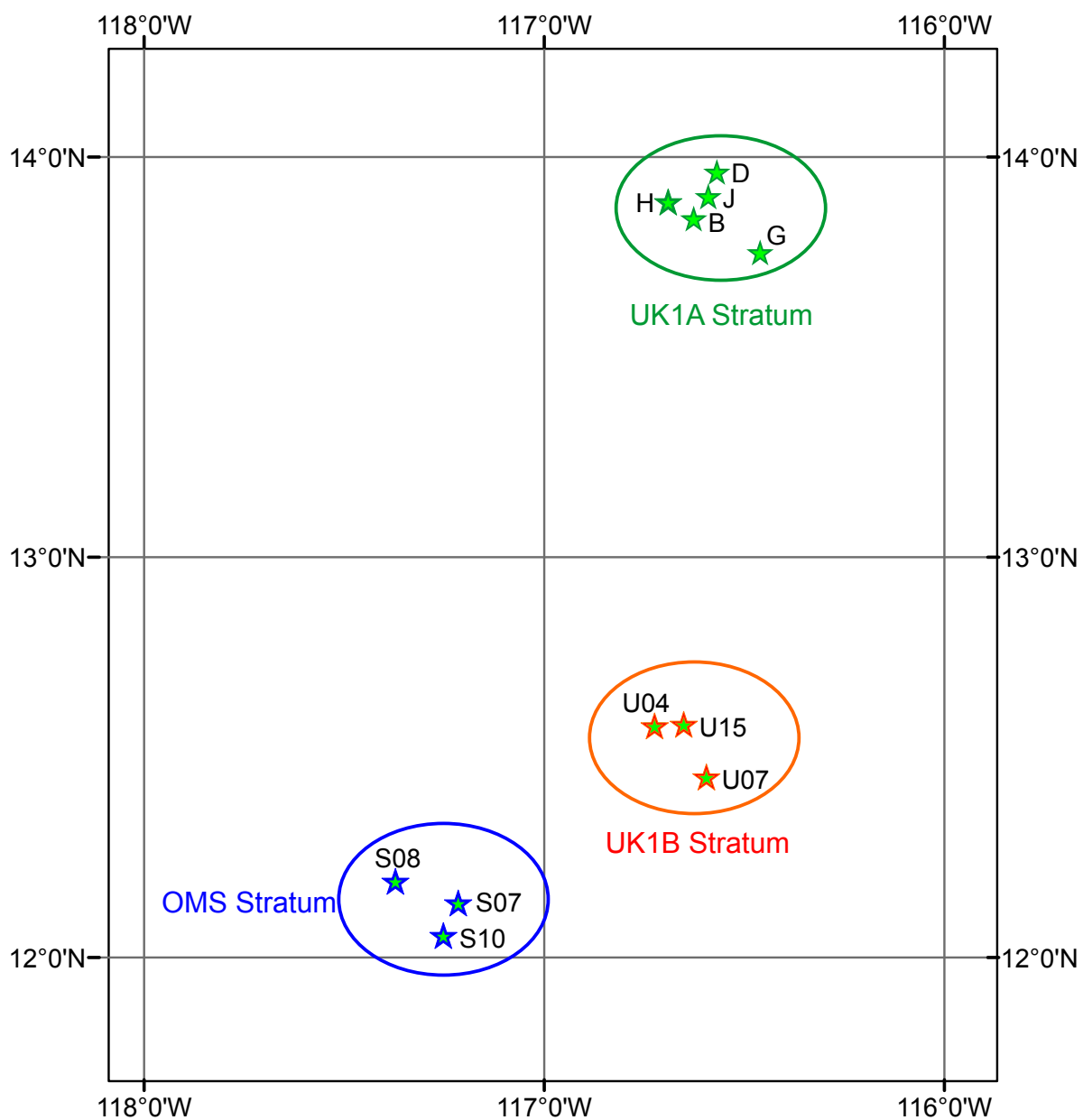


Figure S2

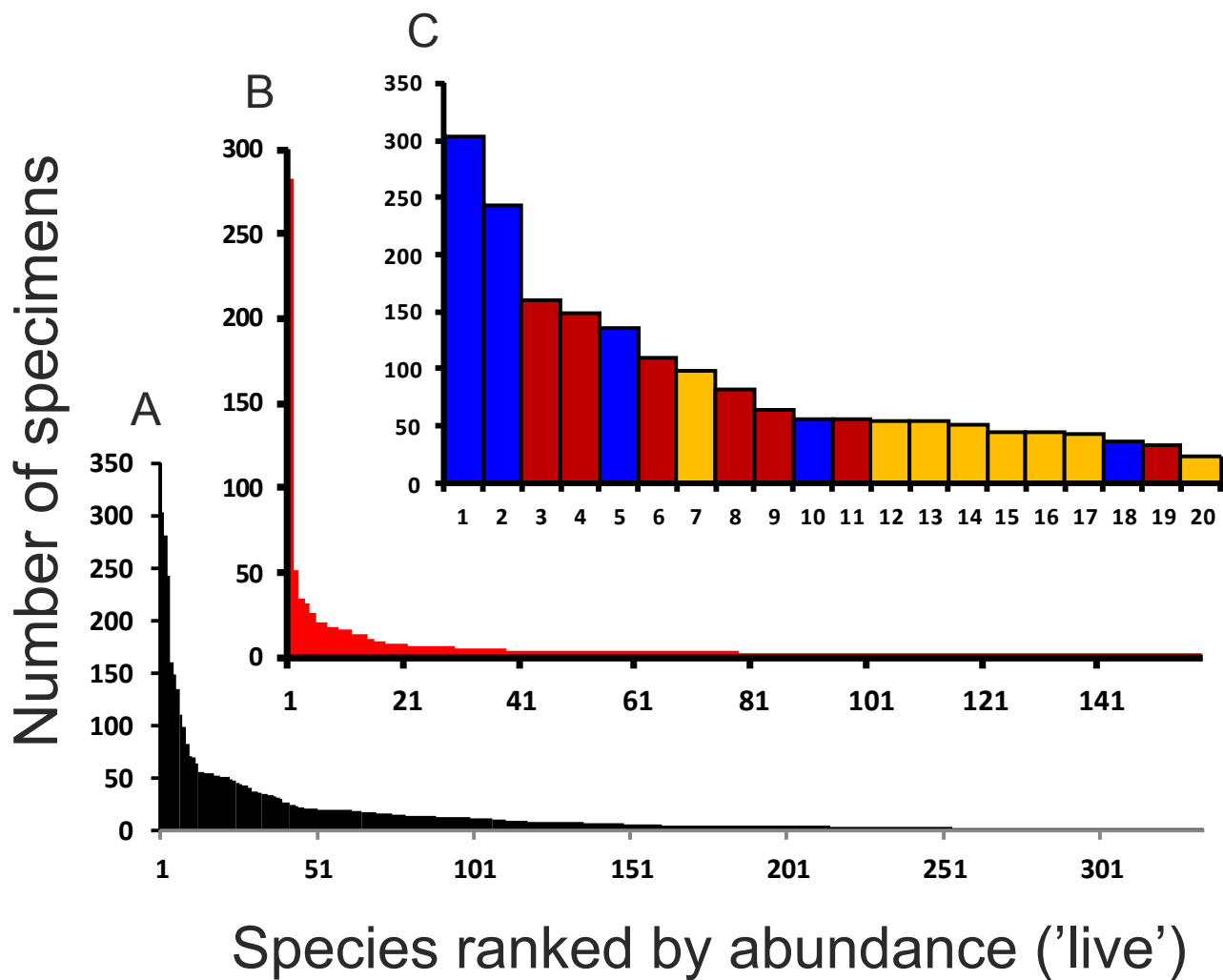
