



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

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The sieve mesh sizes used in benthic foraminiferal studies exert a strong influence on faunal densities and composition. We examined the consequences of including finer (63–150 μm) size classes in a study of Rose Bengal stained ('live') and dead foraminifera in 5 Megacorer samples (0–1 cm layer) from abyssal sites in the eastern Clarion-Clipperton Zone (CCZ; equatorial Pacific), a region with commercially significant deposits of polymetallic nodules. More than 60% of intact specimens originated from the finer (<150 μm) fractions, with over half being picked from 63 to 125 μm residues. Test fragments, mainly agglutinated tubes, were also abundant but were more evenly distributed between coarser and finer residues. The two fractions yielded the same main groups (a mixture of formal taxa and informal groupings) and were dominated by single-chambered forms ('monothalamids'), the majority undescribed. Some were disproportionately abundant in finer fractions: rotaliids in the stained ('live'), textulariids in the dead, and trochamminids, *Lagenammia* spp., *Nodellum*-like forms, saccamminids and spheres in both assemblages. However, the most striking difference was the much greater abundance of tiny, largely undescribed spherical agglutinated morphotypes in the <150- μm fractions. Our 5 samples yielded 462 morphospecies, of which 313 occurred in <150- μm fraction and 170 were confined to this fraction. Twelve of the 31 top-ranked species in the stained assemblage were more or less limited (>90%) to the finer fractions; the corresponding number for the stained + dead assemblage was 12 out of 35. Of the 46 most abundant species in the stained + dead assemblage, 35 were monothalamids (mainly spheres, *Lagenammia* spp., *Nodellum*-like forms, and saccamminids), the remainder being rotaliids (3), hormosinids (3), trochamminids (3) and textulariids (2). By far the most abundant species overall, a tiny agglutinated sphere, was almost entirely confined to the finer fractions. Although small foraminifera that pass through a 150- μm screen are time-consuming to analyze, they constitute an important

part of abyssal Pacific assemblages and may include opportunistic species that respond to episodic food pulses as well as pioneer recolonizers of defaunated substrates. It is therefore important to consider them in studies of possible mining impacts on abyssal benthic communities.

Keywords: polymetallic nodules, Clarion-Clipperton Zone, baseline survey, abyssal benthic foraminifera, sieve mesh size, biodiversity, recolonization

INTRODUCTION

The use of different sized meshes to sieve sediment samples is an important issue in meiofaunal research, the mesh acting as a filter that strongly influences important assemblage metrics, notably faunal densities, biomass, diversity and taxonomic composition of taxa such as nematodes (Leduc et al., 2010). A mesh size of 32 μm is now the widely accepted lower limit for the metazoan meiofauna. In the case of foraminifera, however, different studies have used a variety of different sized meshes (Sen Gupta et al., 1987). The most common are 150, 125, and 63 μm , although larger (250 or 300 μm ; e.g., Bernstein et al., 1978; Lutze and Coulbourne, 1984; Gooday et al., 2001) or smaller (45 or 32 μm ; e.g., Gooday, 1986; Pawlowski and Lapierre, 1988; Pawlowski, 1991; Gooday et al., 1995; Nozawa et al., 2006; Szarek et al., 2007) sizes have been adopted occasionally. The need to analyze finer sieve fractions (63–125 μm or 63–150 μm) becomes more pressing in deep-sea settings, where benthic organisms are generally small in size compared to shallower waters (Thiel, 1975, 1983; Shirayama and Horikoshi, 1989). Although this involves a larger investment of time compared to the analysis of larger-sized fractions, Schröder et al. (1987) argue that the extra effort is worthwhile because valuable faunal information, including a large proportion of specimens belonging to environmentally important ‘indicator’ species, is lost by ignoring sieve residues <150 μm . For example, at bathyal depths in the North Atlantic, small-sized species include several that respond opportunistically to seasonally pulsed food inputs (Gooday and Hughes, 2002; Duchemin et al., 2007; Phipps et al., 2012).

Relatively few studies based on fine sieve fractions have been undertaken in the Pacific Ocean. Snider et al. (1984) analyzed the 45–150 and 150–300 μm fractions for meiofaunal organisms, mainly foraminifera, many of them single-chambered forms (monothalamids). More recently, Nozawa et al. (2006) used a 32 μm mesh in a study of foraminifera, again dominated by monothalamids, from the ‘Kaplan East’ site in the eastern Clarion-Clipperton Zone (CCZ, abyssal equatorial Pacific), a region where large tracts of seafloor are covered with commercially significant deposits of polymetallic nodules. Radziejewska et al. (2006) presented some preliminary observations of monothalamids and other foraminifera based on the >32- μm fractions of samples from the same general area. Ohkawara et al. (2009) described a tiny new spherical monothalamid that was abundant in samples from the Kaplan Central site in the deeper and more central part of the CCZ. The present contribution is part of the ABYSSLINE (ABYSSal baseLINE) project, a baseline survey of foraminifera in two

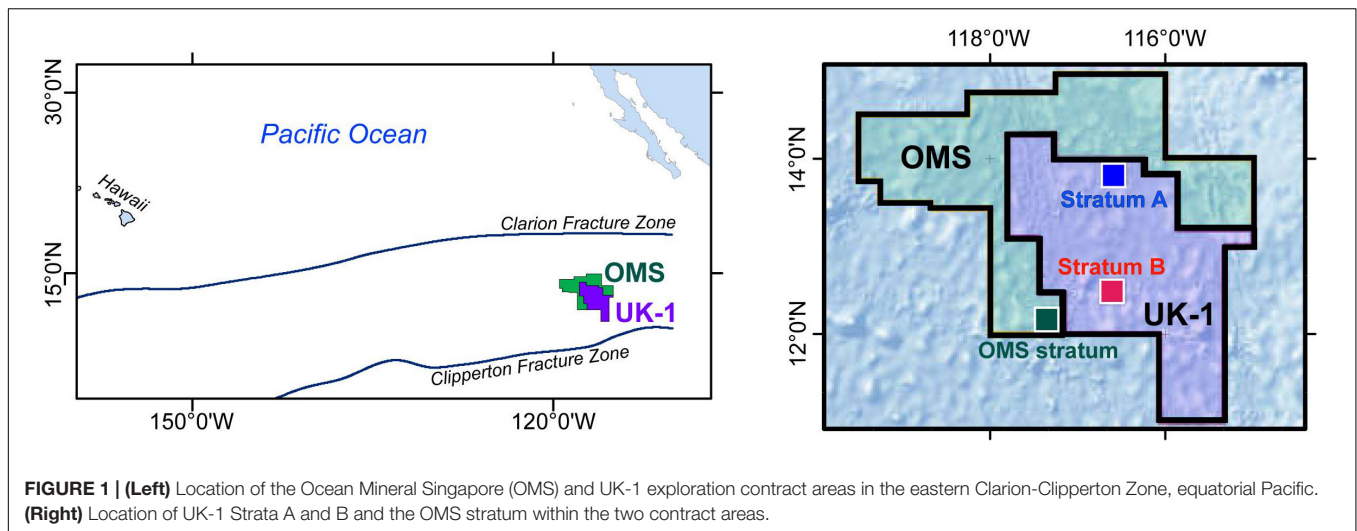
areas, also in the eastern CCZ, licensed by the International Seabed Authority for seabed exploration to the UK Seabed Resources Ltd. (UK-1 area), and Ocean Mineral Singapore Pte Ltd. (OMS area). The UK-1 area was sampled in 2013 and both areas were sampled in 2015 during ABYSSLINE research cruises. Previous studies on meiofaunal foraminifera within the framework of this project have described novel species that use radiolarian shells as microhabitats (Goineau and Gooday, 2015) and foraminiferal composition and diversity in >150 μm size fractions (Goineau and Gooday, 2017). Here, we extend this earlier research by describing assemblages of stained and dead benthic foraminifera retained on 63 and 125 μm mesh sieves and comparing them with assemblages in residues >150 μm . We address two main questions. (1) How much information on foraminiferal abundance and diversity is added by analyzing these finer fractions? (2) What are the differences in foraminiferal assemblage composition between the larger and smaller size fractions?

MATERIALS AND METHODS

General information about the ABYSSLINE project is given by Glover et al. (2015). For environmental information about the study area see Amon et al. (2016) and Goineau and Gooday (2017). Pape et al. (2017) provide further environmental data (sediment granulometry, porosity and sorting, total organic carbon and total nitrogen content) for the GSR license area, located to the west of the UK-1 and OMS areas and in somewhat deeper water (~4500 m). In general terms, our shipboard and laboratory methods followed those described by Goineau and Gooday (2017). We use the term ‘stained’ to refer to specimens that were inferred to be alive when stained.

Sampling

Samples were collected during two ABYSSLINE cruises at 5 sites (**Supplementary Table S1**) in three 30 × 30 km study areas (‘strata’) located within the UK-1 and OMS exploration contract areas (**Figure 1**). Two were obtained in Stratum A of the UK-1 license area, centered around 13°49′ N, 116°36′ W, during the first cruise (AB01, R/V *Melville*, cruise MV1313, 3–27 October 2013), two in UK-1 Stratum B, centered around 12° 28.9′ N, 116° 36.3′ W, and one in the OMS Stratum, centered around 12° 8.2′ N, 117° 17.7′ W during the second cruise (AB02: R/V *Thomas G Thompson* cruise TN319; 12 February to 25 March, 2015). In each case the samples were recovered using a hydraulically dampened Megacorer (BCMega OSIL Bowers & Connelly type), equipped with 12 polycarbonate coring tubes. As soon as possible



after collection, the cores were sliced, using a metal plate, into 0.5-cm thick layers to 2 cm depth and 1-cm thick layers from 2 to 10 cm depth and each layer preserved separately in a 500 ml plastic bottle with 10% formalin buffered with borax. Any nodules present in the core were carefully removed in order to facilitate slicing and sediment adhering to them washed into the appropriate sample bottle.

