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Radiolarian tests as microhabitats for novel benthic foraminifera: observations from the abyssal eastern equatorial Pacific (Clarion–Clipperton Fracture Zone).

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1. Introduction

The work of H.L. Sanders and R.R. Hessler in the 1960s led to a realisation that the metazoan macrofauna (>300 µm fraction) inhabiting sedimented deep-sea habitats are much more diverse than had been realised (Hessler and Sanders, 1967; Sanders and Hessler, 1969). Early studies likewise suggested that the diversity of the metazoan meiofauna increased with increasing water depth (e.g. Tietjen, 1976). Stimulated by these discoveries, the late 1960s and 1970s saw the publication of a series of papers documenting biodiversity trends with depth among benthic foraminifera, based mainly on the study of 'total' (live plus dead) assemblages (reviewed in Douglas and Woodruff, 1981; Gooday et al., 1998). These also revealed high levels of foraminiferal species richness and diversity at abyssal depths.

These earlier studies of deep-sea benthic foraminifera were geologically orientated and focussed mainly on calcareous and multichambered taxa with fossilisable tests, together with robust monothalamous taxa (single-chambered 'monothalamids'). An important development was the recognition, in the 1970s, that delicate agglutinated foraminifera, which had been largely overlooked and have little fossilization potential, are an important component of foraminiferal assemblages in the deep sea, particularly at abyssal depths (Hessler, 1974; Tendal and Hessler, 1977; Bernstein et al., 1978; Schröder, 1986). Many belong in the superfamily Komokiacea, a group that often dominates the abyssal macrofauna (Tendal and Hessler, 1977; Gooday et al., 2007). Smaller size fractions also yield a rich variety of single-chambered foraminifera. Snider et al. (1984) found that foraminifera comprised half of the meiofauna (size fraction 42–300 µm) in their samples from the central North Pacific (water depth 5821–5874 m) and that over half of the foraminifera were either branched or spherical monothalamids. At shallower depths on continental margins, soft-shelled 'saccamminids' (agglutinated) and 'allogromiids' (organic walled) are sometimes

common (Gooday, 1986a, 1986b; Gooday et al., 2013a). More recently, Nozawa et al. (2006) described foraminiferal assemblages (>32 µm fraction) from the Clarion–Clipperton Fracture Zone (CCFZ) in the eastern Equatorial Pacific (~4100 m depth) that comprised tiny agglutinated spheres ('psammosphaerids'), fragments of tubular forms and komokiaceans, together with less common saccamminids and allogromiids. Psammospharids were extremely abundant at a deeper site (5042 m depth) located in the central part of the CCFZ (Ohkawara et al., 2009).

One additional component of deep-sea foraminiferal assemblages that has been largely neglected encompasses forms that inhabit cavities. The occupancy of the empty shells of dead foraminifera, as well as other cryptic microhabitats, has been reported by a number of authors from both shallow- and deep-water settings (reviewed by Gooday et al., 2013b). In the deep sea, the shells of planktonic foraminifera are utilised most frequently. Gooday (1986b) illustrated planktonic foraminifera from a bathyal site (1340 m depth) on the Irish margin (Porcupine Seabight) that contained a stained protoplasmic body and bore various agglutinated lumps and branched and unbranched tubes on their exterior. These structures were apparently constructed by the inhabiting organisms, which were interpreted as benthic foraminifera. More recently, Gooday et al. (2013b) described two species, *Hospitella fulva* Rhumbler, 1911 and *Incola inculta* Gooday and Rothe, 2013, that inhabited planktonic foraminiferal shells from a 2300-m-deep site on the Mid Atlantic Ridge. These and other inhabiting species represented a significant proportion of all 'live' (Rose Bengal stained) foraminifera at the two sites, 18% on the Mid Atlantic Ridge (Gooday et al., 2013b) and 4.9– 19% in the Porcupine Seabight (Gooday, 1986b).

Abyssal Pacific samples yield a profusion of foraminiferal taxa, many of them undescribed (Bernstein et al., 1978; Nozawa et al., 2006). The present study is based on samples collected in the eastern part of the CCFZ as part of ABYSSLINE, a biological

baseline study being conducted prior to the planned mining of the polymetallic nodules that are common in this area. The study site is located in the UK-1 Claim Area, which has been licensed for seabed exploration by the International Seabed Authority (ISA). Since the site is situated close to the Carbonate Compensation Depth (CCD), the planktonic foraminiferal tests that are common at similar depths in the North Atlantic are largely absent. Instead, the coarser fractions of the sediment contain numerous tests of 'radiolarians', a polyphyletic grouping that is no longer recognised as a distinct taxonomic unit (Sierra et al., 2013). The majority of these tests appear to be those of polycystines rather than the more dissolution-prone phaeodarians (Takahashi et al., 1983), although we have not attempted to differentiate these two groups rigorously. These exclusively planktonic protists are transported from the upper water column on sinking aggregates of organic material (Takahashi and Bé, 1984; Takahashi, 1987; Lampitt et al., 2009). Here, we describe for the first time the occupancy of empty radiolarian tests by benthic foraminifera, and address the following questions. 1) Are radiolarian tests obligate microhabitats for some benthic foraminiferal species? 2) What is the contribution of these taxa to abyssal foraminiferal density and diversity?

2. Material and methods: sample collection, preparation and observation

The samples analysed in the present study were collected in the northern part of the UK-1 claim area (13°50'N, 116°35'W; ~4080 m water depth; Table 1) during ABYSSLINE 01 cruise on board the R/V *Melville* (MV1313, 3 to 27 October 2013). At 5 sites, one core was selected from those recovered by a megacorer (BCMEGA OSIL Bowers & Connelly type) equipped with twelve 10-cm diameter core tubes (about 78.6 cm² surface area). As soon as possible after recovery, the cores were sliced into horizontal layers every 0.5 cm until 2 cm depth, and then every 1 cm from 2 to 10 cm depth. Each sediment layer was preserved in a

plastic bottle with 10% formalin buffered with sodium borate. For the present investigation, only the 0–1 cm layer was examined. In the laboratory, samples were sieved through 150 and 300 µm mesh screens, which together retain the majority of radiolarians tests. Each of these size fractions (i.e. 150–300 µm and >300 µm) was stained with Rose Bengal (1 $g.l^{-1}$) and all stained foraminifera, including the soft-shelled species as well as radiolarian tests with obvious staining, were hand-picked in water under a binocular microscope. In order to ensure that stained specimens contained protoplasm, they were placed on a glass cavity slide in glycerol for observation under an Olympus BH-2 compound microscope. All specimens were identified at the genus and species level when possible, or classified into informal morphospecies on the basis of test morphology and wall structure. In the case of two cores (MC02, MC04), we analysed all benthic foraminifera inhabiting radiolarian tests in the >150-µm fraction of the 0–1 cm layer. These quantitative data were supplemented by qualitative observations on the three additional cores (MC07, MC09 and MC11).

