**MARINE
MICROPALEONTOLOGY**

Deep-sea benthic foraminiferal recolonisation following a volcaniclastic event in the lower Campanian of the Scaglia Rossa Formation (Umbria–Marche Basin, central Italy)

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Abstract

We studied the distribution of deep water agglutinated foraminiferal (DWAF) assemblages across a 15-cm-thick volcaniclastic layer in the lower Campanian Scaglia Rossa limestones of the Umbria–Marche Basin. Above the volcaniclastic layer, which is devoid of foraminifera, a remarkable pattern of recovery among DWAF has been observed. The complete recovery of DWAF in terms of trophic groups and complexity of assemblages is observed in the first 5 cm above the volcaniclastic layer, representing 4.8 kyr based upon the mean sedimentation rate of the Campanian Scaglia Rossa Formation.

In its initial stage, the recovery pattern is remarkably similar to that observed following the 15 June 1991 Mount Pinatubo ashfall in the abyssal South China Sea where various species of *Reophax*, a small organically cemented species of *Textularia*, and the calcareous species *Quinqueloculina seminula* and *Bolivina difformis* are the earliest recolonisers on top of the tephra layer.

Such similarities between modern and fossil analogues strengthens the reliability of environmental reconstructions based on DWAF. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: Benthic foraminifera; Volcanic ash; Substrate disturbance; Biotic recovery

1. Introduction

Information on life history and community structure of deep-sea benthic foraminifera is a prerequisite for understanding the processes related to disequilibrium in deep-sea benthic communities, which constitute a key component of the Earth's largest biotope. Recolonisation of deep-sea substrates, in particular, is a topic that has received growing interest in recent years with several studies on both modern and fossil benthic foraminiferal communities following major envi-

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ronmental disturbances (see Alve, 1999 for a re-view of the topic).

In the fossil record, attention has recently fo-cused on recolonisation patterns by benthic fora-minifera following global catastrophic events such as the Cretaceous Oceanic Anoxic Events (Kuhnt, 1992; Coccioni et al., 1995; Peryt and Lamolda, 1996), the Cretaceous–Tertiary Boundary event (Kuhnt and Kaminski, 1993, 1996; Coccioni and Galeotti, 1994, 1998; Speijer and van der Zwaan, 1994, 1996; Galeotti, 1998), and the Palaeocene–Eocene Boundary event (Kaminski et al., 1996; Speijer et al., 1995, 1997). Successive recolonisa-tion of the sea floor has also been suggested to explain the patterns observed in the vertical suc-cession of 'flysch-type' foraminiferal assemblages within turbidite sequences in alpine and boreal regions (Grün et al., 1964; Butt, 1981; Verdenius and Van Hinte, 1983; Kuhnt and Kaminski, 1989).

In the modern ocean, recolonisation by benthic foraminifera has been observed in shallow water environments following artificial disturbance (El-lison and Peck, 1983; Schafer, 1983), in the deep sea following bottom current disturbance (Kamin-ski, 1985), and after local volcanic ashfalls (Finger and Lipps, 1981). In an experiment using recolo-nisation trays at an abyssal site in the Panama Basin, Kaminski et al. (1988a,b) identified several species of benthic foraminifera as opportunistic, including *Psammosphaera*, *Reophax excentricus* and *Reophax dentaliniformis*.

Deep-sea basins that experience seasonal dys-oxia also support communities of opportunistic benthic foraminifera. In a study of the deep San Pedro Basin off southern California, Ka-minski et al. (1995) reported a faunal assem-blage consisting of *Psammosphaera, Reophax*, and a minute organically cemented species of *Textularia* that was interpreted as opportunistic. Many of the species were the same as those found in the recolonisation trays in the Panama Basin, suggesting that different types of distur-bance may result in similar benthic communities. The sole observations of in situ recolonisation by modern deep-sea benthic foraminifera in a vast disturbed habitat were carried out by Hess and Kuhnt (1996), Hess (1998), and Hess et al.