Laboratory Processes

The 0–0.5 and 0.5–1.0 cm sediment layers were used for this study. In the laboratory, the volume of each slice was measured by settling the sediment in a graduated cylinder for 2 days (after which the volume stabilized) followed by splitting into 8 parts using a wet splitter (Jensen, 1982). One split was selected for analysis and its volume measured in the same way. It was then sieved on a series of meshes (300, 150, 125, 63 μm) and each residue stained overnight on the sieve in Rose Bengal solution (1 g in 1 l of tapwater). The stained residues were transferred in water to a Petrie dish and examined under a stereo-microscope. All foraminifera (stained and unstained) and metazoan meiofaunal animals were removed using a glass pipette. In most cases they were stored on cavity slides in a small volume of glycerol, the cavities being left uncovered in order to allow easy access to the specimens. Some delicate organic-walled foraminifera that shrank in glycerol were placed in 1.25 ml Nalgene® cryovials, while calcareous foraminifera, which were rare, were placed on dry slides in order to avoid dissolution in the glycerol. Foraminifera with stained cytoplasm and (if present) fresh stercomata were considered to have been alive when sampled (see **Supplementary Material** for discussion of criteria for distinguishing stained from dead tests).

All foraminiferal specimens were examined under an Olympus BH-2 compound microscope and photographed using an SLR digital camera (Canon EOS 350D) attached to the microscope. Calcareous and delicate organic-walled foraminifera were placed in a cavity slide with water for this purpose, but the majority of specimens were photographed in glycerol. Specimens were grouped into working morphospecies based mainly on

observations of test morphology and wall structure, and assigned to genera or species where possible. Those that could not be placed in known taxa were given a descriptive working name.

Some of the methodological challenges involved in analyzing benthic foraminifera in sediment residues from the abyssal CCZ are outlined in the **Supplementary Material**.

Statistical Methods

T-tests to compare the relative abundances of major groups in the >150 and <150 μm fractions were computed using Excel. Based on complete specimens only (stained and stained plus dead combined), we used the open source software EstimateS (Version 9) (Colwell et al., 2012) to calculate the Fisher alpha (α) and Shannon (H' ; using natural logarithm) diversity indices, and rarefied species richness values [$E(S_{100})$] – the expected number of species represented by 100 individuals) using the open source software EstimateS (Version 9) (Colwell et al., 2012).

RESULTS

Abundance

We picked a total of 2341 complete stained ('live') foraminiferal tests, 1093 complete dead tests, and 1381 fragments (stained and dead combined) from the >300 , 150–300, 125–150, and 63–125 μm fractions combined of the five 1/8th sample splits. Individual splits yielded 269–777 ($=274\text{--}791.10\text{ cm}^{-2}$) stained tests, 125–329 ($=127\text{--}335.10\text{ cm}^{-2}$) dead tests and 115–497 ($=117\text{--}506.10\text{ cm}^{-2}$) test fragments.

A majority (62.2%) of complete stained foraminiferal tests originated from the two finer sieve fractions (<150 μm ; i.e., 63–125 and 125–150 μm combined), with more than half (52.7% overall) being found in the 63–125 μm fraction alone (**Table 1**). The dead assemblage showed a similar proportion; 64.8% overall in the two finer fractions with 53.7% in the 63–125 μm fraction. Fragmented tests (live + dead combined, mainly tube fragments) were more evenly distributed between the two fractions, with 47.5%

TABLE 1 | Numbers and percentages of complete foraminiferal tests (stained + dead) in the 5 sample splits of which the > 150 μm and 63–150 μm fractions were analyzed.

	N range	%range	Mean N	Mean%	
Stained					
300 μm	8–56	2.48–7.99	29.8	6.15	37.8% > 150 μm
150–300 μm	43–284	13.3–35.3	153	31.6	
125–150 μm	26–72	4.97–13.6	46.0	9.49	62.2% < 150 μm
63–125 μm	137–330	44.5–70.6	121	52.7	
Dead					
300 μm	7–17	3.35–8.08	11.6	5.73	35.2% > 150 μm
150–300 μm	39–71	14.5–46.2	55.8	29.5	
125–150 μm	13–46	7.92–15.2	22.6	11.1	64.8% < 150 μm
63–125 μm	42–190	35.3–70.6	121	53.7	

originating from the > 150 μm and 52.5% from the < 150 μm fraction (Table 2).

Main Groups

Species were divided into a series of main categories, a mixture of formal taxa (e.g., rotaliids, hormosinids, trochamminids) and informal morphology-based groupings (e.g., spheres, tubes, and ‘other monothalamids’). The latter encompasses monothalamids that are difficult to categorise morphologically; some examples are illustrated in **Supplementary Figures S1A–C,E–G, S2A,B**. The same main taxa and morphological groupings are represented in both the > 150 μm and < 150 μm fractions (Tables 3, 4). Among groups represented by complete tests (stained and dead), most tend to be more abundant in absolute terms in the finer fractions. This difference is particularly clear in the case of rotaliids and trochamminids (Figures 2A,D–H and **Supplementary Figures S3C–E, S4A–D**), *Lagenammina* spp. (**Supplementary Figures S5A–F**), *Nodellum*-like forms (**Supplementary Figure S6**), saccamminids (**Supplementary Figure S7**), spheres (Figure 4; **Supplementary Figure S8**), and organic-walled forms (**Supplementary Figures S9A–E**) in the live assemblage, and textualariids (Figures 2B,C and **Supplementary Figures S4E,F**), trochamminids, *Lagenammina* spp., *Nodellum*-like forms, saccamminids, and spheres in the dead assemblage. On the other hand, complete tubes and spindles, chains, ‘other monothalamids’ and Komokiacea (‘komoki’; families Baculellidae and Komokiidae, putative monothalamids; **Figure 3K** and **Supplementary Figure S1D**) are more abundant in the coarser fractions, particularly in the case of stained specimens. The only groups that are

significantly more abundant in the finer fractions, however, are the saccamminids and spheres (Tables 3, 4). The difference is particularly striking in the case of the stained spheres, which, on average, are some 5 times more abundant in the 63–150 μm than in the > 150 μm fraction. This difference is highly significant ($p < 0.001$) for stained specimens (Table 3) and significant ($p < 0.05$) for the dead specimens (Table 4). These tiny spheres form a substantial proportion of the stained assemblage. They are largely undescribed and in most cases regarded as indeterminate since it was not possible to consistently distinguish morphologically distinct types amongst them. Some examples of the more common forms are shown in **Figure 4** and **Supplementary Figure S8**.

Test fragments (stained and dead combined) are dominated by tubes and spindle-shaped morphotypes (grouped together), with lesser contributions from komokiaceans (Baculellidae and Komokiidae) (Figure 3). However, the only clear differences between fractions are the greater average absolute and relative abundance of baculellid fragments in the coarser fractions and, to a lesser extent, of komokiids in the finer fractions (**Supplementary Table S2**). The differences were not significant ($p > 0.05$), however. In the case of the komokiids, it reflected the large number of small fragments of a *Reticulum* species (Figure 3K) in the 63–125 and 125–150 μm fractions of the MC13 sample.

Table 5 presents data for the calcareous and agglutinated taxa that have more robust tests and therefore the potential to survive in the fossil record. We include here all of the multichambered foraminifera (Globothalamea and Tubulothalamea) (Figure 2 and **Supplementary Figures S3A–E, S4**), together with species of *Lagenammina* (**Supplementary Figures S5A–F**), which,

TABLE 2 | Numbers and percentages of fragmentary foraminiferal tests (stained + dead) in the 5 sample splits of which the > 150 μm and 63–150 μm fractions were analyzed.

	N range	%range	Mean N	Mean%	
300 μm	15–46	6.38–34.3	34.6	13.0	
150–300 μm	20–308	14.9–52.7	160	34.5	47.5% > 150 μm
125–150 μm	27–95	8.87–20.1	53.6	15.2	
63–125 μm	41–246	24.5–62.1	140	37.3	52.5% < 150 μm
Total per 10 cm^2	17–84				

TABLE 3 | Mean and percentage abundances (\pm standard deviations) of major groups based on complete stained specimens in the two size fractions and both fractions combined of 5 samples.