Detailed photographs of each species and morphospecies were taken using a SLR digital camera (Canon EOS 350D) fitted to the Olympus stereo microscope. Photographs of the most distinctive and representative specimens were taken at different focal depths and combined into fully focused images using the open source image processing software package Combine ZP.

3. Results

Quantitative data on radiolarian inhabitants were obtained from two samples (MC02 and MC04). The more distinctive and obvious inhabitants found in three other samples (MC07, MC09, MC11) were also examined. The majority of the radiolarian tests that host foraminifera belong in the polycystine order Spumellaria and are spherical in form with a

lattice-like construction, although a few host tests (belonging, for example, to the genera *Spongaster* and *Dictyocoryne*) have a flattened morphology (Anderson, 1983). In addition, conical radiolarian tests resembling genera such as *Pterocorys* and *Peripyramis*, members of the polycystine order Nassellaria, are fairly common and are occasionally inhabited by foraminifera.

3.1. Radiolarian inhabitants

Radiolarian tests and their inhabitants were retained almost exclusively (99%) in the 150–300 µm size fraction. The inhabitants were more abundant in the 0.5–1.0 cm layer (70–85%) compared to the 0–0.5 cm layer of our samples. Among the total of 288 specimens recovered, only a few could be placed with any confidence in a described genus (e.g. *Lagenammina, Thurammina*, *Hormosinella*). The majority were therefore assigned to informal morphotypes (Table 2). Most of the morphotypes were found only within radiolarian tests but a few also occurred outside these microhabitats. For convenience, we grouped the morphotypes into six main categories based on wall type (e.g. organic, agglutinated) and the organisation of the test (e.g. single-chambered, multichambered). One of these groupings includes forms resembling members of the superfamily Komokiacea but the others are informal categories that have no phylogenetic significance.

3.1.1. Komokiacean-like forms

Komokiacean-like forms account for about 15% (MC04) and 26% (MC02) of the total number (288) of radiolarian inhabitants in our two quantitatively-analysed samples. This category is dominated by clusters of globular chambers apparently connected to each other and often obscured by a fine-grained sediment coating (Fig. 1A, B). A second morphotype

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has a flimsy organic wall with sparse fine-grained sediment coating, enclosing a dense mass of stercomata (Fig. 1C, D). The third morphotype is characterised by masses of stercomata within a test that is compartmentalized to resemble a honeycomb, and extends into a tubular structure; the test wall is composed of organic material overlain by a fine-grained veneer (Fig. 1E). Another form with a similar honeycomb test but darker stercomata lacks a tube and has an entirely organic wall (Fig. 1F)

3.1.2. Orange-brownish organic-walled, pseudo-chambered forms

This category includes forms with tests comprising several globular compartments ('pseudo-chambers' rather than true chambers), sometimes linked by tubular stolons. The wall has a characteristic orange-brownish colour and appears relatively rigid. We distinguish two morphotypes: 1) with regular, smooth globular uniserial or biserial compartments (Fig. 2A–C), and 2) with more irregular globular to ovate compartments arranged in a single row or irregularly branching (Fig. 2D–F). In both forms, the final chamber can give rise to a neck terminating in an aperture and sometimes projecting outside the radiolarian test. They typically occupy the entire available space inside the host test, in one case several chambers extend outside the radiolarian (Fig. 2D). These morphotypes resemble two brown, organic-walled genera, *Hospitella* Rhumbler, 1911 and *Placopsilinella* Earland, 1934, the former known mainly from two North Atlantic records and the latter widely distributed in deep water (Gooday et al., 2013b and references therein). In our samples, they account for about 4% of all radiolarian inhabitants.

3.1.3. Organic-walled forms

This category makes up 22% of radiolarian inhabitants. It comprises several morphotypes with transparent, organic test walls. The most common types are spherical to

oval in shape, 50 to 100 µm in diameter and lack a visible aperture. In some cases, the cell body contains many dark stercomata (Fig. 3A–C) whereas in others the cytoplasm is devoid of stercomata (Fig. 3D–F). The second most abundant morphotype has an elongate tubular test, >300 µm long and about 30 µm wide, again with no obvious aperture (Fig. 3K). Specimens are typically curved to resemble a horseshoe inside the radiolarian test. The protoplasm is relatively homogeneous without stercomata. Another form has a more or less spherical test, 90–130 µm diameter, with at least one or two elongate papillae, possibly associated with apertures, and containing dark cytoplasm (Fig. 3I). Several other distinctive morphotypes are represented by single specimens. The first has an approximately spherical test, ~130 µm diameter, filling much of the interior of the radiolarian and with at least four conical papillae (about 20 µm height) that abut against the internal surface of the radiolarian test. The red-stained cell body contains large dark stercomata (Fig. 3G). The second has an oval test, ~90 µm long, with finely granular cytoplasm. The aperture is situated at the end of a tapered neck arising from one end of the individual (Fig. 3H). The third form has a more complex, lobed test that occupies much of the interior of the host radiolarian (Fig. 3J). Finally, a form resembling an undescribed morphotype observed living freely in the sediment residue has a crooked tubular shape with regular constrictions and enclosing clumps of dark stercomata (Fig. 3L).