(2001), who documented the initial stage of re-colonisation on top of the tephra layer deposited in the South China Sea as a result of the 1991 eruption of Mount Pinatubo in the Philippines. The initial observations suggest that faunal re-covery (largely by species of *Reophax*, *Subreo-phax*, and a minute organically cemented species of *Textularia*) had begun as early as 3 years fol-lowing the eruption.

The process of faunal decimation and recovery following tephra falls must undoubtedly be a common occurrence in the geological record, con-tributing to local differences in the patch structure and successional patterns observed in deep-sea benthic foraminifera. However, a major unknown question is whether or not this process leaves an observable fossil record, and if so what the time-scale of faunal recovery in the deep sea is. In this paper we address these questions by documenting the pattern of the recolonisation through a high resolution study of deep water agglutinated fora-miniferal (DWAF) assemblages from below, with-in, and above a 15-cm-thick volcaniclastic layer in a deep-sea sequence of the Scaglia Rossa Forma-tion exposed in the Furlo Gorge (Umbria–Marche Apennines, central Italy).

2. Geological and stratigraphical setting

The upper Turonian–middle Eocene Scaglia Rossa Formation in the Umbria–Marche Basin consists of regularly bedded pink and reddish limestones interbedded with reddish marly layers deposited under well oxygenated conditions in a lower bathyal depositional environment (Arthur and Fischer, 1977; Kuhnt, 1990). The faunal and floral associations of the Scaglia Rossa mostly consist of calcareous nannofossils and subordi-nate planktonic foraminifera along with rare benthic foraminifera (mainly DWAF). The DWAF assemblages in these limestones are highly diversified and are unique within the Upper Cretaceous. They include elements of mixed calcareous and organically cemented bathy-al assemblages, purely agglutinated 'flysch-type' assemblages, and a number of species known from Upper Cretaceous sequences deposited be-
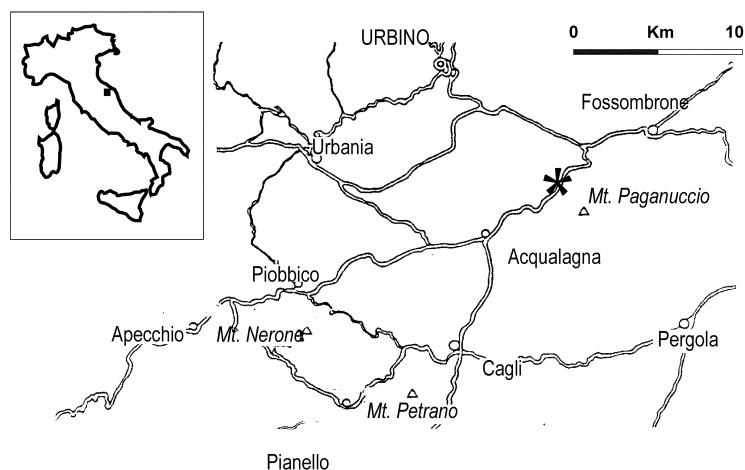
Fig. 1. Location map of the studied section.

low the Carbonate Compensation Depth. According to Kuhnt (1990), the agglutinated foraminiferal assemblage of the Scaglia Rossa is indicative of a water depth between 1500 m and 2000 m.

In outcrops of the lower Campanian Scaglia Rossa sequence at Furlo (Marche region of Italy, Fig. 1), Mattias et al. (1988) described a discrete 15-cm-thick bentonitic layer. According to the litho-, magneto- and biostratigraphic investigation of the Furlo sequence by Alvarez and Lowrie (1984), this bentonitic layer falls within the *Globotruncana elevata* planktonic foraminiferal zone, and within the lower part of Chron 33r of early Campanian age. Based on detailed geochemical and mineralogical analyses, Mattias et al. (1988) suggested a volcanic origin for this bentonite. The layer is predominantly comprised of calcium dioctahedric montmorillonite derived from the transformation, in a marine environment, of fine volcanic glass originating from sub-aerial volcanic activity. The sudden deposition of a 15-cm-thick (post-compaction thickness) volcanic ash layer would have created a sudden disturbance of the sea floor ecosystem, including mass mortality of benthic organisms. This event, therefore, represents an interesting case for a high-resolution study of the pattern of recolonisation of the benthic community, which in this bathyal environment is normally characterised by a highly diversified assemblage of DWAF.