	All fractions		>150 μ m		63–150 μ m	
	N	%	N	%	N	%
Foraminiferal group						
Rotaliids	12.8 \pm 8.47	3.01 \pm 2.61	3.80 \pm 2.86	3.92 \pm 6.83	9.20 \pm 5.81	3.12 \pm 1.94
Miliolids	1.60 \pm 1.34	0.35 \pm 0.35	0.40 \pm 0.55	0.15 \pm 0.23	1.40 \pm 1.14	0.44 \pm 0.39
Lagenids	0.60 \pm 0.89	0.15 \pm 0.25	0	0	0.60 \pm 0.89	0.20 \pm 0.30
Ammosclerids	0.20 \pm 0.45	0.04 \pm 0.08	0.20 \pm 0.45	0.10 \pm 0.25	0.20 \pm 0.45	0.06 \pm 0.13
Textulariids	3.20 \pm 1.00	0.65 \pm 0.18	1.20 \pm 0.45	1.00 \pm 0.80	2.40 \pm 1.67	0.79 \pm 0.45
Trochamminids	5.00 \pm 4.36	1.04 \pm 1.04	0.40 \pm 0.55	0.19 \pm 0.28	4.40 \pm 4.28	1.32 \pm 1.34
Hormosinids	14.8 \pm 6.38	3.04 \pm 1.16	6.20 \pm 5.45	3.28 \pm 2.23	6.60 \pm 5.37	2.65 \pm 1.90
<i>Nodellum</i> -like	14.4 \pm 12.1	2.74 \pm 2.01	2.4 \pm 2.07	1.21 \pm 1.17	11.6 \pm 10.0	3.64 \pm 2.70
<i>Lagenammina</i>	21.0 \pm 8.94	4.44 \pm 2.19	2.40 \pm 1.67	2.56 \pm 3.77	18.6 \pm 8.17	5.80 \pm 1.90
Flasks	16.4 \pm 12.7	3.41 \pm 2.64	8.40 \pm 5.55	5.03 \pm 5.10	8.00 \pm 9.30	2.32 \pm 2.65
Chambers 2 tubes	5.60 \pm 3.21	1.15 \pm 0.57	1.60 \pm 1.82	1.04 \pm 1.60	4.00 \pm 2.83	1.19 \pm 0.67
Saccamminids	17.6 \pm 6.58	4.05 \pm 1.96	<u>2.20 \pm 2.59</u>	0.90 \pm 1.18	<u>15.4 \pm 8.02</u>	5.39 \pm 2.77
Spheres	171 \pm 36.8	37.6 \pm 8.11	<u>27.8 \pm 18.3</u>	14.94 \pm 5.86	<u>143 \pm 22.1</u>	49.4 \pm 13.3
Organic-walled	14.0 \pm 7.87	2.88 \pm 1.31	3.80 \pm 3.90	1.58 \pm 0.92	10.2 \pm 5.63	3.56 \pm 2.13
<i>Hyperammina</i>	0.60 \pm 1.34	0.08 \pm 0.19	0.20 \pm 0.45	0.06	0.40 \pm 0.89	0.102 \pm 0.22
Tubes/spindles	56.2 \pm 38.2	11.1 \pm 4.43	38.4 \pm 22.4	21.4 \pm 5.85	20.2 \pm 17.3	6.12 \pm 3.82
Other monothalamids	59.8 \pm 65.1	10.5 \pm 8.40	36.2 \pm 38.0	18.2 \pm 8.48	23.6 \pm 27.4	6.47 \pm 6.76
Chains	4.00 \pm 3.87	0.69 \pm 0.64	2.80 \pm 3.83	1.18 \pm 2.00	1.20 \pm 1.30	0.34 \pm 0.34
Komoki-like	14.4 \pm 11.5	2.54 \pm 1.59	6.25 \pm 5.54	3.12 \pm 2.51	8.40 \pm 8.53	2.37 \pm 1.98
Komoki: baculellids	10.4 \pm 8.41	1.91 \pm 1.05	9.60 \pm 8.02	4.52 \pm 1.89	0.80 \pm 0.83	0.24 \pm 0.25
Komoki: komokiids	4.60 \pm 1.81	0.97 \pm 0.24	<u>4.40 \pm 1.95</u>	2.96 \pm 1.71	<u>0.20 \pm 0.45</u>	0.07 \pm 0.15
Radiolarian Inhabitants	22.4 \pm 12.4	5.44 \pm 2.80	17.6 \pm 14.0	10.9 \pm 7.10	5.00 \pm 6.40	1.69 \pm 2.17
Total numbers	2386		929		1457	
Gromiids (n = 21)	4.80 \pm 4.44	1.08 \pm 1.22	0.40 \pm 0.89	0.125	4.40 \pm 4.16	1.41 \pm 1.38

Values that are significantly different between the two fractions are underlined ($p < 0.05$) or bold and underlined ($p < 0.001$).

although monothalamous, have more or less rigid test walls and are known as fossils. Hormosinids (23.2% of stained and 25.1% of dead specimens) and *Lagenammina* species (40.8% of stained and 25.0% of dead specimens) are abundant constituents of the both stained and dead assemblages when the coarser and finer fractions are combined, and are joined in the dead assemblage by the textulariids (21.5%). Rotaliids are relatively more common in the stained (19.6%) than in the dead (8.38%) assemblage. The overall composition of the >150 μ m and <150 μ m assemblages is similar. However, hormosinids are relatively less abundant in the finer fractions (stained 19.1% vs. 33.7%; dead 23.2% vs. 30.2%), a pattern reversed in the case of *Lagenammina* spp. (stained 42.7% vs. 36.0%; dead 30.2% vs. 11.3%).

Common Species

Supplementary Tables S3–S6 detail the 30 or so most abundant species in the stained + dead and stained only assemblages; in each case, data for all fractions combined, and the <150 μ m fraction only, are shown separately. All 44 species listed in these tables are illustrated in Figures 2–4 and the Supplementary Figures and brief descriptions are given the taxonomic notes included in the Supplementary Material. More than three-quarters (34) are monothalamids, among which

spheres, *Lagenammina* species, and ‘other monothalamids’ make up the majority. Most of the multichambered species are textulariids, including several *Reophax* species. By far the most abundant species, both overall and in particular categories, is a small agglutinated sphere (*Psammosphaerid* sp. 20) that is almost entirely confined (99.4%) to the finer residues. Seven other species (*Spiroplectammina subcylindrica*, ‘lobed spheres’, *Lagenammina* yellowish with long neck, *Lagenammina* sp. 9, *Saccamminid* sp. A, *Saccamminid* sp. 5) are found exclusively in the <150 μ m fractions (stained + dead assemblage). The 30 most common species (stained + dead) in the <150- μ m fraction include 23 that are also in the top 32 for the combined residues (>150 + <150 μ m). In the case of the stained-only assemblage in the <150- μ m fraction, the top 30 species include 22 that are also among the top-ranked species in the two residues combined; these include all of the 17 most abundant species.

Diversity

The five samples combined yielded a total of 462 provisional morphospecies of testate protists (stained and dead, complete and fragmentary tests) that were regarded as foraminifera. Of these, 54 were represented only by fragmented specimens, 279 occurred in the >150 μ m fraction, 313 occurred in

TABLE 4 | Mean and percentage abundances (\pm standard deviations) of major groups based on complete dead specimens in the two size fractions and both fractions combined of 5 samples.

	All fractions		>150 μm		63–150 μm	
	N	%	N	%	N	%
Foraminiferal group						
Rotaliids	12.6 \pm 19.3	4.83 \pm 6.34	5.80 \pm 8.58	7.38 \pm 10.0	6.80 \pm 10.8	3.62 \pm 4.58
Miliolids	0.60 \pm 0.55	0.28 \pm 0.28	0.50 \pm 0.55	0.80 \pm 0.74	0	0
Lagenids	0.80 \pm 1.30	0.31 \pm 0.48	0.20 \pm 0.45	0.26 \pm 0.58	1.00 \pm 1.41	0.69 \pm 0.98
Ammosclerids	5.80 \pm 4.09	2.64 \pm 1.47	2.60 \pm 2.70	4.03 \pm 4.57	4.20 \pm 4.44	2.98 \pm 2.27
Textulariids	24.6 \pm 15.9	11.2 \pm 5.95	8.00 \pm 2.83	11.8 \pm 5.11	17.0 \pm 14.4	12.03 \pm 8.37
Trochamminids	13.8 \pm 11.5	6.22 \pm 3.94	4.20 \pm 3.56	6.01 \pm 5.00	9.60 \pm 8.73	6.64 \pm 4.01
Hormosinids	30.2 \pm 18.3	13.2 \pm 4.94	9.80 \pm 4.44	14.7 \pm 8.32	20.4 \pm 15.0	12.6 \pm 3.79
<i>Nodellum</i> -like	12.0 \pm 7.84	5.87 \pm 3.46	0.60 \pm 0.89	0.82 \pm 1.19	11.4 \pm 7.60	8.88 \pm 4.58
<i>Lagenammina</i>	29.6 \pm 17.8	12.7 \pm 3.68	4.80 \pm 3.56	6.69 \pm 4.42	24.8 \pm 12.0	15.1 \pm 4.92
Flasks	6.80 \pm 3.83	3.52 \pm 2.16	2.60 \pm 2.07	3.70 \pm 2.96	3.60 \pm 2.69	2.64 \pm 2.72
Chambers 2 tubes	7.00 \pm 2.82	3.51 \pm 1.48	2.80 \pm 2.77	4.16 \pm 4.25	4.20 \pm 2.81	2.58 \pm 1.16
Saccamminids	8.25 \pm 3.77	3.85 \pm 0.85	<u>1.60 \pm 1.67</u>	2.40 \pm 2.54	<u>6.80 \pm 3.03</u>	4.96 \pm 1.43
Spheres	28.8 \pm 13.7	13.7 \pm 3.57	<u>5.60 \pm 2.97</u>	7.76 \pm 3.58	<u>23.2 \pm 14.3</u>	16.78 \pm 7.87
Organic-walled	0.40 \pm 0.55	0.16 \pm 0.16	0	0	0.40 \pm 0.55	0.22 \pm 0.32
<i>Hyperammina</i>	1.20 \pm 0.84	0.57 \pm 0.38	0.60 \pm 0.89	0.98 \pm 1.48	0.60 \pm 0.89	0.36 \pm 0.58
Tubes/spindles	11.0 \pm 4.85	5.59 \pm 2.27	5.40 \pm 2.07	7.96 \pm 3.22	6.60 \pm 5.94	4.85 \pm 3.89
Other monothalamids	10.0 \pm 2.55	4.91 \pm 1.44	6.00 \pm 3.39	8.84 \pm 5.20	4.00 \pm 2.92	2.52 \pm 0.95
Chains	1.80 \pm 3.49	1.00 \pm 2.28	0.80 \pm 1.79	1.04 \pm 2.32	1.00 \pm 1.73	0.92 \pm 1.82
Komoki-like	1.80 \pm 2.39	0.93 \pm 1.64	1.40 \pm 2.61	1.80 \pm 3.39	0.40 \pm 0.55	0.23 \pm 0.32
Komoki: baculellids	3.20 \pm 3.11	1.55 \pm 1.93	2.80 \pm 2.68	3.72 \pm 3.56	0.40 \pm 0.55	0.34 \pm 0.49
Komoki: komokiids	2.20 \pm 1.79	1.07 \pm 0.76	2.00 \pm 1.87	2.64 \pm 2.20	0.20 \pm 0.45	0.13 \pm 0.30
Radiolarian inhabitants	2.20 \pm 1.79	1.07 \pm 0.71	2.20 \pm 1.79	3.05 \pm 2.47	0	0
Total numbers	1140		413		727	
Gromiids	0	0	0	0	0	0