3.1.4. Agglutinated monothalamids

Agglutinated monothalamids constitute 26% (MC02) and 35% (MC04) of all radiolarian inhabitants, making them the most abundant forms in our samples. They are occasionally found inside the conical tests of nassellarid radiolarians (Fig. 4D) as well as the tests of flattened spumellarid morphotypes (Fig. 5). These monothalamids are morphologically diverse and include some distinctive morphotypes. Agglutinated spheres

(~50 µm diameter), usually with walls that contain noticeable grains, are common. The red-stained cytoplasm often contains stercomata (Fig. 4A, B), although some specimens have homogeneous cytoplasm (Fig. 4C). An organic layer is sometimes discernible below the agglutinated wall. One to several (up to six) individuals, without any obvious connection between them, may inhabit the same host test. Two egg-shaped specimens, about 90 and 110 µm in maximum dimension with a thin, finely agglutinated test wall and containing red-stained homogeneous cytoplasm, were found inside two conical radiolarians (Fig. 4D). A peanut-shaped chamber, about 100 µm long, has a fairly coarsely agglutinated wall and contains small dark stercomata (Fig. 4F). A relatively large (about 250 µm diameter) and distinctive agglutinated chamber, brownish-orange in colour with at least ten short tubular to conical processes (about 30 µm height; Fig. 4E) represents the genus *Thurammina*. Another distinctive form comprises a spherical agglutinated test that gives rise to one to three narrow rigid tubes (about 20 µm diameter and 30 to 80 µm long), although sometimes only the base of the tube is present (Fig. 4G). The wall is thick and rather coarsely agglutinated. Specimens with a single tubular extension are assigned to the genus *Lagenammina* (Fig. 4H, I). Tubular morphotypes are less common. They include narrow crooked tubes with one closed end (about 25µm diameter and 150–500 µm long) containing red-stained cytoplasm without stercomata (Fig. 4J, K). The wall is quite thick and fine-grained. Finally, a distinctive form that is partly hidden by sediment that completely fills the radiolarian test has a wide, sigmoidal test. The fine-grained wall contains brightly stained protoplasm devoid of stercomata (Fig. 4L).

3.1.5. Multichambered agglutinated forms

Occasional agglutinated specimens comprise two or more chambers. The simplest consist of 2–3 chambers with rather sparse agglutination overlying an inner organic layer

(Fig. 6A) and containing dense cytoplasm with small dark stercomata. More complex forms comprise 8 or more chambers with relatively thick and coarsely agglutinated wall (Fig. 6B, C); these can occupy almost the entire interior of the host test. In some cases, the chambers appear to be arranged trochospirally, although surrounding fine-grained sediment often makes their arrangement difficult to discern. Three specimens consist of several globular to droplet-shaped swellings ('pseudo-chambers') arranged in a linear sequence (Fig. 6D–F). The first morphotype consists of globular pseudo-chambers joined by tubular stolons, suggesting a placement in the genus *Hormosinella* (*Hormosinella* sp.1, Fig. 6D). The second form, also assigned to the genus *Hormosinella* (*Hormosinella* sp.2, Fig. 6E), has droplet-shaped pseudo-chambers filled by dark cytoplasm and stercomata. The third form has fine-grained, droplet-shaped pseudo-chambers joined end to end, with sparse small dark stercomata (Fig. 6F).

3.1.6. Inhabitants constructing external structures on radiolarian tests

Forms in which the cell body occupies the interior of a radiolarian test and is associated with an agglutinated construct on the test exterior are an interesting, albeit minor, component of the assemblage. A number of different structures can be recognised. In most cases, tubular structures extend out on one or both sides of the host test. These include rigid tubes that are either branched (Fig. 7A) or narrow, straight and unbranched (about 10 µm diameter and 100 µm long) (Fig. 7B). In other cases, the structures are more flexible and branched distally (Fig. 7C). In many cases, the cell body is tiny (about 40 to 60 µm diameter), approximately spherical, and enclosed in a thin-walled organic test. Sample MC04 yielded a single example of a form resembling *Incola inculta* Gooday and Rothe, 2013, that has constructed a conical lump on the test exterior (Fig. 7F). Also included for convenience in this group are two agglutinated tests that may be the same as the form illustrated in Fig. 7C;

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one is perched on the exterior of a radiolarian (Fig. 7D) and the other inside the host (Fig. 7E). Both are characterised by short tubular extensions and enclose a well-stained cell body.

3.1.7. Possible inhabitants

One form could not be assigned to any of the informal groupings. Specimens comprise a mass of large brightly red-stained stercomes that are not enclosed by an obvious wall (Fig. 8A–C). However, a fine-grained sediment veneer is typically developed on the outside of the radiolarian test.

3.2. Contribution to the density and diversity of benthic foraminiferal assemblage

When all stained foraminifera, including those inhabiting radiolarians and other 'free-living' forms (both complete and fragmentary), are considered, the >150 μm size fraction (i.e. 150–300 µm and >300 µm size fractions combined from the 0–1 cm layer) yielded densities of 1204 ind./100 cm² and 965 ind./100cm² at MC02 and MC04 sites, respectively. The forms inhabiting radiolarian tests considered here represented ~9% of this 'entire live' assemblage in the MC02 sample (109 ind./100 cm²) and ~27% in the MC04 sample (257 ind./100 cm²). They also probably make an important contribution to species richness. The number of inhabiting species that are confined to this microhabitat in our material cannot be accurately determined because some are poorly defined morphologically or obscured by sediment that partly fills the host test. However, among the 35 morphotypes that we recognised at the five investigated sites, 27 can be assigned to described genera or confidently regarded as distinct morphospecies. Of these 27 morphospecies, 19 appear to be confined to radiolarian tests, i.e. they have not been encountered amongst the 'free-living' assemblage in the sediment residue.

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4. Discussion

The inhabitants of radiolarian tests constitute only one element, albeit an important one, of the diverse foraminiferal assemblages that characterise the abyssal CCFZ. A preliminary account of species encrusting the surfaces of polymetallic nodules in our study area is given elsewhere (Gooday et al., 2015) and a separate paper will describe the associated sediment-dwelling faunas (Goineau and Gooday, in prep.). Because these analyses are very time-consuming, we limited our quantitative treatment of the inhabiting foraminifera to the upper 1-cm layer of two cores (MC02, MC04), which nevertheless yielded a total of 288 specimens. These data are supplemented by qualitative records of some morphospecies from three additional cores (MC07, MC09, MC11).