3. Material and methods

To document changes in benthic foraminiferal assemblages and recolonisation patterns above the volcaniclastic layer, a quantitative analysis of DWAF was carried out on acid residues or washed residues obtained from 18 samples. Samples were collected across a 255-cm interval, from 125 cm below the volcaniclastic layer (FB1 to FB6), within it (FB7a, b), to 115 cm above it (FB8 to FB17). The interval spanning the first 5 cm above the volcaniclastic layer was sampled every centimetre (FB8 to FB12).

Considering the duration of Chron 33r (Gradstein et al., 1995) and its thickness in the Furlo section (Alvarez and Lowrie, 1984), the mean sedimentation rate during the early Campanian at Furlo was about 8.6 m/Myr. Therefore, assuming a constant sedimentation rate and geologically instantaneous deposition of the volcaniclastic layer, the studied interval represents approximately 370 kyr. Although a hiatus is known to occur within the Scaglia Rossa within the basal Palaeocene (e.g. Dingus, 1984), there is no visible evidence of hiatuses or turbidites within the studied interval.

Limestone samples were soaked in 5% diluted HCl, wet sieved with tap water and a 63-μm screen, and oven dried. The > 63-μm residues were split with a microsplitter into subsamples containing approximately 300–400 specimens

Table 1
Morphology and inferred life position of DWAF genera identified across the volcaniclastic layer at Furlo

Genus	Morphology	Inferred Life Position
Hippocrepina	Tubular (tapering)	Erect Epifaunal
Hyperammina		
Saccorhiza	Tubular	
Rhizammina	Tubular (branching)	
Rhabdammina		
Ammosphaeroidina	Rounded trochospiral	Surficial Epifaunal
Trochammina	Planoconvex trochospiral	
Turritellella	Irregular	
Glomospira		
Lituotuba	Flattened streptospiral	
Ammodiscus	Flattened planispiral	
Glomospirella		
Haplophragmoides		
Paratrochamminoides		
Trochamminoides		
Rzehakina	Flattened	
Recurvoides	Globular (streptospiral)	Shallow Infaunal
Aschemocella	Globular	
Saccammina	Globular (monothalamous)	
Karreriella	Lanceolate	Deep Infaunal
Pseudobolivina		
Spiroplectammina		
Uvigerinammina	Tapered	
Karrerulina	Elongate tapered	
Ammobaculites	Elongate subcylindrical	
Bulbobaculites		
Dorothia		
Hormosina		
Hormosinella		
Kalamopsis		
Reophax		
Subreophax		

each, which were all picked, counted, mounted on micropalaeontological slides for quantitative analysis, and then stored in the collections of the Palynology Center at the University of Urbino. The two samples representing the bentonite layer were washed with tap water through a 63-μm sieve.

We largely adopted species concepts of Kaminski et al. (1988a,b), Kuhnt (1990), Kuhnt and Kaminski (1990, 1993), Wightman and Kuhnt (1992), Kaminski and Geroch (1993), and Kuhnt et al. (1998). Specimens not identified to the generic level are reported as indeterminate forms. For each sample, the Fisher-α index and the percentages of epifaunal, shallow infaunal, and deep infaunal forms were calculated. The identification of epifaunal v. infaunal groups was carried out using the morphogroup classification of Jones and Charnock (1985), Tyszka (1994), Nagy et al. (1995), and Van Den Akker et al. (2000). The inferred mode of life for each taxon is reported in Table 1.