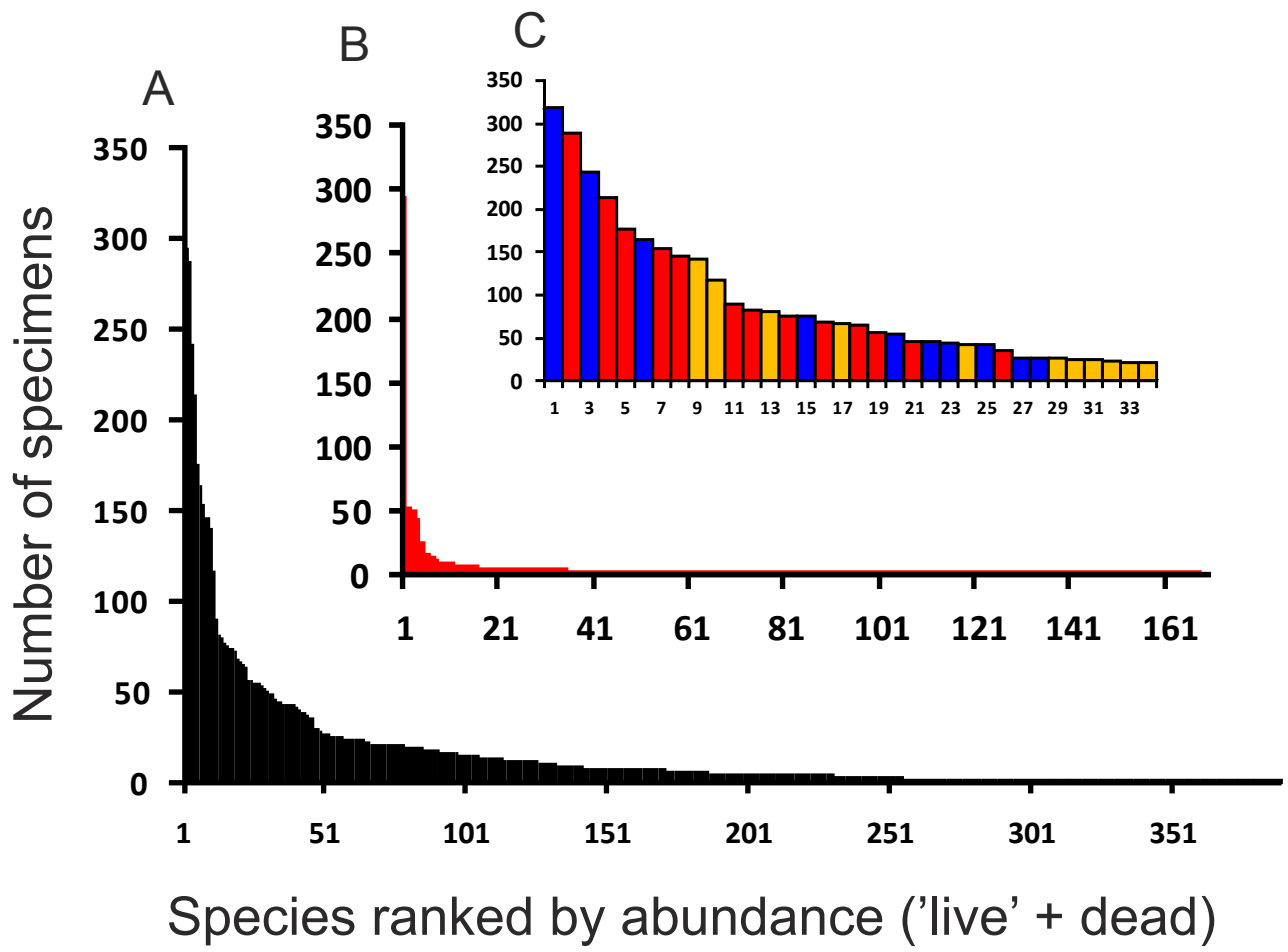
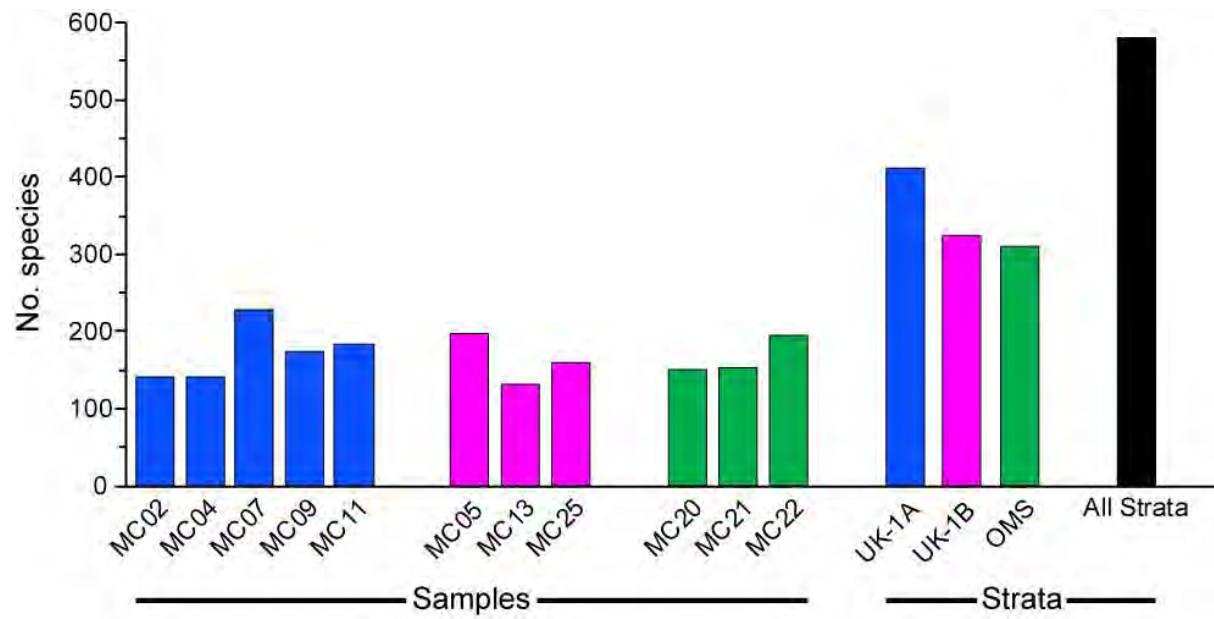


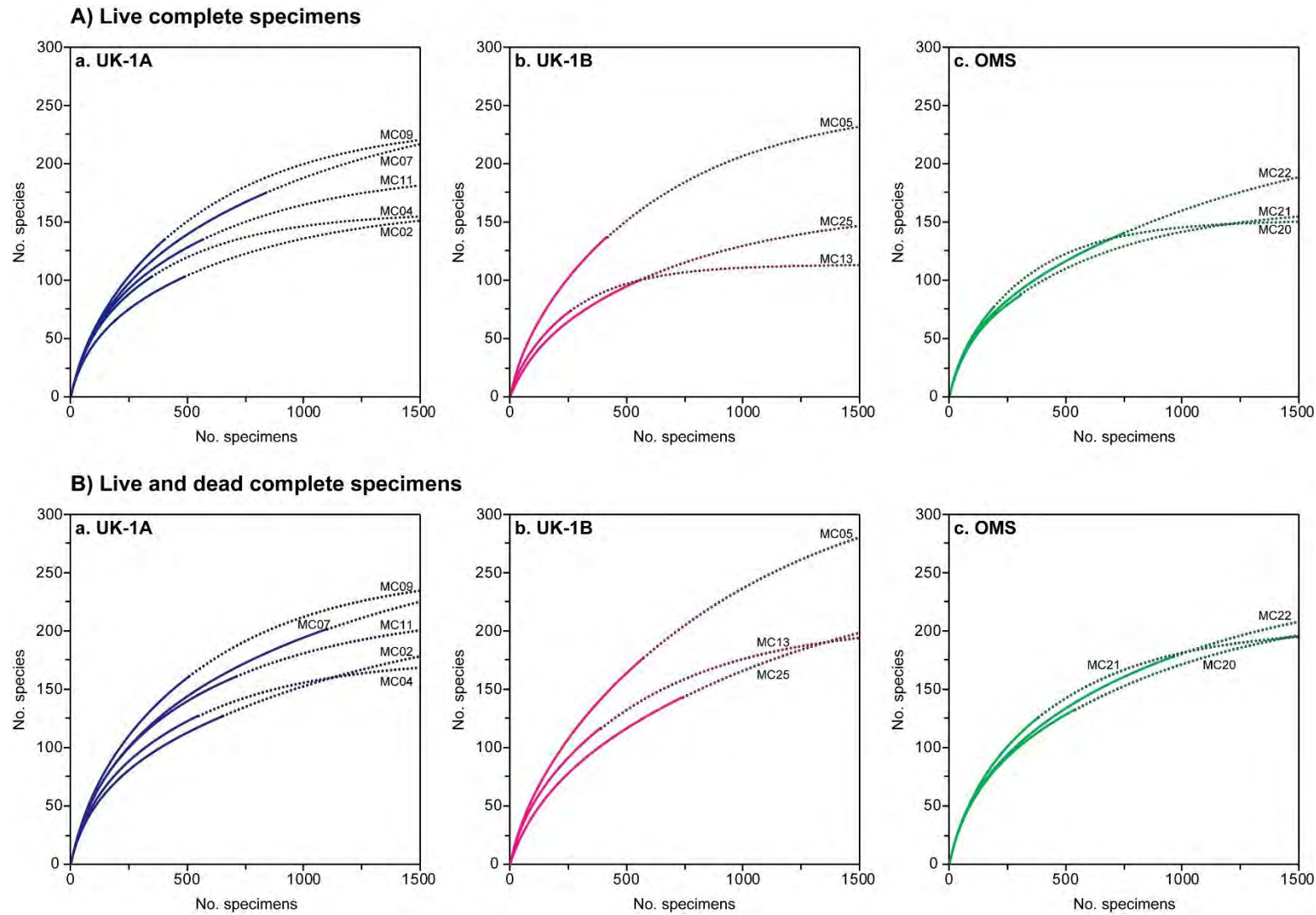