4.1. Recognition of radiolarian inhabitants

Many of the stained structures within radiolarian tests are organic-walled or agglutinated monothalamous or occasionally polythalamous forms that are consistent with known foraminiferal morphologies. We are confident that these organisms are secondary inhabitants of the radiolarians. However, we also observed other stained formations that were probably not inhabiting organisms. These usually consist of clusters of discrete, light greenish to brownish stercomata masses, that are not enclosed by an obvious wall (Fig. 8D), although they are sometimes surrounded by, or embedded within, unstained material resembling fine-grained sediment. The nature of these formations is unclear. However, it is possible that at least some of them represent the remains of the original radiolarian cell, particularly where the stained material is located in the central capsule of the radiolarian test. Radiolarians produce 'minipellets' that closely resemble foraminiferal stercomata (Gowing and Silver,

1985; Riemann, 1989). Rapid transport through the water column on sinking aggregates (Takahashi et al., 1983; Lampitt et al., 2009) may deliver radiolarians to the seafloor in a relatively fresh condition (Thiel et al., 1989). Additional analyses, for example, using Transmission Electron Microscopy, would be necessary to determine whether some stained specimens are radiolarian remains or foraminifera.

Soft-shelled monothalamids with clearly-developed apertures and agglutinated or organic-walled tests (so-called 'saccamminids' and 'allogromiids', respectively) sometimes occupy the empty tests of other foraminifera (Gooday et al., 2013b). For example, Rhumbler (1894) described five 'allogromiid' species from the empty shells of the large agglutinated foraminifera *Saccammina spherica* and Moodley (1990) observed a saccamminid entering an empty *Quinquiloculina* test. Both of these examples are from sublittoral settings in the North Sea. Our material from the abyssal CCFZ includes 'allogromiids' with spherical, oval or elongate tests (Fig. 3 H, I, K), as well as spherical agglutinated forms without an obvious aperture ('psammosphaerids'; Fig. 4A–D). Saccamminids have not been recognised, although we have observed one example of a saccamminid inhabiting a radiolarian test in the NE Atlantic (Fig. 9 C–D).

There are closer parallels between the foraminifera inhabiting planktonic foraminiferal tests in the bathyal and abyssal Atlantic and those inhabiting radiolarian tests in the abyssal Pacific. Forms resembling the genera *Hospitella* and *Placopsilinella* in our Pacific material (Fig. 2) are comparable to *Hospitella fulva* Rhumbler, 1911 and *Placopsilinella aurantiaca* Earland, 1934 from lower bathyal depths (~2500 m) on the Mid-Atlantic Ridge (MAR) (Gooday et al., 2013b). Our samples yielded a single specimen (Fig. 7F) resembling *Incola inculta* Gooday and Rothe, 2013, an inhabiting species common in the MAR samples that constructs an agglutinated lump on the exterior of the host test. Similarly, inhabitants that construct external agglutinated tubes, either branched or unbranched, are

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represented in both the Atlantic and Pacific material. In particular, the form with two straight tubes arising from opposite sides of the radiolarian test (Fig. 7B) has close parallels among inhabitants of planktonic foraminiferal tests at shallower depths in the NE Atlantic (Gooday, 1986b, Fig. 3K therein; Gooday, 1990b, Pl. 4, Fig. E therein). These similarities suggest that some of the species (or at least morphotypes) found in our samples from the CCFZ have wide distributions.

4.2. Why do foraminifera occupy radiolarian tests?

In the bathyal and abyssal North Atlantic, benthic foraminiferal 'squatters', many of them monothalamids, occupy the empty calcareous shells of planktonic foraminifera (Gooday, 1986b; Gooday et al., 2013b). Our present results suggest that the siliceous tests of radiolarians provide comparable shelters for benthic foraminifera in the Pacific, where the CCD is shallower than in the Atlantic and calcareous planktonic tests dissolve before they can accumulate in abyssal sediments. Thus, despite their small size (<500 µm), the tests of these exclusively planktonic protists can be important microhabitats for abyssal benthic foraminifera. The dead tests of somewhat larger benthic agglutinated foraminifera (multichambered trochamminaceans and hormosinaceans) also hosted occasional inhabitants in our Pacific samples. Many of these resemble the organic-walled horseshoe-shaped form illustrated in Fig. 3K.

Benthic foraminiferal microhabitats are usually thought of in terms of where species live in the sediment profile (Jorissen, 1999). The vertical distribution of species from surface to deeper sediment layers is believed to reflect a balance between the amount of available food and dissolved oxygen concentrations (Jorissen et al., 1995). In well-oxygenated abyssal regions, including our UK-1 study area, food availability will exert the main control. Linke

and Lutze (1993) introduced the concept of dynamic foraminiferal microhabitats, according to which species will adapt their behaviour to optimise food acquisition, for example, by attaching to elevated substrates such as worm tubes and sponges where they have access to a higher food flux. In the abyssal Pacific, polymetallic nodules provide this kind of microhabitat for sessile foraminifera (Veillette et al., 2007; Gooday et al., 2015). Planktonic foraminiferal tests in the Atlantic, and radiolarian tests in the Pacific, may represent another kind of abyssal microhabitat where food is concentrated. Potential food sources could include bacteria associated with the decayed remains of the host organism. A small body of largely circumstantial evidence suggest that deep-sea monothalamids ('allogromiids' and saccamminids) consume bacteria (Gooday et al., 2008). They have been reported from other potentially food-rich microhabitats, including crustacean moults (Gooday, 1990a) and the organic tube ('granellare') systems of xenophyophores (Hughes and Gooday, 2004). However, there is often no trace of obvious organic remains that could support bacterial populations within the radiolarian tests. Protection, combined with the provision of a rigid framework on which to construct agglutinated structures and the shear abundance and therefore easy availability of radiolarian tests in Pacific abyssal sediments, may therefore be important drivers of 'squatter' behaviour.

In sublittorial and bathyal settings, calcareous foraminiferal species may exhibit considerable flexibility in their occupancy of microhabitats, in some cases moving between elevated and sedimentary substrates according to which offers the greatest access to food (Linke and Lutze, 1993). In contrast, at our abyssal site, the occupancy of radiolarian tests, as well as the colonisation of nodule surface, appears to be largely habitual rather than opportunistic. A mainly sedentary lifestyle would also be consistent with the fact that many different forms are represented amongst the 'squatter' assemblage in our material. This may reflect a much lower degree of activity among some of the 'basal' monothalamous taxa (e.g.