Tubular forms occurring in the studied material (mainly *Rhizammina indivisa*, *Rhizammina algaeformis* and *Rhabdammina* sp.) have been combined into a single group. Since only small fragments of these delicate forms occur in the studied material, counting them as individual specimens would overestimate their relative abundance. At the same time, considering the numbers of fragments as counts, as is often the case, affects the relative abundance of the non-tubular taxa. As a compromise, we subdivided the number of fragments by a constant value of 15. This number was derived by considering the minimum number of unbranched fragments obtainable from the holotype of *R. algaeformis* (which comprises the largest proportion of the tubular fragments). Although arbitrary, this method enables us to obtain an estimate of tubular specimens that is closer to reality than counting single fragments as specimens.

Statistical tests, including R-mode principal component analysis (PCA) and Q-mode cluster analysis, have been performed on the untransformed data set after exclusion of rare species (those that occur as one or two specimens in fewer than three non-adjacent samples) and grouping species that have a discontinuous, scattered distribution to the generic level. For cluster analysis, groups of com-positionally similar samples were identified using the Bray–Curtis dissimilarity index (Bray and Curtis, 1957) in association with the nearest neighbour, or single linkage, clustering technique.

4. Results

Results are summarised in Table 2 together with the mean distance of each sample from the bentonitic layer. DWAF assemblages from the surveyed interval are rich and highly diversified, consisting of not fewer than 70 species representing 33 genera. A minor degree of uncertainty concerning the number of occurring species is due to the presence of specimens not identified to the generic level in some samples. Preservation is generally good, though one of the samples above the bentonitic layer (FB10) exhibits a relatively poor state of preservation. The most common components of the DWAF assemblage are *Paratrochamminoides* spp., *Trochamminoides dubius*, *Trochammina* spp., *Subreophax* spp., *Saccammina* spp., and tubular forms (mainly *Rhizammina algaeformis*). Other important components are *Haplophragmoides* spp., *Reophax* spp., and *Ammosphaeroidina pseudopauciloculata*.

The relative abundance of each species fluctuates greatly in the surveyed interval, and the largest fluctuations are observed just above the volcaniclastic layer (see Table 2 and Fig. 2). The bentonitic layer itself is virtually devoid of foraminifera (both benthic and planktonic). Our examination of a large volume of material collected from the lower half of the ash layer revealed just one specimen of *Glomospira serpens*, while the samples collected from the upper half of the layer were completely barren.

Major differences in diversity, community structure, feeding and habitat preferences are observed among benthic foraminiferal assemblages below and above the volcaniclastic layer. Cluster analysis clearly separates two major branches at a Bray–Curtis index value of 0.3 (Fig. 3). The first group consists of four samples, representing the first 4 cm above the volcaniclastic layer (the 'recolonisation interval'), whereas the second group includes all the remaining samples. A further sub-