Values that are significantly different are underlined ($p < 0.05$).

the <150- μm fractions and 170 were confined to these fine fractions (Table 6). The most diverse groups were the tubes with 77 species, 20 of them confined to fractions <150 μm , and the spheres, with 61 species, 25 confined to the fine fractions. Among multichambered groups, textulariids (32 species, 18 only in <150 μm fractions) and hormosinids (30 species, 6 only in <150 μm fractions) were the most speciose. If the >150 μm dataset is expanded to include six additional sample splits for which the fine fractions were not analyzed (Goineau and Gooday, unpublished), then the number of morphospecies found only in the >63 μm fraction is halved from 170 to 84.

Detailed diversity metrics based on complete individuals are summarized in Table 7 (stained plus dead specimens combined) and Table 8 (stained specimens only). Species numbers and diversity indices [H' , Fisher α , $E(S_{100})$] are generally higher in samples that include the 63–125- μm plus 125–150- μm fractions compared to those based on only the 150–300- μm plus >300 μm fractions. Except for sample MC21, where stained specimens were 3.5 times more abundant in the finer than the coarser residues, Rank 1 Dominance (R1D) is higher in the case of the <150- μm assemblages. However, inclusion of the finer fractions has

an inconsistent influence on R1D values when the two fractions are combined.

Gromiids, Unknown Testate Structures, and Metazoan Meiofauna

The <150- μm residues yielded 21 specimens with transparent organic tests that were regarded as gromiids based on the presence of an oral capsule (Hedley, 1960; Rothe et al., 2010). Most had more or less elongate, droplet-like tests that tapered toward the oral capsule (Supplementary Figures S9G,I), but a few were sausage-shaped (Supplementary Figure S9F) or spherical (Supplementary Figure S9H). They are tentatively assigned to 8 morphospecies, all confined to the fine fractions, although variability in test morphology made it difficult to discriminate between some of these forms.

The fine fractions (mainly the 63–125 μm fraction) of some samples also yielded a variety of more or less spherical, organic-walled structures that gave rise to relatively short blind-ending processes (Figure 5). They were concentrated in the MC11 and MC13 samples and included three main types. Type A varies in shape from spherical to oval or somewhat irregular and is characterized by a variable number (2–10) of short tubular

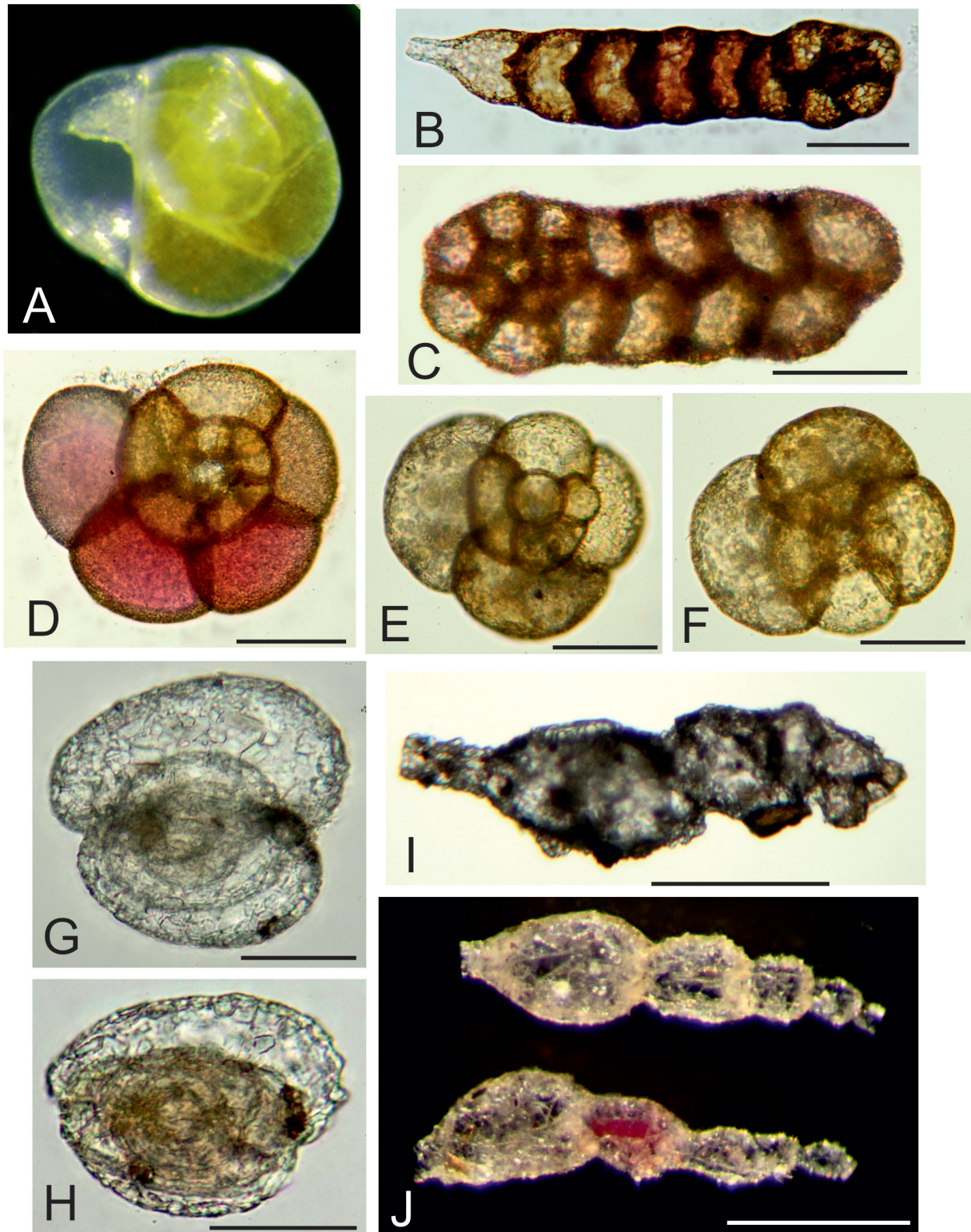


FIGURE 2 | Multichambered foraminifera. **(A)** *Epistominella exigua* Brady; 'live' specimen with green cytoplasm, picked from > 150 μm residue at sea. **(B)** *Ammobaculites filiformis* Earland; MC09, 0–0.5 cm, 63–125 μm fraction. **(C)** *Spiroplectammina subcylindrica* Earland; MC21 G 0–0.5 cm, 63–125 μm . **(D)** Trochamminacean sp. 1; MC21, 0.5–1.0 cm, 63–125 μm fraction. **(E,F)** Trochamminacean sp. 2; MC21, 0.5–1.0 cm, 63–125 μm fraction. **(G,H)** *Adercotryma* sp.; MC21, 0.5–1.0 cm, 63–125 μm fraction. **(G)** Rounded specimen. **(H)** More elongate specimen. **(I)** *Reophax scorpiurus* Montfort, MC11, 0.5–1.0 cm, 150–300 μm fraction. **(J)** *Reophax* sp. 1, MC05, 0–0.5 cm, >300 μm fraction. Scale bars = 50 μm **(A–H)**, 250 μm **(I)**, 500 μm **(J)**.