Cedhagen and Mattson, 1991; Cedhagen and Frimanson, 2002) that typically dominate abyssal foraminiferal assemblages. The complex morphologies of radiolarian inhabitants such as the komokiacean-, *Hospitella*- and *Placopsilinella*-like forms (Figs 1–2) would probably place severe limits on their mobility. On the other hand, experimental studies indicate that some monothalamous foraminifera are quite mobile (e.g. *Allogromia* spp., *Bathysiphon* spp., and *Saccammina* sp.; Gross, 2000). In a culture experiment, Moodley (1990) observed an organic-walled monothalamid that was able to change its shape and squeeze into the aperture of an empty miliolid (*Quinquiloculina* sp.) test. Some of the radiolarian inhabitants with simpler morphologies, such as those illustrated in Fig. 3, may also be mobile. However, in most cases it seems unlikely that these forms could change their shape sufficiently to allow them to pass through the tight meshwork of the host test, effectively trapping them inside these microhabitats.

The inhabiting foraminifera presumably enter the radiolarians as propagules which, unlike fully-grown individuals, are small enough to pass through the perforations in the walls of the radiolarian tests. Evidence for the existence of tiny dispersive juvenile stages of foraminifera (either naked zygotes or 1–2-chambered juveniles) has emerged from the elegant experiments of Alve and Goldstein (2003, 2010). However, if propagules are passively dispersed, then the apparent restriction of some morphospecies to radiolarian tests suggests that they require these microhabitats to develop beyond the propagule stage.

4.3. Role in maintaining local foraminiferal biodiversity

Benthic foraminiferal species richness and diversity is typically very high in abyssal settings (Buzas and Gibson, 1969; Bernstein et al., 1978; Gooday et al., 1998), as it is for many other faunal components (Snelgrove and Smith, 2002; Rex and Etter, 2010). At the

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MC02 and MC04 sites, each core sample yielded well over 100 distinct morphospecies, making a combined total of 222 sediment-dwelling species (1703 stained specimens). Among the 27 morphospecies that were found inside radiolarians at the five investigated sites, 8 were also observed in sediment residues or occupying other microhabitats (e.g. the tests of agglutinated foraminifera, surfaces of polymetallic nodules). The remaining 19 morphospecies were apparently confined to radiolarian tests. At MC02 and MC04 sites, these 19 morphospecies represented about one third (~25–34%) of all radiolarian inhabitants, at least 9% of all stained specimens (free-living plus inhabitants), and about 8% of species, suggesting that they make a non-negligible contribution to the diversity and density of foraminifera in the UK-1 area.

At small spatial scales (<1 meter to 100s of metres), deep-sea macro- and meio-faunal diversity has been linked to spatial heterogeneity, for example, in the distribution of phytodetritus, *Sargassum* and other organic material on the seafloor, leading to a patchwork of communities at different successional states (Grassle and Morse–Porteous, 1987; Grassle and Grassle, 1994; Rice and Lambshead, 1994; Snelgrove and Smith, 2002). Some of the earlier literature on deep-sea diversity maintenance emphasised the possible role of small-scale biogenic structures (<0.01 m²), approaching the size of individual macrofaunal organisms, in creating small-scale heterogeneity that can be used as habitat structures by other organisms (Jumars, 1975; Jumars and Eckman, 1983). Jumars (1976) mentions two examples from bathyal settings that illustrate this 'grain-matching' model; a limpet species that was always found attached to blades of eelgrass or on one occasion a piece of wood in samples from the San Diego Trough, and entoprocts and foraminifera attached to the surface of a centimetre-sized 'faecal pellet' (more likely a gromiid protist) from the Santa Catalina Basin. The higher diversity in the San Diego Trough of polychaetes that were inferred to be active over small areas compared with more mobile polychaetes supports this hypothesis

(Jumars, 1975). Among the meiofauna, Thistle (1979) found that harpacticoid copepods were significantly associated with a variety of biogenic structures (mudballs created by cirratulid polychaetes, large foraminiferal tests, tanaid tubes) in the San Diego Trough. A later study revealed an association between one harpacticoid species and occupied cirratulid mudballs (Thistle and Eckman, 1988). In the NE Atlantic, the empty tubes of agglutinated foraminifera and structures created by komokiaceans provide centimetre-scale habitats for a variety of metazoans and foraminifera (Gooday and Haynes, 1983; Gooday, 1984; Gooday and Cook, 1984; Buhl–Mortensen et al., 2010). At a somewhat larger scale, morphologically complex xenophyophore tests create microhabitat structure for numerous macro- and meio-faunal organisms (Levin and Thomas, 1988) as well as other foraminifera (Hughes and Gooday, 2004). The present study, and the earlier work of Gooday et al. (2013b), suggests that planktonic foraminiferal and radiolarian tests create even smaller (<1 mm) microhabitats that can be utilized by meiofaunal organisms. An important feature, particularly of the radiolarian tests, is that, although small, they are relatively robust structures that persist much longer in the sediment than more ephemeral biogenic sources of small-scale heterogeneity, such as faecal casts and mudballs. They clearly provide an important microhabitat, at least for other foraminifera, and probably thereby contribute towards the maintenance of high species diversity.

5. Concluding remarks

Our observations highlight the lack of attention paid to species occupying inconspicuous microhabitats. The recognition in samples from the Mid-Atlantic Ridge of *Hospitella fulva*, a species of benthic foraminifera inhabiting the shells of planktonic foraminifera that had not been reported since it was described more than a hundred years

previously (Gooday et al., 2013b), and occupancy by foraminifera of cavities inside porous nodules from the Peru Basin (Maybury, 1996), provide other examples. Recent analyses of environmental DNA ('eDNA') in deep-sea sediment samples have revealed numerous sequences ('barcodes') that are impossible to assign to any described foraminiferal taxa. These undetermined Operational Taxonomic Units (OTUs) constituted 25–55% of foraminiferal sequences in the study of Lecroq et al. (2011). Some of them could correspond to novel species occupying cryptic microhabitats, which are not represented in the molecular database. This potential important source of novel biodiversity needs to be kept in mind when conducting baseline surveys of small-sized, deep-sea organisms, particularly in remote abyssal regions.