Figure S4



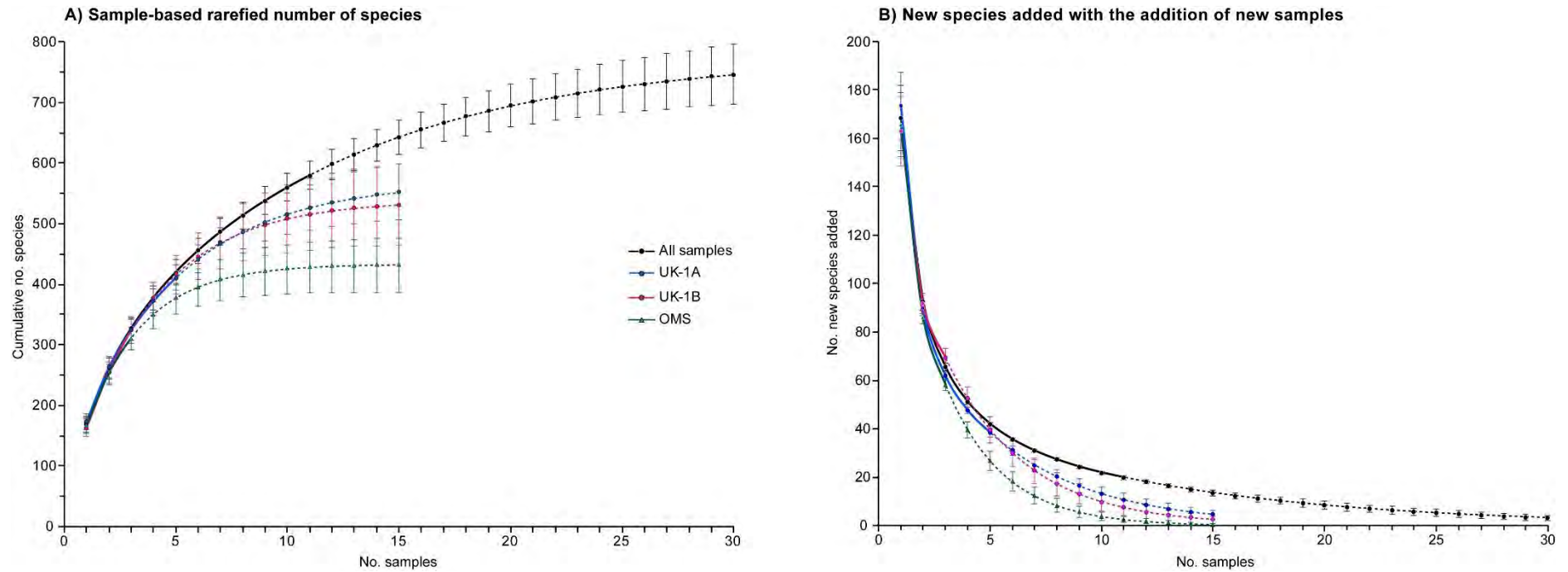
Supplementary Fig. S5: Total number of species recognised in individual samples (MC02, MC04 etc), individual strata (UK1-A, UK1-B, OMS) and all strata combined.