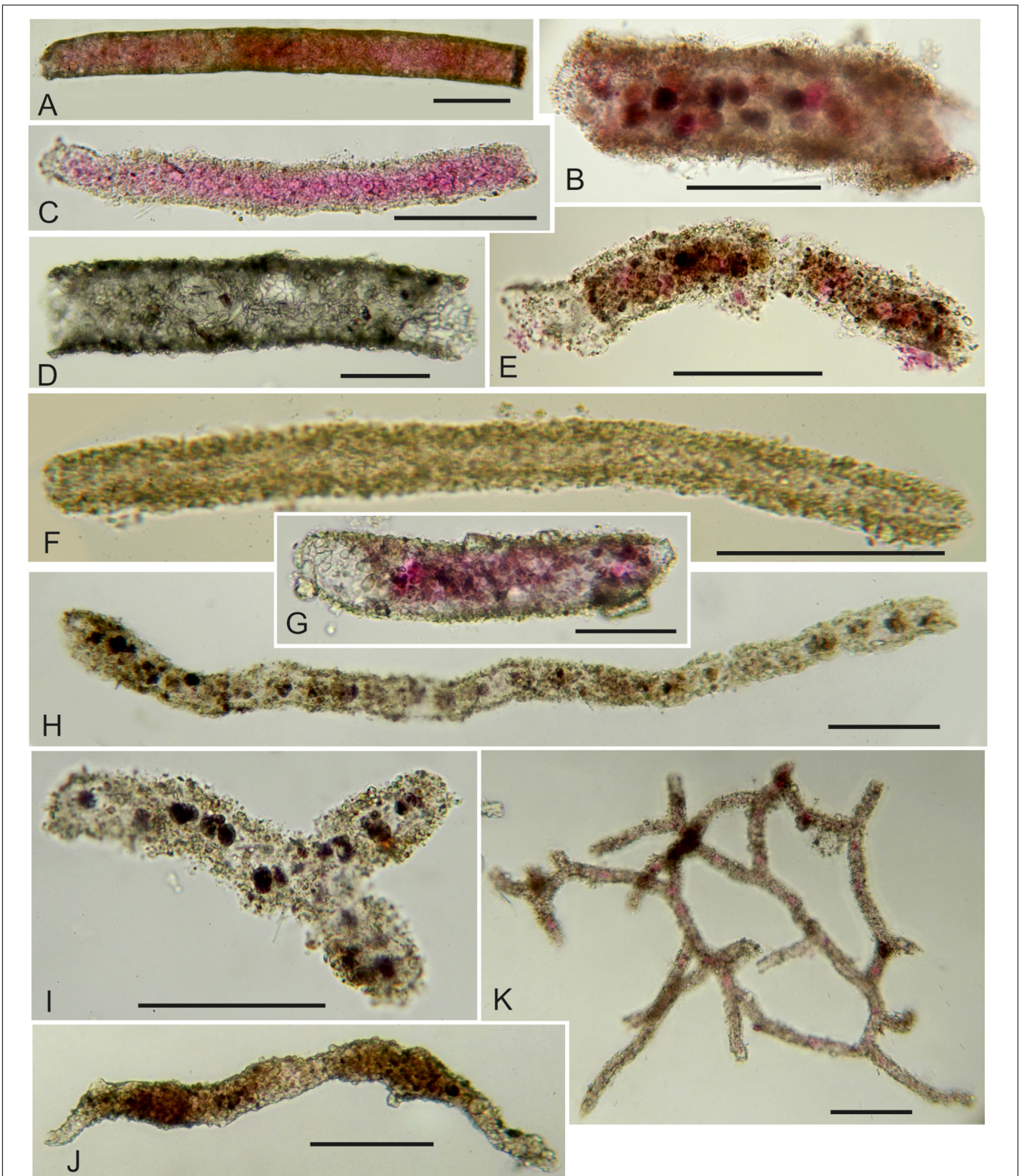


FIGURE 3 | (A–F) Undescribed tubular foraminifera (fragments unless stated otherwise). **(A)** Stained; MC21, 0.5–1.0 cm, 63–125 μm fraction. **(B)** Stained with stercomata; MC13, 0–0.5 cm, 125–150 μm fraction. **(C)** Stained; MC11, 0–0.5 cm, 63–125 μm fraction. **(D)** Dead; MC13, 0–0.5 cm, 125–150 μm fraction. **(E)** Stained; MC09, 0–0.5 cm, 63–125 μm fraction. **(F)** Dead; MC21, 0.5–1.0 cm, 63–125 μm fraction. **(G)** Stained, complete test; MC05, 0.5–1.0 cm, 63–125 μm fraction. **(H)** Dead tubular fragment with stercomata; MC11, 0–0.5 cm, 63–125 μm fraction. **(I)** Complete tubular specimen; MC11, G, 0–0.5 cm, 63–125 μm fraction. **(J)** *Marsipella* sp.; MC11, 0–0.5 cm, 63–125 μm fraction. **(K)** Stained fragment of *Reticulum* (komokiacean); MC13, 0–0.5 cm, 125–150 μm fraction. Scale bars = 100 μm .

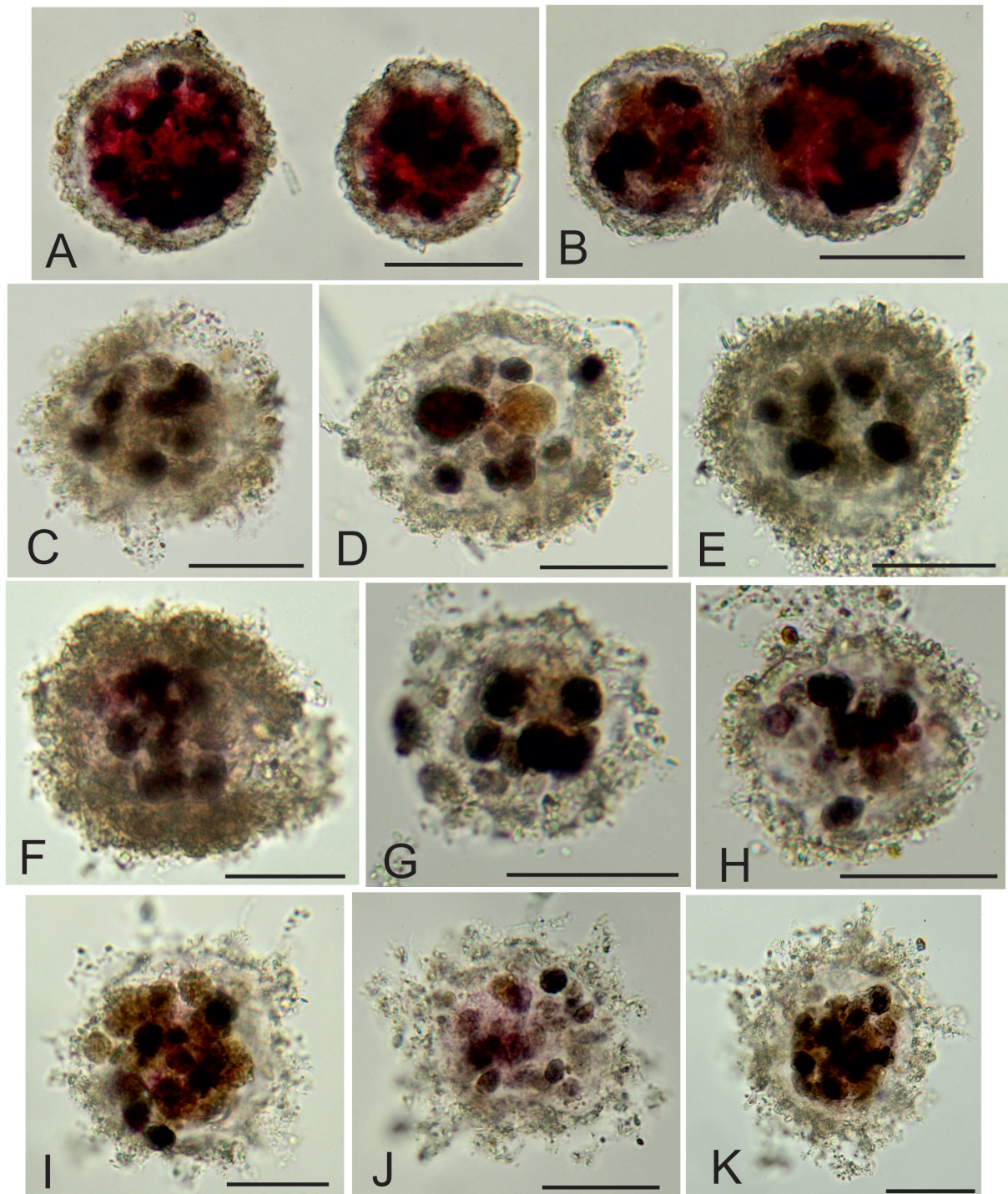


FIGURE 4 | Undescribed spherical foraminifera from 63 to 125 μm fractions. **(A,B)** *Psammosphaerid* sp. 20, the most abundant morphospecies species in the stained assemblage; MC13, 0.5–1.0 cm. **(C–H)** Morphotype with delicate, fine-grained wall enclosing stercomata and sparse cytoplasm; all are from sample MC05. **(I–K)** Similar morphotype in which the wall includes an organic layer with finely agglutinated particles and gives rise to short filament-like structures; all are from sample MC05. Scale bars = 50 μm .

extensions with longitudinal striations and ending in a thin-walled bulb. This was by far the commonest form, particularly in the MC13 sample where it was represented by 174 specimens.