The agglutinated foraminifera that inhabit the nodule crevice microhabitat in the Peru Basin are mainly monothalamids, notably a species of *Thurammina,* a genus with a fossil record extending back to the Palaeozoic (Maybury, 1996). In our material, *Thurammina* is represented by a single unstained individual (Fig. 4E). The vast majority of the radiolarian inhabitants are delicate forms that have very little fossilisation potential. The only possible exceptions are the multichambered forms resembling the genera *Hospitella* and *Placopsilinella,* which have fairly rigid walls composed of orange-brownish organic material. However, neither of these genera has a proven fossil record (Loeblich and Tappan, 1988).

Our observations help to establish the importance of radiolarian tests as microhabitats for some benthic foraminifera in the abyssal Pacific. However, we can only speculate at present on the advantages for the foraminifera of occupying these small spaces. Future studies focussing on the variability of environmental parameters in relation to these and other sources of fine-scale heterogeneity of deep-sea sediments might lead to a better understanding of abyssal foraminiferal ecology. For example, it might be possible to examine

the effect of radiolarian tests on the micro-distribution of oxygen using planar optode techniques (Glud et al., 2009; Stahl et al., 2012).

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Tables

Table 1. Station data for the four sampling sites in the UK-1 claim area.

Sampling sites	Samples	Latitude (°N)	Longitude (°W)	Water depth (m)
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

Table 2. Quantitative counts (MC02 and MC04), and qualitative records (MC07 and MC11) of the morphotypes inhabiting radiolarian tests (0–1 cm, >150 µm size fraction). 'N' refers to the number of specimens, and the percentage (%) to the relative abundance of each morphotype to the total inhabiting fauna. 'X' indicates presence.

Morphotypes	Figure	MC02 N	MC02 %	MC04 N	MC04 %	MC07	MC09	MC11
Komokiacean-like forms	1							
Cluster of globular chambers	1A,B	16	18.6	25	12.4			X
Flimsy wall, very dense stercomata *	1C,D	–	–	2	1.0	X		
'Honeycomb' komokiacean sp.1 *	1F	6	7.0	2	1.0	X		
'Honeycomb' komokiacean sp.2 **	1E	–	–	1	0.5	X		
Orange-brownish organic-walled, pseudo-chambered forms	2							
Globular chambers arranged in regular spiral or biserial pattern *	2A–C	–	–	1	0.5			X
Forms with more or less globular chambers arranged irregularly *	2D–F	2	2.3	8	4.0	X		
Organic-walled monothalamids	3							
Elongate test	3K	7	8.1	2	1.0		X	
More or less spherical test, cell body with stercomata	3A–C	1	1.2	10	5.0			
More or less spherical test, cell body without stercomata	3D–F	11	12.8	15	7.4			
Spherical test with 4 conical papillae *	3G	–	–	1	0.5			
More or less spherical test with aperture(s) sp.1 *	3I	1	1.2	–	–			
More or less spherical test with aperture(s) sp.2 *	3H	–	–	1	0.5			
Red tube with constrictions **	3L	–	–	1	0.5			
Other organic-walled monothalamids	3J	3	3.5	10	5.0			
Agglutinated monothalamids	4,5							
Spherical test, cell body with stercomata *	4A,B	4	4.7	34	16.8			
Spherical test, cell body without stercomata, red interior *	4C; 5A,B	–	–	2	1.0	X		
Tube with red-stained interior *	4J,K	–	–	2	1.0		X	
Chamber with tubes *	4G	2	2.3	1	0.5		X	X
Lagenammina spp. **	4H,I	2	2.3	14	6.9			X
Egg-shaped, very finely agglutinated wall **	4D; 5C,D	1	1.2	1	0.5		X	
Coarse-grained peanut-shaped test *	4F	1	1.2	–	–			
Sigmoidal test *	4L	–	–	1	0.5			
Thurammina sp. **	4E	–	–	–	–	X		

	Fig.	n	%	n	%			
Other agglutinated monothalamids		12	14.0	15	7.4			X
Agglutinated multichambered	6							
Trochospiral with relatively thick agglutinated wall	6B,C	1	1.2	11	5.4			
Two or more chambers, sparse agglutination, organic layer	6A	7	8.1	13	6.4			
Droplet-shaped swellings arranged in a single row **	6F	–	–	–	–			X
Hormosinella sp.1 *	6D	–	–	1	0.5			
Hormosinella sp.2 **	6E	–	–	1	0.5			
Inhabitants constructing external structures on radiolarian tests	7							
Red cell: flexible branching tubes on test exterior **	7C–E	7	8.1	15	7.4	X	X	X
Red cell: straight rigid unbranched tubes on test exterior *	7B	–	–	1	0.5		X	X
Rigid branching tube *	7A	–	–	1	0.5			
Incola inculta-like form *	7F	–	–	1	0.5			
Possible inhabitant	8							
Radiolarian with red stercomata and external sediment veneer *	8A–C	2	2.3	9	4.5		X	X
Tot. 'live' radiolarian inhabitants		86		202			–	–

* Morphotypes considered as distinctive morphospecies.
** Morphotypes considered as distinctive morphospecies and observed in other microhabitats in our samples (e.g. sediment residue, surface of polymetallic nodules, empty test of agglutinated foraminifera).

Figure captions

Figure 1. Komokiacean-like morphotypes inhabiting radiolarian tests (scale bars: 100 µm). Clusters of globular chambers (A–B). Form with a flimsy wall, very dense stercomata (C, D). One inhabitant gives rise to one globular chamber extending outside the radiolarian test (*co*; D). Tests comprising honeycomb-like compartments containing stercomata (E, F), with either a flexible tube (arrowed) and a fine-grained wall (E), or without a tube, containing darker stercomata, and an entirely organic wall (F).