Table 2
Distribution of DWAF across the volcaniclastic layer at Furlo

Sample	FB1	FB2	FB3	FB4	FB5	FB6	FB7a	FB7b	FB8	FB9	FB10	FB11	FB12	FB13	FB14	FB15	FB16	FB17
Mean distance from the bentonite layer (cm)	−125	−85	−40	−15	−5	−0.5	0	0	+0.5	+1.5	+2.5	+3.5	+4.5	+10	+19,5	+27	+36	+100
Ammobaculites sp.	–	0.5	–	–	–	0.5	–	–	–	–	1.5	0.5	–	–	–	–	2.0	0.5
Ammodiscus cretaceus	–	–	0.5	–	–	0.5	–	–	–	–	–	–	–	–	1.0	–	–	–
Ammodiscus glabratus	1.7	–	–	1.9	0.9	1.5	–	–	1.4	0.4	0.5	0.5	2.8	1.5	1.0	–	0.5	–
Ammodiscus peruvianus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.5
Ammodiscus planus	2.6	–	0.5	4.9	1.8	2.9	–	–	1.4	1.8	–	1.5	1.4	5.8	2.4	0.4	0.5	–
Ammodiscus sp.	–	1.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ammosphaeroidina pseudopauciloculata	7.7	3.0	10.0	8.7	8.5	7.8	–	–	7.1	8.3	0.5	5.8	6.2	3.4	2.9	6.7	12.7	10.2
Aschemocella sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.5	–	–	–
Bulbobaculites problematicus	2.1	1.0	1	1.0	1.8	–	–	–	2.8	1.3	1.0	1.5	1.9	3.4	1.4	4.5	1.0	0.9
Dorothia sp.	0.4	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Glomospira charoides	–	–	–	0.5	–	–	–	–	0.5	–	–	–	0.9	–	–	–	0.5	0.5
Glomospira glomerata	–	0.5	2.0	1.0	0.4	0.5	–	–	–	–	–	–	–	–	–	–	–	–
Glomospira gordialis	–	2.0	2.5	1.0	6.3	1.0	–	–	1.4	–	1.0	2.9	3.8	3.4	2.4	–	2.4	1.9
Glomospira serpens	0.4	0.5	–	0.5	0.9	–	–	–	–	0.4	–	0.5	–	0.5	–	0.4	–	0.5
Glomospira spp.	3.0	0.5	–	1.0	0.9	2.0	–	–	–	–	–	–	–	–	–	0.9	0.5	0.4
Glomospirella gaultina	2.6	1.0	–	2.9	1.3	2.0	–	–	1.4	2.2	0.5	1	–	4.9	1.4	0.4	1.0	1.9
Haplophragmoides suborbicularis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Haplophragmoides walteri	5.1	11.4	4.5	2.9	3.6	2.4	–	–	2.4	7.0	7.0	0.5	–	12.6	6.3	4.5	6.3	10.2
Haplophragmoides sp.	–	–	–	–	0.4	–	–	–	–	0.4	1.5	–	1.4	–	–	0.4	0.5	0.5
Hippocrepina depressa	–	–	0.5	–	–	–	–	–	–	–	0.5	–	–	–	–	0.4	–	–
Hormosina excelsa	–	–	1.5	1.0	0.4	0.5	–	–	–	–	–	–	–	–	–	0.9	–	0.5
Hormosina sp.	1.3	0.5	–	–	–	0.5	–	–	–	0.4	–	–	–	–	–	–	–	–
Hormosinella cf. *distans*	3.0	2.5	5.5	1.0	4.0	2.4	–	–	5.7	5.3	7.0	2.4	6.2	4.9	4.3	4.5	1.5	2.3
Hyperammina dilatata	–	–	–	0.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Hyperammina sp.	0.4	1.5	–	–	–	0.5	–	–	–	0.4	–	–	0.5	–	–	0.4	1.5	1.4
Kalamopsis grzybowskii	–	–	1.5	2.4	0.4	2.0	–	–	–	–	–	–	–	–	–	–	1.0	–
Karreriella conversa	0.4	–	–	–	–	–	–	–	–	0.4	–	–	–	–	–	–	0.5	–
Karrerulina sp.	0.9	4.5	4.5	1.0	5.4	2.0	–	–	2.4	0.9	4.5	10.2	1.4	4.4	5.3	4.5	4.4	6.9
Lituotuba lituiformis	0.4	–	–	1.9	–	1.0	–	–	0.5	–	–	–	2.8	–	0.5	–	–	0.5
Lituotuba sp.	–	–	–	–	–	0.5	–	–	–	–	–	–	–	–	–	0.4	–	–
Paratrochamminoides heteromorphus	–	–	0.5	–	–	–	–	–	–	–	–	1	–	–	–	–	0.5	–
Paratrochamminoides sp. 1 (Kuhnt, 1990)	7.2	9.4	3.0	6.3	10.7	5.4	–	–	3.3	5.7	3.0	4.4	10.4	6.3	13.0	9.4	4.9	6.0
Paratrochamminoides sp. 2 (Kuhnt, 1990)	6.0	5.9	2.5	3.9	6.3	2.0	–	–	2.4	4.4	3.5	3.4	5.2	7.2	12.5	5.8	8.8	6.0