Type B has relatively longer, narrower, and often somewhat tapered tubular processes, sometimes ending in a small bulb. Three specimens were found inside other structures in the MC11

TABLE 5 | Absolute and relative abundance of complete foraminifera belonging to more robust (fossilizable) taxa, mainly multichambered.

	> 150 μm				<150 μm				Combined			
	'Live'		Dead		'Live'		Dead		'Live'		Dead	
	N	%	N	%	N	%	N	%	N	%	N	%
Rotalliids	19	22.1	24	15.1	41	18.6	24	5.80	60	19.6	48	8.38
Miliolids	0	0	3	1.89	6	2.73	0	0	6	1.96	3	0.52
Ammodiscids	0	0	9	5.66	2	0.91	25	6.04	2	0.65	34	5.93
Lageniids	0	0	1	0.63	6	2.73	8	1.93	6	1.96	9	1.57
Textulariids	4	4.65	36	22.6	9	4.09	87	21.0	13	4.24	123	21.5
Trochamminids	3	3.49	20	12.6	20	9.09	49	11.8	23	7.52	69	12.0
Hormosinids	29	33.7	48	30.2	42	19.1	96	23.2	71	23.2	144	25.1
<i>Lagenammina</i>	31	36.0	18	11.3	94	42.7	125	30.2	125	40.8	143	25.0
Total	86		159		220		414		306		573	

The numbers are totals from all 5 samples. L = 'Live' (stained); D = Dead.

TABLE 6 | Number of morphospecies assigned to different foraminiferal groups, and to gromiids.

Foraminiferal group	All species	>150 μm	<150 μm	<150 only
Rotalliids	19	11	14	8
Miliolids	4	1	3	3
Ammodiscids	6	1	6	5
Lageniids	5	3	5	2
Textulariids	32	13	24	18
Trochamminids	18	10	16	8
Hormosiniids	30	23	20	6
<i>Lagenammina</i>	15	4	13	11
<i>Nodellum</i> -like	17	8	15	8
Flasks	4	3	4	1
Droplet chambers	2	0	2	2
Chambers 2 tubes	2	0	2	0
Saccamminids	28	8	22	19
Spheres	61	35	36	25
Organic-walled (allogromiids)	19	6	15	13
<i>Hyperammina</i>	6	3	3	3
Tubes/spindles	77	54	57	20
Other monothalamids	56	43	25	12
Chains	10	9	6	0
Komoki-like	15	13	9	2
Komoki: baculellids	19	19	9	0
Komoki: komokiids	17	12	7	4
Total number of species	462	279	313	170
Gromiids	8	0	8	8

The numbers are totals from all 5 samples.

sample. Type C is spherical and was represented by 2 specimens from the MC13 sample with several (3 and 5) rounded bumps on the surface of the organic wall.

A total of 167 metazoan meiofaunal organisms (not counting 7 polychaete fragments without heads), all of which were well stained and assumed to have been alive when collected, were picked from the 5 sample residues (i.e., 1/8th splits of the top 1-cm layer of five 10-cm diameter sediment cores). This number

corresponds to an overall density of 34.0 individuals per 10 cm². Nematodes were the most common metazoans (62.3%), followed by harpacticoid copepods (19.7%), nauplii (15.6%), 2 ostracods, 1 bivalve and 1 kinorhynch.

DISCUSSION

Stained complete foraminiferal tests were more than an order of magnitude more abundant in our five sample splits from the eastern CCZ than metazoan meiofaunal animals (i.e., 2341 stained tests compared with 167 metazoans, corresponding to overall densities of 496 and 34 individuals per 10 cm², respectively). The metazoan densities are generally lower than those typical for the CCZ (11–394 individuals per 10 cm² in nine studies; summarized in Radziejewska, 2014, Table 3.4 therein) and the mean values (88 ± 55 to 151 ± 54 individuals per 10 cm²) recently reported by Pape et al. (2017) from the GSR license area in the northeastern CCZ. Moreover, the proportion (62.3%) of nematodes is relatively low and the proportion of nauplii relatively high (15.6%), compared to previous studies. For example, nematodes represented 85–93% and nauplii 1.1–7.1% of the metazoan meiofauna in the study of Pape et al. (2017). These discrepancies probably reflect methodological differences. In particular, while the 63 μm lower limit used in the present study is normal for foraminifera (Murray, 2014), it is not appropriate for analyzing metazoan meiofauna, for which 32 μm is now the generally accepted lower limit (Leduc et al., 2010). Nevertheless, although metazoans were not adequately sampled, our results do suggest that stained foraminifera outnumber metazoan meiofaunal animals in CCZ sediments.

The nature of the organic-walled structures with blind-ending processes remains unresolved. They are almost certainly not dinoflagellate cysts (Dr. Ian Harding, University of Southampton, personal communication). The most likely identification, at least for the common forms from sample MC13 (Figures 5A–D), are that they are metazoan eggs, possibly those of a crustacean (Dr. Manuel Bringué; Geological Survey of Canada – Calgary).

TABLE 7 | Diversity metrics for the stained + dead assemblage in different samples.

	MC09			MC11			MC05			MC13			MC21		
	UK-1 Stratum A			UK-1 Stratum A			UK-1 Stratum B			UK-1 Stratum B			OMS Stratum		
	>150	<150	Total	>150	<150	Total	>150	<150	Total	>150	<150	Total	>150	<150	Total
N	208	340	547	345	426	771	208	233	442	144	161	305	99	350	448
S	95	100	164	99	113	177	82	89	150	57	57	100	50	120	150
H'(log _e)	4.27	4.03	4.59	3.96	4.07	4.55	3.95	4.02	4.52	3.57	3.22	3.96	3.53	4.19	4.38
Fisher α	67.6	47.7	85.0	47.2	50.2	74.0	49.9	52.6	83.1	37.3	32.1	56.9	40.3	64.5	79.1
E(S ₁₀₀)	63.6	52.0	63.3	50.4	52.2	60.2	52.4	54.9	62.1	46.7	44.0	53.0	50.0	56.0	59.0
R1D	7.21	9.71	6.63	10.14	12.7	7.03	6.44	12.4	6.58	24.1	44.7	26.1	15.1	10.0	7.81

TABLE 8 | Diversity metrics for the stained assemblage in different samples.

	MC09			MC11			MC05			MC13			MC21		
	UK-1 Stratum A			UK-1 Stratum A			UK-1 Stratum B			UK-1 Stratum B			OMS Stratum		
	>150	<150	Total	>150	<150	Total	>150	<150	Total	>150	<150	Total	>150	<150	Total
N	152	171	323	292	307	597	123	167	290	85	114	199	42	170	212
S	74	72	129	80	87	144	61	61	115	30	36	57	26	70	83
H'(log _e)	4.03	3.844	4.438	3.69	3.756	4.260	3.69	3.635	4.293	2.883	2.492	3.209	3.072	3.820	3.851
Fisher α	58.7	46.29	84.92	36.3	40.93	60.27	36.35	35.19	69.52	16.20	18.77	27.40	29.11	44.25	51.89
E(S ₁₀₀)	58.8	52.3	65.1	44.2	47.6	54.2	44.2	47.0	59.8	30.0	34.2	39.60	26.0	51.7	52.75
R1D	7.89	11.6	10.9	12.0	17.3	8.88	8.12	16.5	9.18	24.1	46.8	27.1	9.52	11.7	17.1

The majority of complete stained (61.1%) as well as dead (63.8%) foraminiferal tests originated from the 63–150 μm fractions. These results are consistent with previous studies of deep-sea meiofauna, including foraminifera (e.g., Gooday, 1986; Schewe, 2001), as well as with the general tendency for small-sized organisms to become increasingly important with increasing water depth (Thiel, 1975, 1983). Duchemin et al. (2007) report that the 63–150 μm fraction of the top 1-cm of a core from 1000 m in the Bay of Biscay yielded the vast majority (97.5%) of stained foraminifera. In one of the most comprehensive studies, Phipps et al. (2012) found that stained foraminiferal densities in the 63–150 μm fraction of samples taken along a down-slope transect (262 – 4987 m water depth) on the Portuguese margin were consistently more than twice those in the >150 μm fraction. Interestingly, the proportion increased with depth, reaching a peak at 3908 m, where 88% of stained foraminifera were picked from the fine sieve residues.

Comparison With Modern Abyssal Assemblages

Fractions <150-μm were dominated by monothalamids, many of them more or less spherical forms. These tiny spheres represented an average of 37.6 ± 8.1% of complete stained foraminifera in all fractions combined and 49.4 ± 13.3% in the 63–150 μm fraction, with a significantly lower numbers in the 150–300 μm compared to the 63–150 μm fraction (Table 1). Many have delicate, fine-grained test walls and contain stercomata (Figures 4C–K). Numerous agglutinated spheres are also reported in previous

studies of abyssal Pacific samples. According to Snider et al. (1984), spherical ('sac-shaped') morphotypes made up almost third (31.3%) of meiofaunal foraminifera in the central North Pacific (5800 m depth). Nozawa et al. (2006), found an even greater predominance (33.5 – 94.5%) of tiny, undescribed 'psammospaerids' in small samples from the Kaplan East site, located immediately to the west of the UK-1/OMS area and at a similar water depth. The higher proportion probably reflects the fact that Nozawa et al. (2006) examined even finer fractions (>32 μm) fractions than those analyzed for the present study. Later, Ohkawara et al. (2009) established a new species, *Saccamina minimus*, based on numerous tiny agglutinated spheres from the deeper (~5000 m) Kaplan Central site, located in the central part of the CCZ (~14°N, 130°W). The majority of spheres in our samples are undescribed, but some are probably the same as *S. minimus*, while other somewhat larger forms resemble *Thuramina albicans*. Small agglutinated spheres also occur in the abyssal North Atlantic. They represented 7.2 – 12.4% of assemblages >63 μm at the Porcupine Abyssal Plain and an even higher proportion (17.8%, 21.0%) in two samples from the Cape Verde Abyssal Plain (Gooday, 1996). Very small agglutinated tests were reported by Gooday et al. (1995) in North Atlantic sediments sieved on 32 and 20 μm meshes. However, the spheres with a soft 'fluffy' wall and containing stercomata (Figures 4C–K), which are common in our samples, have not been observed in the Atlantic material.