Figure 2. Orange-brownish organic-walled multichambered morphotypes inhabiting radiolarian tests (scale bars: 100 µm). Forms with globular to ovate 'pseudo-chambers' arranged in a fairly regular spiral (A, B) or biserial pattern (C) resembling the genus *Placopsilinella* Earland, 1934. Forms with more or less globular chambers arranged in an irregular manner resembling the genus *Hospitella* Rhumbler, 1911 (D–F). A neck (arrowed) arising from the final chamber is sometimes visible in both forms (B, E, F). Several chambers (*co*) may extend outside the radiolarian test (D).

Figure 3. Organic-walled foraminiferal morphotypes inhabiting radiolarian tests (scale bars: 100 µm). Spherical to oval test without visible aperture, and with cell-body either containing stercomata (A–C) or without stercomata (D–F). Some individuals have a 'peanut'-shaped test, possibly as a result of shrinkage (F). Spherical morphotype with at least four conical papillae abutting against the internal surface of the radiolarian test (G). Oval test with an aperture situated at the end of a short tapered terminal neck (arrowed) (H). More or less spherical test with dark cytoplasm and one elongate papilla (arrowed), presumably an apertural structure (I). More complex, lobate morphotype with dark stercomata (J). Elongate

tubular morphotype curved into a horseshoe shape without obvious aperture (K). Tubular morphotype with constrictions and clumps of dark stercomata (L).

Figure 4. Agglutinated single-chambered morphotypes inhabiting radiolarian tests (scale bars: 100 µm). Spheres with noticeable agglutinated particles and containing either stercomata (A, B) or homogeneous red-stained protoplasm (C); a single radiolarian can contain one or multiple spheres. Egg-shaped morphotype with finely agglutinated wall inside a conical nasselarid radiolarian (possibly *Peripyramis*) (D). Brownish-orange agglutinated chamber with several short processes, assigned to the genus *Thurammina* (E, from sample MC07). Peanut-shaped coarsely agglutinated chamber filled with few small dark stercomata (F). Spherical chamber giving rise to two short rigid tubes (arrowed) (G). Spherical chambers giving rise to one long narrow tube (arrowed), assigned to genus *Lagenammina* (H, I). Narrow crooked tubes with one closed end and red-stained protoplasm (J, K). Sigmoidal, brightly stained inhabitant partly hidden by sediment filling the radiolarian test (L).

Figure 5. Agglutinated single-chambered morphotypes inhabiting flattened radiolarian tests from MC09 (scale bars: 100 µm). Spherical agglutinated monothalamid, possibly the same as the 'sphere with noticeable agglutinated particles and homogeneous red-stained protoplasm' illustrated in Fig. 4C, located inside a test of the radiolarian *Spongaster* sp. (A, B). Egg-shaped monothalamid with very finely agglutinated wall inside the radiolarian *Dictyocoryne* sp. (C, D). Note that the foraminifera are located inside the radiolarian tests, not on their outer surfaces.

Figure 6. Multichambered agglutinated morphotypes inhabiting radiolarian tests (scale bars: 100 µm). Specimen with two or more chambers ('pseudo-chambers'), sparse agglutination

overlying organic layer (A). Trochospiral specimens with a relatively thick agglutinated wall (B, C). Forms assigned tentatively to the genus *Hormosinella* (D, E). Spherical pseudo-chambers joined by tubular stolons (*Hormosinella* sp.1, D); droplet-shaped pseudo-chambers filled by dark cytoplasm and stercomata (*Hormosinella* sp.2, E). Fine-grained, droplet-shaped pseudo-chambers joined end to end in a single row (F, from sample MC11).

Figure 7. Morphotypes constructing external structures on radiolarian tests (scale bars: 100 µm). Forms with rigid, branched tube (A), narrow, rigid, straight tubes on opposite sides of host test (B) and narrow, flexible, branched tube on exterior of host test (C). Chamber attached to the surface of host test giving rise to two short tubes (D). Similar form enclosed entirely within host test (E). Form with conical lump on the test exterior, penetrated by an organic tube (arrowed), resembling *Incola inculta* Gooday and Rothe, 2013 (F). Asterisks (A, B, F) indicate the Rose-Bengal-stained cell body.

Figure 8. Unclassified forms (scale bars: 100 µm). Radiolarian tests filled by large brightly red-stained stercomata with more or less well-developed fine-grained sediment veneer on the outside of the test (A–C); these are interpreted as secondary inhabitants. Radiolarian tests with a central mass of stercomata without any clear wall; this may represent the remains of the original radiolarian cell (D).
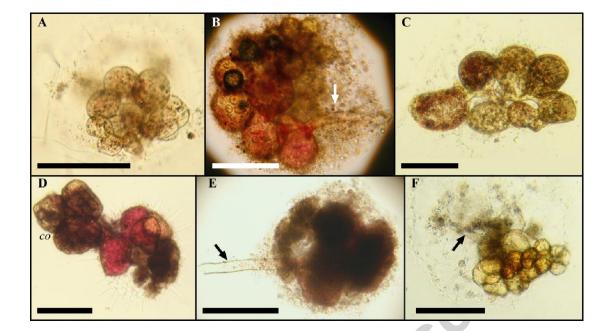
Figure 9. Foraminifera inhabiting two large radiolarian tests from the Whittard canyon (south-west of Ireland, North Atlantic, 2300 m depth). Intact radiolarian test with inhabiting organisms (A). Test broken open to reveal a thread-like organic-walled foraminifera (?*Nemogullmia*; arrowed) and a spherical cell body without an obvious wall (B). Intact radiolarian test containing a silvery saccamminid (C). Saccamminid removed from test (D).
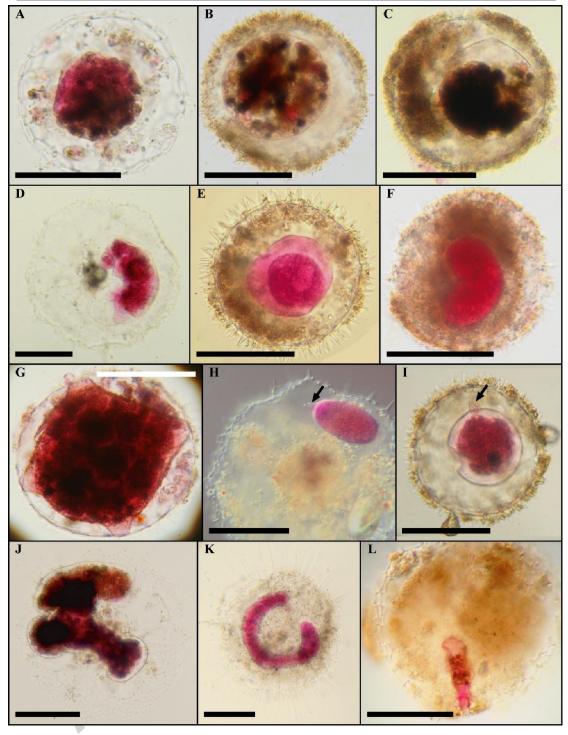
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Highlights

* We investigated live benthic foraminifera from the abyssal eastern equatorial Pacific.