Table 2 (continued)

| Sample | FB1 | FB2 | FB3 | FB4 | FB5 | FB6 | FB7a | FB7b | FB8 | FB9 | FB10 | FB11 | FB12 | FB13 | FB14 | FB15 | FB16 | FB17 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Mean distance from the bentonite layer (cm) | −125 | −85 | −40 | −15 | −5 | −0.5 | 0 | 0 | +0.5 | +1.5 | +2.5 | +3.5 | +4.5 | +10 | +19,5 | +27 | +36 | +100 |
| Paratrochamminoides/ Trochamminoides juvenile | 0.9 | – | 0.5 | – | – | 1.0 | – | – | 4.7 | 4.8 | 7.5 | 4.9 | – | – | – | – | 1.0 | – |
| Pseudobolivina lagenaria | – | – | – | – | – | – | – | – | – | – | – | 0.5 | – | – | – | – | – | – |
| Pseudobolivina cf. munda | 0.4 | 0.5 | – | 1.0 | 0.4 | 0.5 | – | – | 6.1 | 6.1 | 3.0 | 3.9 | 4.3 | 1.9 | 1.0 | 0.4 | 1.5 | 0.5 |
| Pseudobolivina variabilis | 0.9 | – | – | – | – | 0.5 | – | – | 0.5 | 0.9 | – | – | – | – | – | 0.9 | – | – |
| Recurvoides nucleosus | – | – | 1.0 | 0.5 | 0.4 | 0.5 | – | – | – | – | 1.0 | – | – | – | 2.4 | – | 0.5 | – |
| Recurvoides sp. | 0.4 | – | 2.0 | 0.5 | – | 1.0 | – | – | 0.9 | 0.4 | – | 1 | – | 1.0 | – | – | 1.0 | 0.5 |
| Reophax minutus | 3.8 | 5.4 | 3.5 | 3.4 | 3.6 | 2.9 | – | – | 14.6 | 7.9 | 8.5 | 8.7 | 6.6 | 2.9 | 10.1 | 4.9 | 6.3 | 5.6 |
| Reophax subnodulosus | – | 2.5 | 2.0 | – | – | 1.0 | – | – | 0.5 | – | 0.5 | – | 0.9 | – | 1.0 | – | 0.5 | 0.5 |
| Reophax sp. 5 (Kuhnt, 1990) | – | – | – | 1.0 | – | 1.0 | – | – | 2.4 | – | 1.0 | – | 1.4 | – | – | – | 1.0 | 0.9 |
| Reophax spp. | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – |
| Rzehakina epigona | – | – | – | – | – | – | – | – | 0.5 | – | 0.5 | – | – | – | – | – | 0.5 | – |
| Saccammina grzybowskii | 3.0 | 2.5 | 2.0 | 2.9 | 0.9 | 2.0 | – | – | 0.9 | 3.9 | 1.5 | 7.3 | 3.3 | 2.4 | 2.4 | 8.5 | 0.5 | 2.8 |
| Saccammina placenta | 5.5 | 6.9 | 5.0 | 4.9 | 5.8 | 4.4 | – | – | 4.7 | 4.4 | 3.0 | 5.3 | 5.2 | 10.2 | 6.3 | 6.7 | 4.9 | 3.2 |
| Saccammina sphaerica | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | 0.4 | – | – |
| Saccorhiza ramosa | – | – | 1.0 | 1.0 | – | 1.0 | – | – | – | – | – | – | – | – | – | – | – | 0.9 |
| Spiroplectammina dentata | 0.4 | – | 1.0 | 0.5 | – | – | – | – | – | – | – | – | – | – | – | 0.4 | – | – |