The finer residues yielded many tubular and spindle-shaped morphotypes (Figure 3). Stained specimens judged to be complete were again more common in the >150-μm

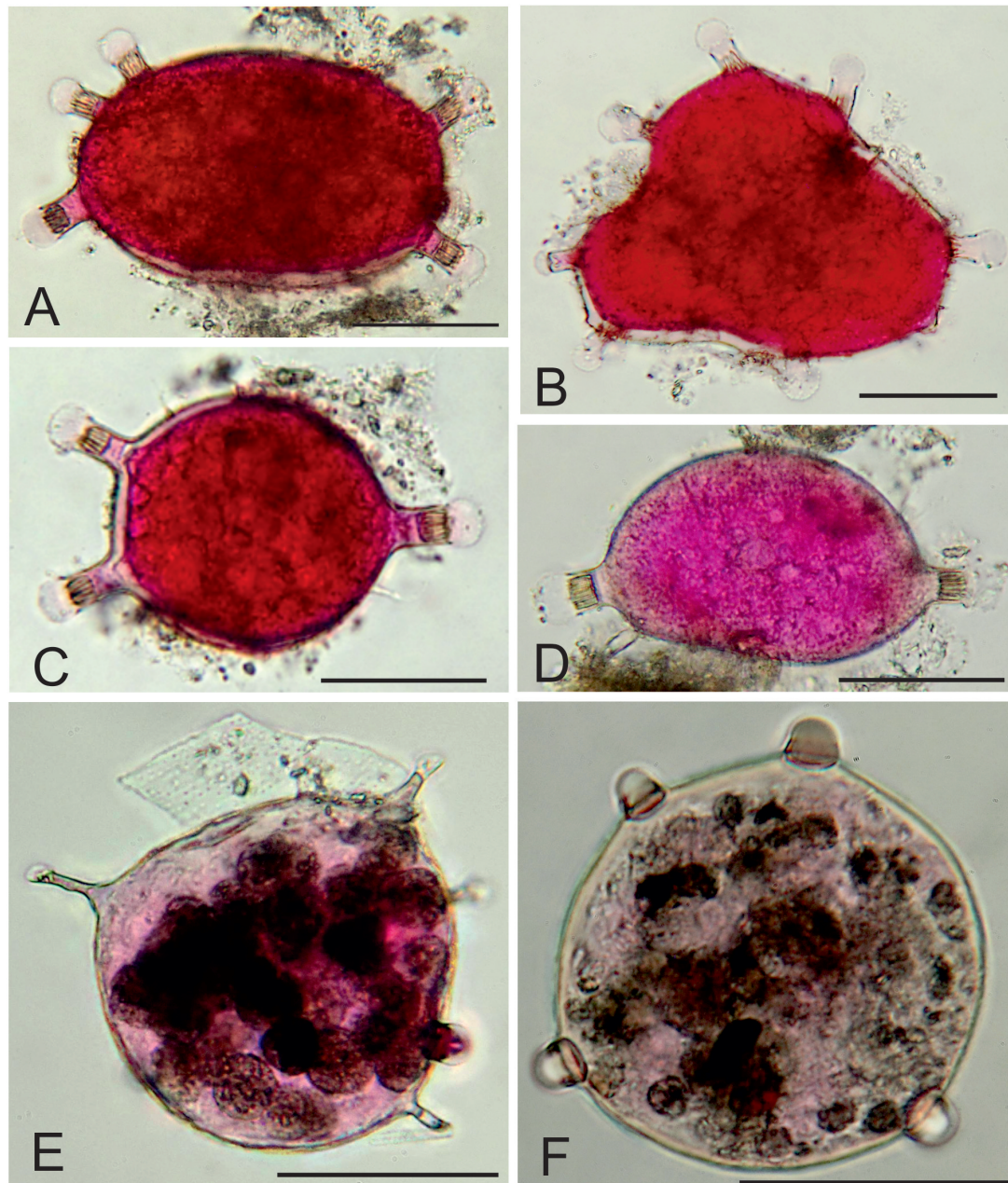


FIGURE 5 | Unidentified organic-walled structures (?metazoan eggs) from 63–125 μm fractions. **(A–C)** Type A with short striated tubes ending in thin-walled bulbs; MC11, 0–0.5 cm layer. **(D,E)** Type B with relatively long slender tubes, sometimes ending in a small thin-walled bulb; MC11, 0–0.5 cm. **(F)** Type C with rounded bumps; MC13, 0.5–1.0 cm layer. Scale bars = 50 μm .

(mean 21.4%) than the $<150\text{-}\mu\text{m}$ (mean 6.12%) fraction (Table 3). Tubular fragments (stained as well as stained and dead combined) were also very numerous, representing $>60\%$ in both size fractions (Supplementary Table S2). Similar fragments are often common in abyssal samples. Bernstein et al. (1978) recorded 30,938 fragments compared to 5,079 complete foraminiferal tests in 5 unstained box-corer residues ($>297\text{ }\mu\text{m}$ fraction) from the central North Pacific. Snider et al. (1984) likewise found numerous fragments in their North Pacific

samples (42–1000- μm fraction). Based on the conservative assumption that all fragments of a similar type within a sediment layer and adjacent layers were derived from one individual, they calculated that 24% of monothalamids were tubular forms.

Our samples also yielded small, multichambered foraminifera that are similar to those reported in previous studies of modern abyssal benthic foraminifera. They include agglutinated species (e.g., *Cribrostomoides subglobosum*, *Cyclammina trullisata*, *Cystammina galatea*, *Cystammina pauciloculata*, *Deuterammina*

grahami, *Glomospira* spp., *Hormosinella ovicula*, *Hyperammina cylindrica*, *Lagenammina difflugiformis*, *Paratrochammina scotiaensis*, *Reophax scorpiurus*, *Spiroplectammina subcylindrica*, *Hormosinella distans*, *Veleroninoides wiesneri*), and calcareous species [*Epistominella exigua*, *Nuttallides umbonatus*, *Cibicidoides mundulus* (as *C. cf. mundulus*), *Fissurina staphyllearia* and *Melonis pompilioides*] previously reported from abyssal depths in the North and equatorial Pacific by authors such as Smith (1973), Burministrova et al. (2007), and Enge et al. (2012). Many of these are well-known morphospecies that are widely distributed in modern ocean basins (Gooday and Jorissen, 2012; Holbourn et al., 2013).

Comparison With Fossil Assemblages

There are some similarities between the agglutinated foraminifera in our samples and certain assemblages of multichambered taxa of Late Cretaceous and Paleogene age recovered in Deep-Sea Drilling Project (DSDP) and Ocean Drilling Project (ODP) cores. Krasheninnikov described Upper Cretaceous faunas devoid of calcareous foraminifera in red-brown clays from the Pacific (1973) and Indian (1974) Oceans. He interpreted these as having been deposited in oceanic sediments below the CCD. They consisted mainly of small species, often with smooth, fine-grained test walls, assigned to genera such as *Haplophragmoides*, *Labrospira*, *Trochammina*, and *Recurvoides*. Similar abyssal faunas are known from the North Atlantic Plantagenet Formation, where they also include 'rhizamminids' and 'fossil forms which resemble modern Komokiaceans' (Kuhnt et al., 1989). However, our multichambered assemblages also contain some calcareous taxa (mainly rotaliids), reflecting their location close to, rather than well below, the CCD. In this respect, they have more in common with the mixed calcareous and agglutinated assemblages described by Hemleben and Troester (1984) from DSDP Hole 543A in the central Atlantic.

Species of *Reophax* and other hormosinids, which consistently constitute the most common multichambered foraminifera in our samples, are often not well represented in the Late Cretaceous assemblages, possibly a result of the low fossilization potential of their fairly delicate tests (Schröder, 1986). Some more robust species, however, are preserved as fossils in deep-sea sediments (e.g., Kuhnt and Moullade, 1991).

Possible Ecological Significance Responses to Food Inputs

One rationale for including finer sieve fractions (63–150 μm) in ecological studies of bathyal and abyssal foraminifera is that small species often display opportunistic responses to seasonally pulsed food ('phytodetritus') inputs to the seafloor (e.g., Gooday, 1988, 2003; Gooday and Lamshead, 1989; Corliss and Silva, 1993; Silva et al., 1996; Ohga and Kitazato, 1997; Gooday and Rathburn, 1999; Gooday and Hughes, 2002; Kitazato et al., 2003; Heinz and Hemleben, 2006; Duchemin et al., 2007). This suggests that they play an active role in the processing fresh organic carbon on the ocean floor, an inference supported by *in situ* experimental studies using ^{13}C -labeled algae (Moodley et al., 2002), some

of which reveal different species-level responses to food inputs (Nomaki et al., 2005, 2006).