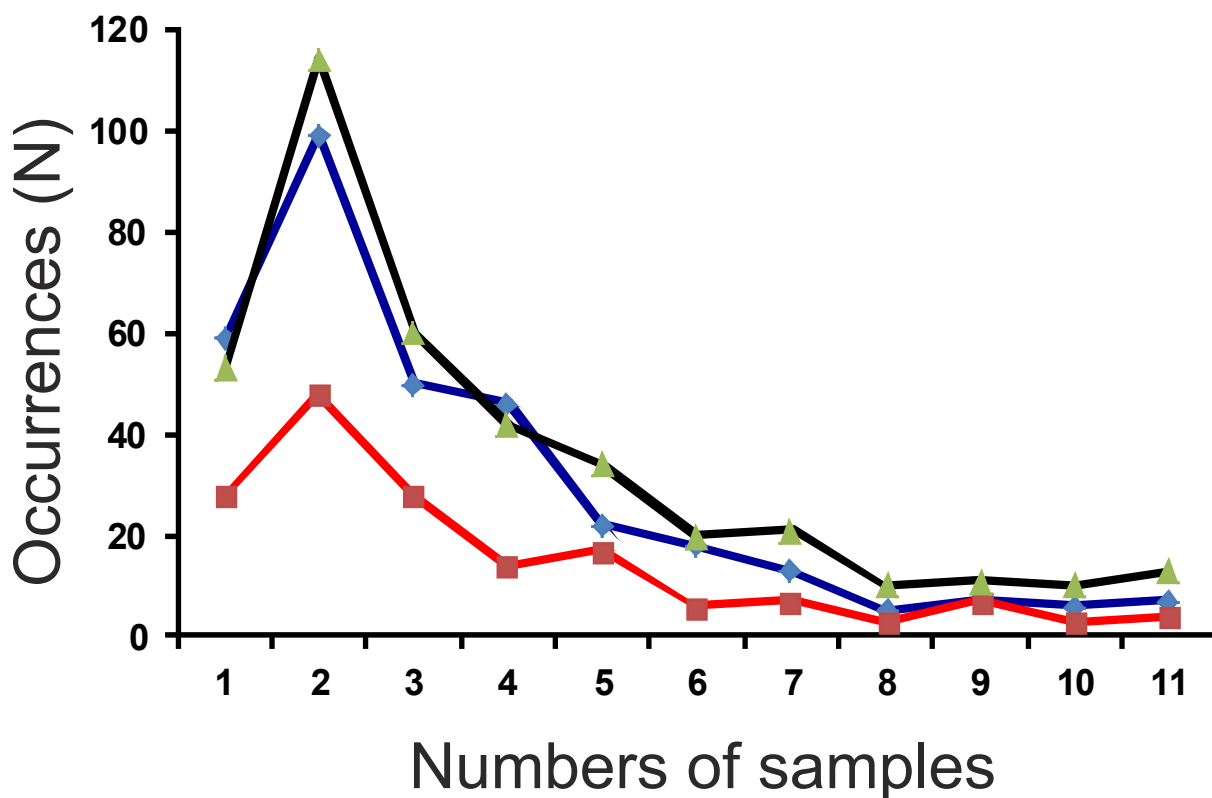
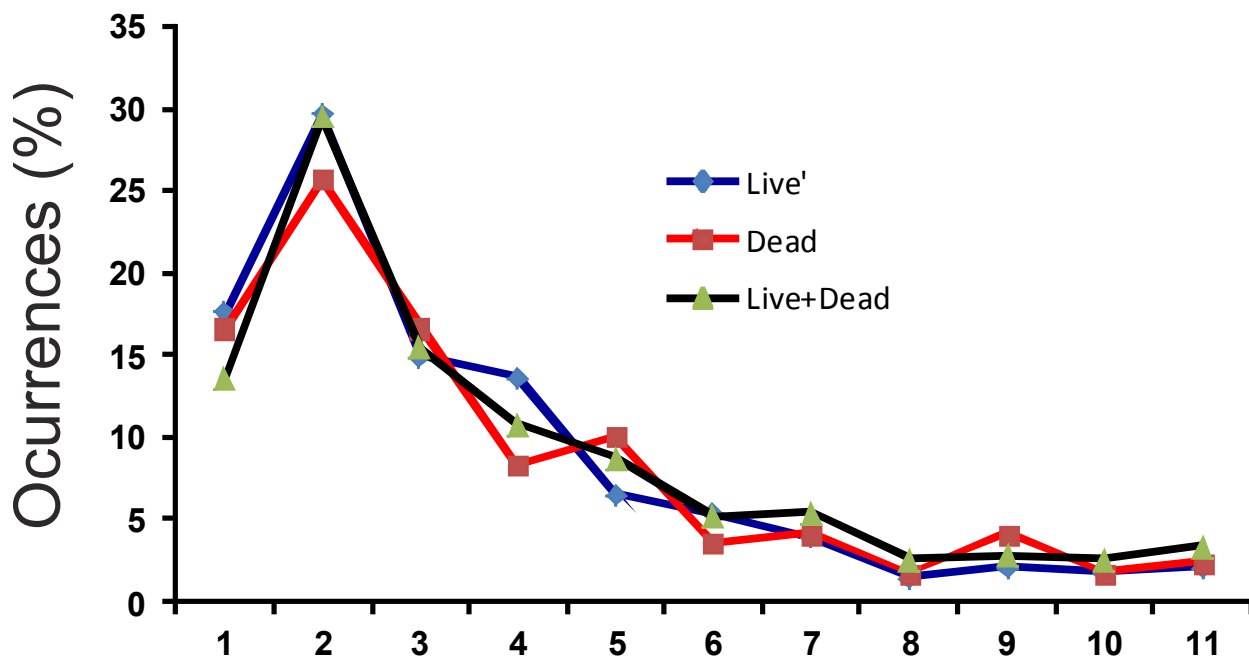
Supplementary Fig. S6: Rarefaction curves based on complete live (A) and complete live and dead (B) specimens. Solid lines are based on actual data; dashed lines are extrapolated curves up to 1,500 specimens for each sample.