* Foraminifera, including novel morphotypes, commonly inhabit empty radiolarian tests.

* We recognised 27 inhabiting morphospecies, 19 confined to radiolarian tests.

* The majority of the inhabiting forms represent undescribed species.

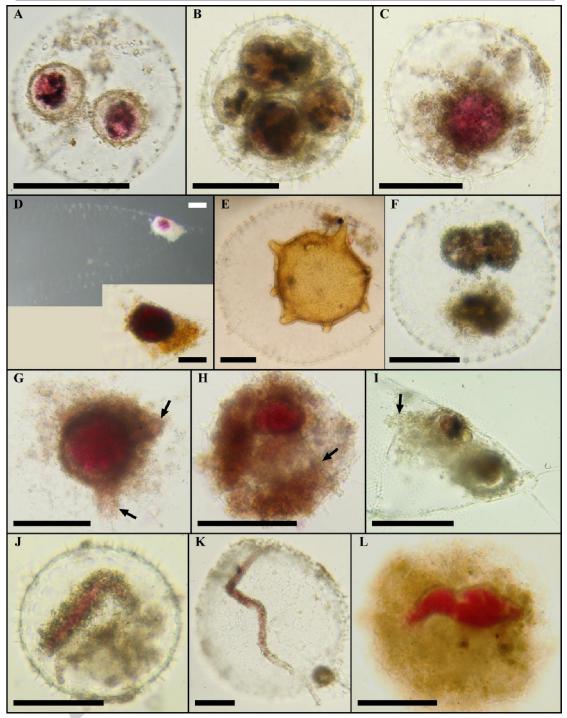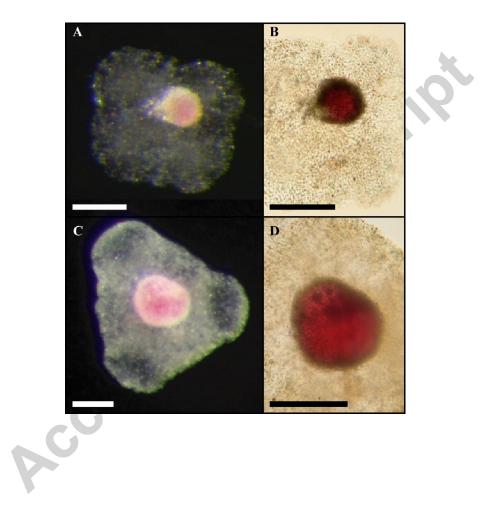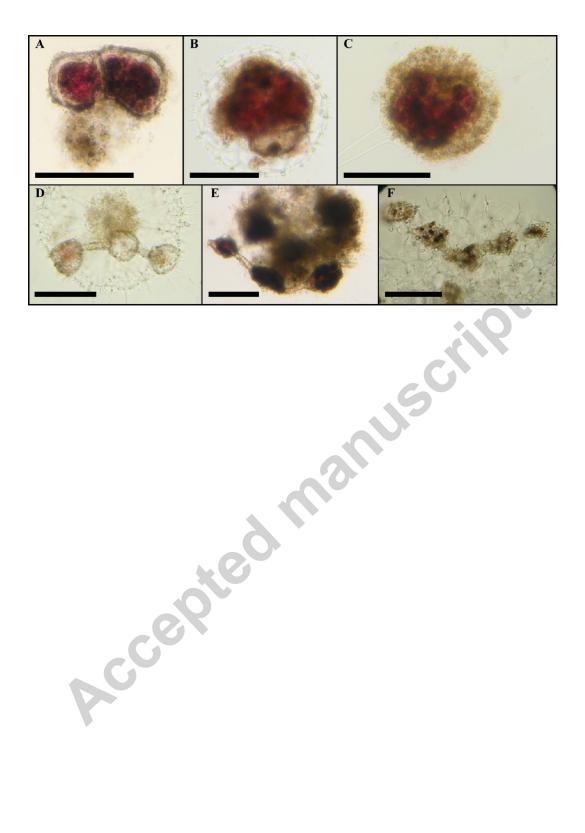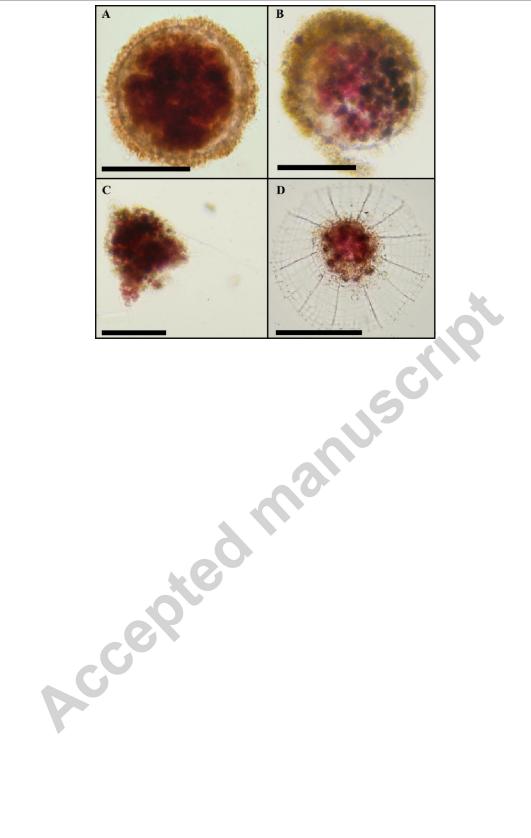* Cryptic microhabitats may help to sustain local foraminiferal diversity.

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