The deposition of phytodetritus on the deep-sea floor is well documented at temperate latitudes in the NE Atlantic. In the Pacific the phenomenon is reported from various sites along the North American continental margin (Beaulieu, 2002), notably at the intensively studied abyssal (4100 m depth) Station M on the Californian margin (Beaulieu and Smith, 1998). Here, as in the NE Atlantic, the presence of these deposits on the seafloor has a distinct seasonal component (Lauerma and Kaufmann, 1998). There is also evidence for seafloor phytodetritus in the abyssal equatorial Pacific. Deposition in this open ocean setting, however, is not seasonal (Beaulieu, 2002) and is linked to upwelling created by easterly trade winds (Smith and Demopoulos, 2003). Gardner et al. (1984) observed 'dark globs of material' that were '1–4 cm across and appear fluffy and organic in nature...' in seafloor photographs taken at a site to the south of the central CCZ (4°N, 136°W; 4469 m depth). Smith et al. (1996) recovered phytodetritus in multicore samples collected along the 140°W line from 5°N to 5°S. Further east, and within the CCZ, Radziejewska (2002) observed a 'very thin layer of a fluffy material, greenish-brown in color' (i.e., phytodetritus) on the surfaces of some cores collected in 1997 in part of the IOM contract area (centered at 11° 04'N, 119° 40'W; 4380–4430 m depth) that had been subject 2 years earlier to an experimental disturbance designed to simulate the effects of nodule mining (see also Radziejewska, 2014). Samples of this material, which was very patchily distributed, contained chloropigments and intact diatoms. Phytodetritus was not present on the surfaces of cores recovered in 1995 or 2000. Its presence in 1997 was believed to be largely responsible for the greatly increased abundance of the nematode genera *Desmoscolex* and *Pareudesmoscolex* compared to 1995 (Radziejewska et al., 2001). Increases in metazoan megafauna in nodule-bearing parts of the IOM area was likewise attributed to the increased food supply originating from phytodetrital inputs (Radziejewska and Stoyanova, 2000).

Small lumps of phytodetritus-like material were occasionally found in our sieve residues, but these deposits were not observed on the surfaces of any megacores collected during the present study. However, our residues yielded small numbers of species, notably *Alabaminella weddellensis* and *Epistominella exigua*, which are known to exploit phytodetrital inputs in the abyssal NE Atlantic (e.g., Gooday, 1988, 1993). *Epistominella exigua*, in particular, contained bright green cytoplasm indicating ingestion of fresh chlorophyll-bearing particles (Figure 2A). Darker green cytoplasm is typical of *Nuttallides umbonifera*, the most common rotaliid in our samples (Supplementary Figure S3D). If inputs of phytodetritus do occur from time to time in the UK and OMS claim areas, as they appear to do in the nearby IOM area, then these and perhaps other species are likely to respond to this fresh food source with rapid reproduction and population growth. All but 2 of the 25 specimens (stained and dead) of *A. weddellensis* and *E. exigua* were extracted from residues <150 μm , demonstrating the importance of examining finer sediment fractions in order to recover small, opportunistic foraminiferal species that may be

important players in the processing of fresh organic matter on the ocean floor.

Possible Importance in Recolonization

Alve (1999) reviewed how sediments that have been defaunated by natural or anthropogenic processes can be repopulated by benthic foraminifera. In relatively tranquil settings, initial recolonization may proceed in a series of stages, starting with quick-growing, opportunists that are succeeded by slower-growing, more specialized species. Relatively few studies of foraminiferal recolonization have been conducted in deep-water settings. Probably the best direct evidence comes from samples collected during 5 cruises (spring 1994, summer and winter 1996, summer 1998, spring 1999) in an area of the South China Sea (~2500 m depth) blanketed by a layer of volcanic ash from the 1991 Mt Pinatubo eruption (Hess and Kuhnt, 1996; Hess et al., 2001; Kuhnt et al., 2005). Although the material involved was different, the ash fall to some extent mimicked the deposition of resuspended sediment expected to result from seabed mining. In samples sieved on a 63- μm mesh, the initial recolonizers of the 2- to 6-cm-thick ash layer appeared to be a small species of *Textularia*, followed by *Reophax dentaliniformis* and later by *R. bilocularis* and *R. scorpiurus*, the rotaliid *Bolivina difformis* and the miliolid *Quinqueloculina seminula* (Hess et al., 2001). A second wave of recolonizers included *Trochammina* spp., *Adercotryma glomerata*, and *Subreophax guttifera*.

Analysis of sediments deposited by turbidity currents in submarine canyons has provided insights into the recolonization by foraminifera of physically disturbed areas of seafloor. According to Duros et al. (2017), the initial recolonizers in the >150 μm fraction of a turbidite deposit at upper bathyal depths (983 m, 1454 m) in the Capbreton Canyon (Bay of Biscay) were *Fursenkoina bradyi*, *R. dentaliniformis* and *Technitella melo*. However, the 63–150 μm fraction from the 983-m site, as well as two shallower sites (251 m, 301 m), were dominated by juveniles of *Bolivina subaenariensis*, which was interpreted as representing a second stage of recolonization. The same species dominated low diversity assemblages (63–150- μm fraction) of two cores collected in the same canyon at a 600 m site that had been impacted by a turbidity current 1.5 years earlier (Hess et al., 2005; Hess and Jorissen, 2009). Here, *B. subaenariensis* may have been responding to organic matter associated with the turbidite, as well as participating in the recolonization process.

These studies suggest that azoic substrates, originating either from deposited material (ash) or physical disturbance of the seafloor (turbidite), are colonized by a succession of foraminiferal species. In both cases, the colonizing species were considered to have been infaunal. Some of these species are larger (e.g., *Reophax* spp., which are fairly common in our samples) and more likely to be retained in the >150- μm fraction, but smaller species or juveniles are also involved. Our finer fractions yielded small agglutinated species belonging to genera such as *Ammobaculites*, *Spiroplectammina*, and *Textularia* that are rare in the stained assemblages. It is possible that such species may be important during initial phases of recolonization following mining-related disturbances.

CONCLUSION

Is the considerable additional effort required to analyze foraminifera in 63–150 μm fractions of samples from areas that could be disturbed by seabed mining worthwhile? In the present study, the fine-fraction assemblages contained >60% of stained and dead test as well as 170 species that were not present in the coarser fractions. They also yielded greater absolute abundances than >150- μm fractions of several monothalamid groups, notably *Lagenammia* spp., *Nodellum*-like forms, saccamminids, and particularly spherical forms, as well as some multichambered taxa, namely rotaliids (stained only), hormosinids (dead only), textulariids (dead only), and trochamminids. An important part of the foraminiferal assemblage was therefore confined to these fine fractions. As argued elsewhere (e.g., Gooday et al., 2008; Goineau and Gooday, 2017), multichambered taxa, particularly the calcareous rotaliids, may be metabolically more active than stercomata-bearing monothalamids in deep-sea settings, and therefore more important in terms of ecosystem functioning. Although rotaliids are relatively uncommon in our samples, their greater absolute (but not relative) abundance in the <150- μm fractions provides one incentive for analyzing fine sieve residues. Another justification is the potentially important role that small multichambered opportunistic species could play in the recolonization of sediments disturbed by mining. Nevertheless, the fact remains that this work is very time-consuming and difficult to undertake routinely.

A number of studies have used foraminiferal faunal data and diversity metrics as bio-indicators of human impacts in marine environments (e.g., Jorissen et al., 2009 and references therein). This has led to the formulation of a series of recommendations, the FOMIBO initiative, aimed at standardizing methodologies applied in such studies (Schönfeld et al., 2012). One of the 'mandatory' recommendations is that, although samples should be sieved on a 63- μm mesh, detailed analysis should be based on the >125- μm fraction. However, they also add the 'advisory' recommendation that in some eutrophic settings, where small opportunistic species are abundant, it may also be necessary to analyze the finer 63–125- μm as well as the >125 μm fraction. A similar conclusion was reached by Sen Gupta et al. (1987). A sensible compromise in the case of baseline studies of foraminifera in Pacific nodule fields would therefore be to concentrate efforts on analyzing coarser residues from all samples but to examine finer fractions (63–150 μm), either quantitatively or qualitatively, in a subset of samples or sample splits. Similar approaches have been adopted by a number of authors working in the NE Atlantic deep-sea samples (e.g., Phipps et al., 2012; Duros et al., 2017). It may be particularly important to do this during monitoring exercises, i.e., where deep-sea sediments have been defaunated by seabed mining and are in the early stages of recolonization by meiofaunal organisms. To conclude, foraminifera and particularly monothalamids are a major constituent of benthic faunas in the CCZ nodule fields. Despite the methodological challenges that they pose, we would encourage other researchers to consider including them in studies of areas where seabed mining may occur in the future.

DATA AVAILABILITY

All datasets generated for this study are included in the manuscript and/or the **Supplementary Files**.

AUTHOR CONTRIBUTIONS

AJG conceived the project, analyzed the <150 μm fractions, and prepared the figures and tables. AG analyzed the >150 μm fractions. Both authors integrated and analyzed the <150 μm and >150 μm fraction data. The manuscript was largely written by AG with contributions from AJG.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2019.00114/full#supplementary-material>

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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