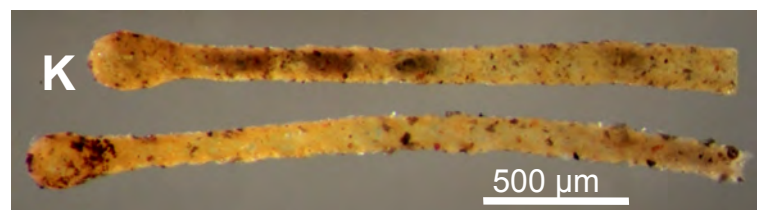
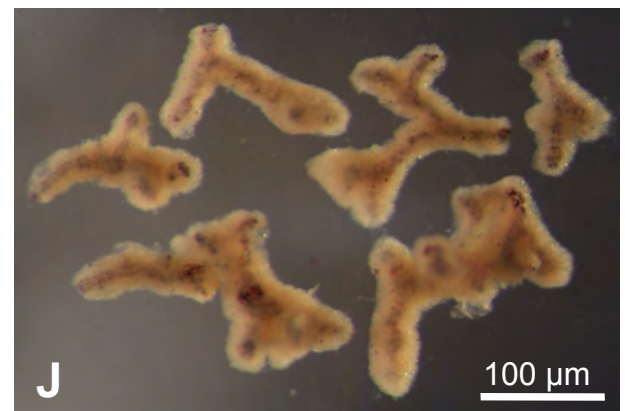
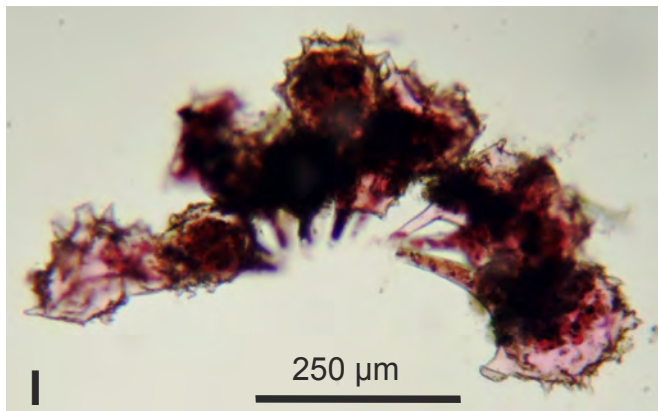
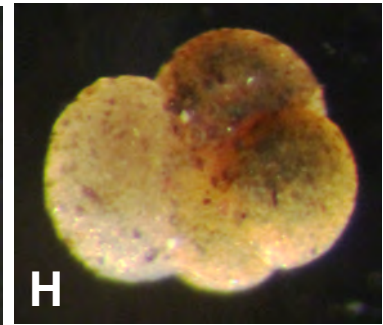
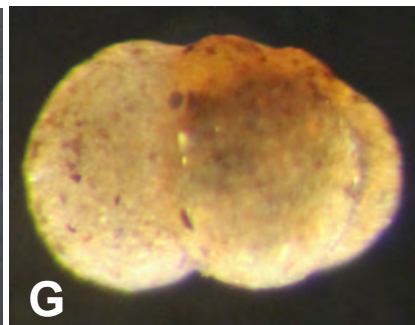
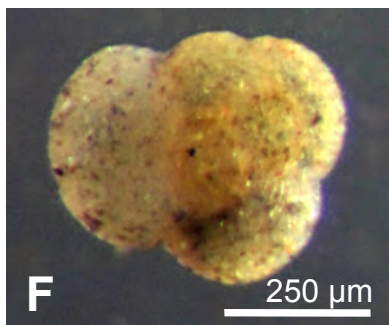
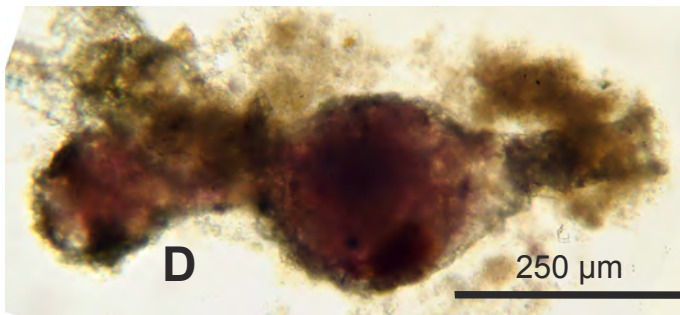
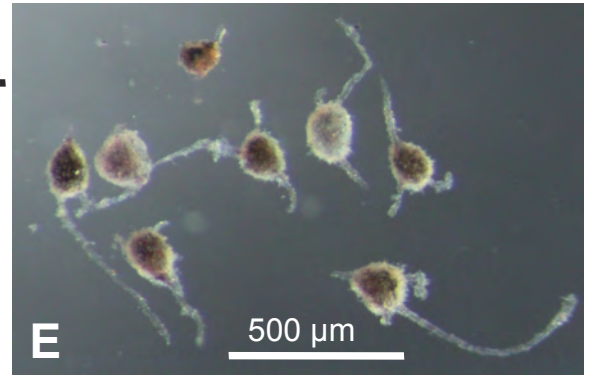
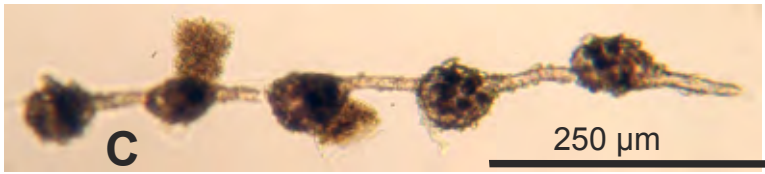
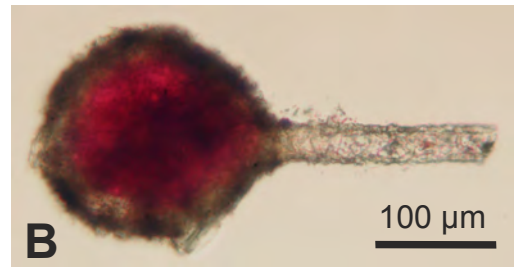
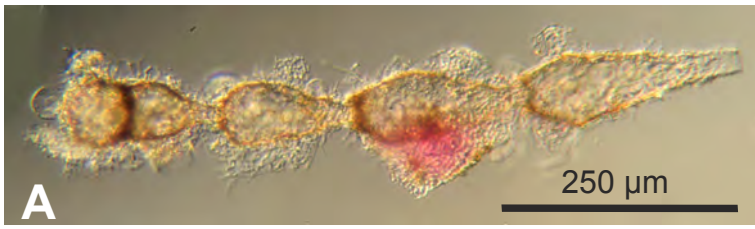
Supplementary Fig. S7: Sample-based rarefaction curves based on the number of complete (live and dead combined) specimens from the 11 analysed samples, and extrapolated up to 15 or 30 samples (A). Corresponding number of new species added per additional sample based on the sample-based extrapolated rarefaction curves (B). Estimates are shown for single strata, and for all strata combined. For each sample, vertical bars indicate the 95% interval confidence.



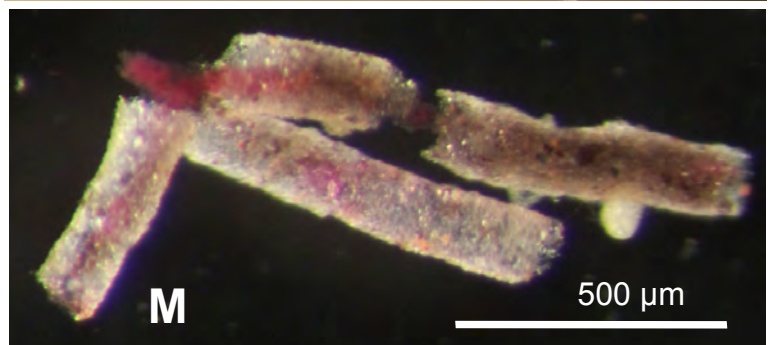
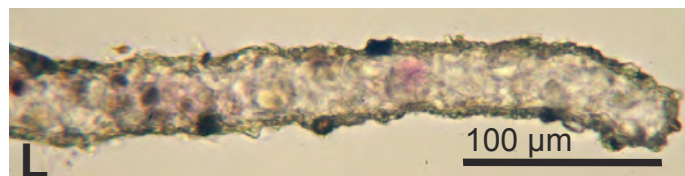
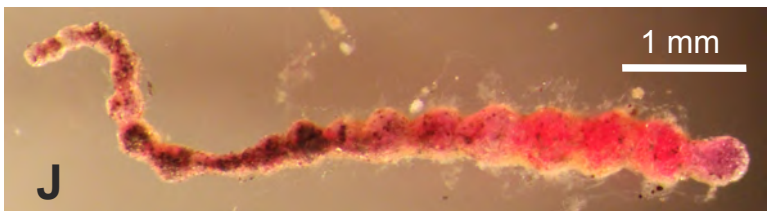
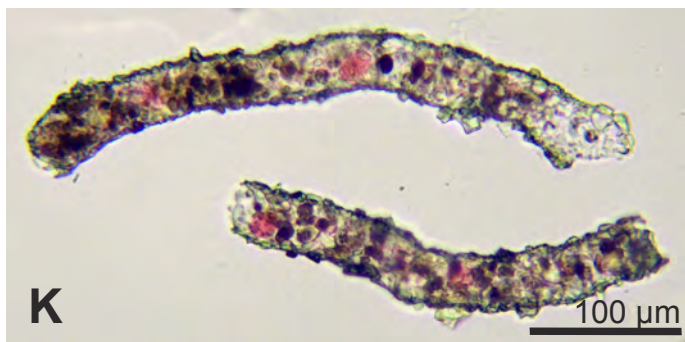
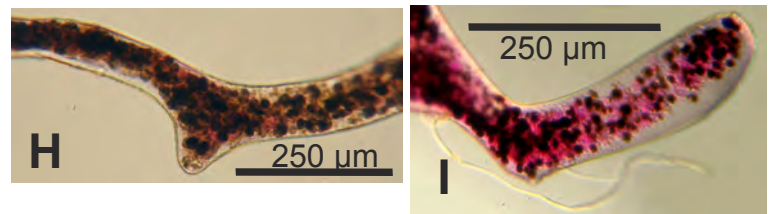
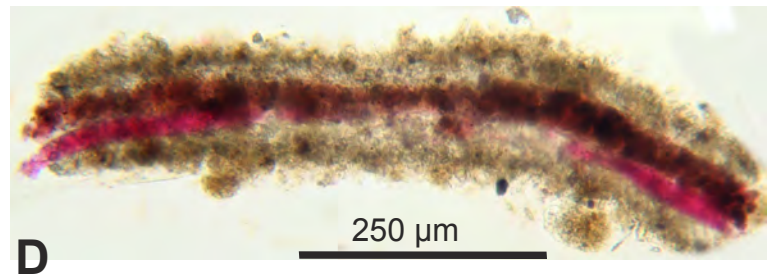
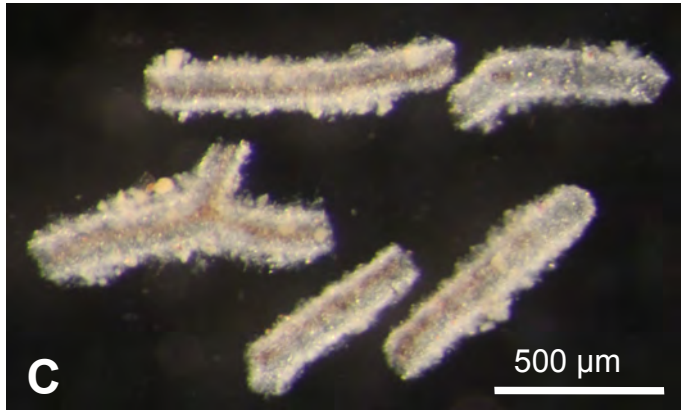
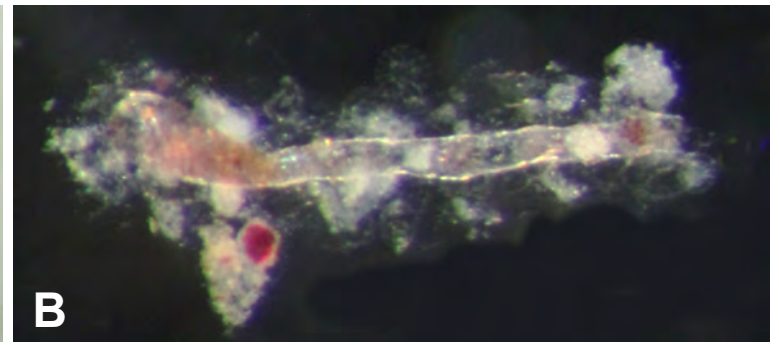
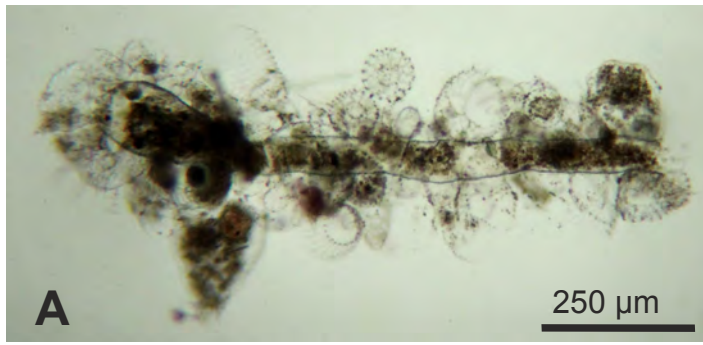
Supplementary Figure S8



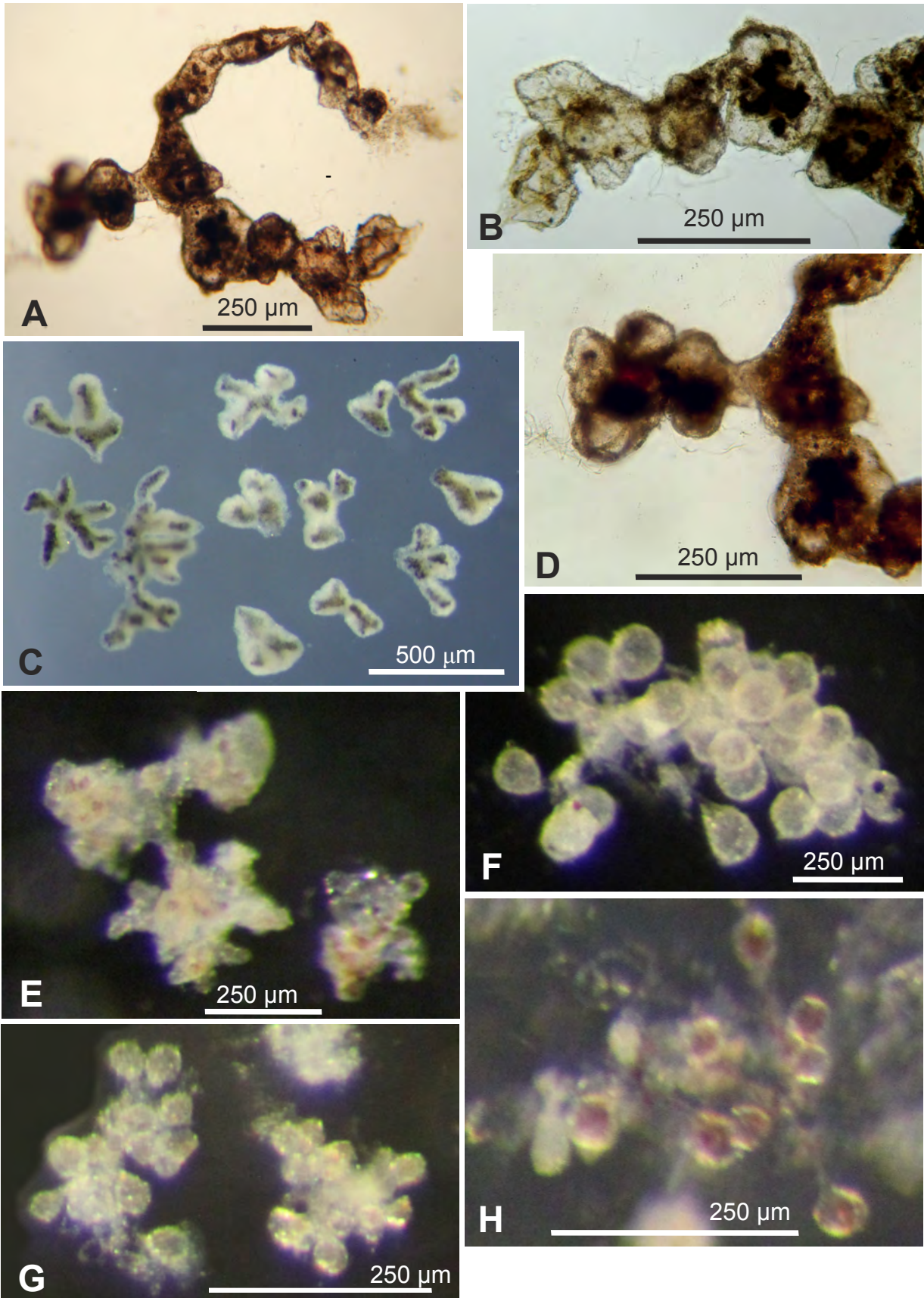
Supplementary Figure S9



Supplementary Fig. S10



Supplementary Figure S11



Supplementary Figure S12