| Spiroplectammina laevis | 0.9 | – | – | 1.0 | – | 1.5 | – | – | – | 3.1 | 1.0 | – | – | – | – | 0.4 | 1.5 | – |
| Spiroplectammina spp. | – | 0.5 | – | – | 0.9 | – | – | – | – | – | 1.0 | 2.4 | 0.5 | – | – | – | – | – |
| Subreophax guttifer | 0.9 | 2.5 | 2.5 | 2.9 | 3.1 | 3.4 | – | – | 2.4 | 6.1 | 3.0 | 1.9 | 0.9 | 1.5 | 0.5 | 0.9 | 3.4 | 2.3 |
| Subreophax pseudoscalaris | 0.4 | – | – | – | – | – | – | – | 0.5 | 1.3 | – | – | – | 1.0 | – | – | 0.5 | 0.5 |
| Subreophax scalaris | 0.4 | 2.0 | 1.0 | 2.4 | 3.6 | 0.5 | – | – | 4.7 | 2.2 | 6.5 | 2.9 | 1.4 | 2.4 | 3.8 | 1.3 | 1.5 | 1.4 |
| Subreophax splendidus | 2.1 | 8.4 | 4.0 | 6.3 | 4.0 | 3.4 | – | – | 6.1 | 2.2 | 7.0 | 9.2 | 5.2 | 3.4 | 6.7 | 6.3 | 3.9 | 7.4 |
| Subreophax spp. | – | – | 1.0 | 0.5 | 0.4 | 2.4 | – | – | – | – | 1.5 | 0.5 | – | – | – | – | – | – |
| Trochammina deformis | 7.2 | 5.9 | 8.5 | 3.9 | 6.3 | 5.4 | – | – | 2.4 | 1.3 | 3.0 | 2.4 | 4.3 | 2.4 | 1.4 | 3.6 | 6.3 | 4.6 |
| Trochammina cf. gyroidiniformis | – | – | 0.5 | 0.5 | – | – | – | – | – | 0.4 | – | – | – | – | – | – | 1.0 | – |
| Trochammina spp. | 2.1 | 4.0 | 4.0 | 6.8 | 4.5 | 5.9 | – | – | 1.4 | – | 3.0 | – | – | – | 0.5 | – | – | – |
| Trochamminoides dubius | 9.4 | 3.5 | 5.5 | 4.4 | 3.6 | 8.3 | – | – | 3.8 | 8.8 | 4.5 | 2.4 | 10.4 | 2.9 | 1.4 | 9.4 | 1.0 | 7.9 |
| Trochamminoides septatus | 0.4 | – | – | – | 0.4 | 0.5 | – | – | – | – | – | – | – | – | – | – | – | – |
| Trochamminoides subcoronatus | – | – | – | – | – | – | – | – | – | – | – | – | – | 0.5 | – | – | – | – |
| Trochamminoides spp. | 3.8 | 2.5 | 3.5 | 3.9 | – | 2.4 | – | – | 4.2 | – | 2.0 | 0.5 | – | 0.5 | 1.4 | 0.9 | 2.0 | 0.5 |
| Tubular forms | 6.0 | 5.9 | 7.0 | 4.9 | 4.0 | 6.3 | – | – | 4.7 | 5.7 | 6.5 | 6.3 | 8.5 | 5.3 | 4.3 | 6.3 | 7.3 | 6.0 |
| Turritellella sp. | – | – | – | – | – | 0.5 | – | – | – | – | – | 0.5 | – | – | – | – | – | – |
| Uvigerinammina jankoi | 4.3 | 1.0 | 4.0 | 1.0 | 1.3 | 6.3 | – | – | 0.5 | – | 1.0 | 1 | 0.9 | 0.5 | 1.4 | 0.4 | – | 0.5 |
| Indeterminate forms | 1.7 | 0.5 | 0.5 | 1.9 | 2.7 | 1.0 | – | – | 0.9 | 0.9 | 1.5 | 2.4 | 0.9 | 2.9 | 0.5 | 2.2 | 2.4 | 1.4 |
| Number of specimens | 235 | 202 | 201 | 206 | 224 | 205 | 0 | 0 | 212 | 228 | 200 | 206 | 211 | 206 | 208 | 223 | 205 | 216 |
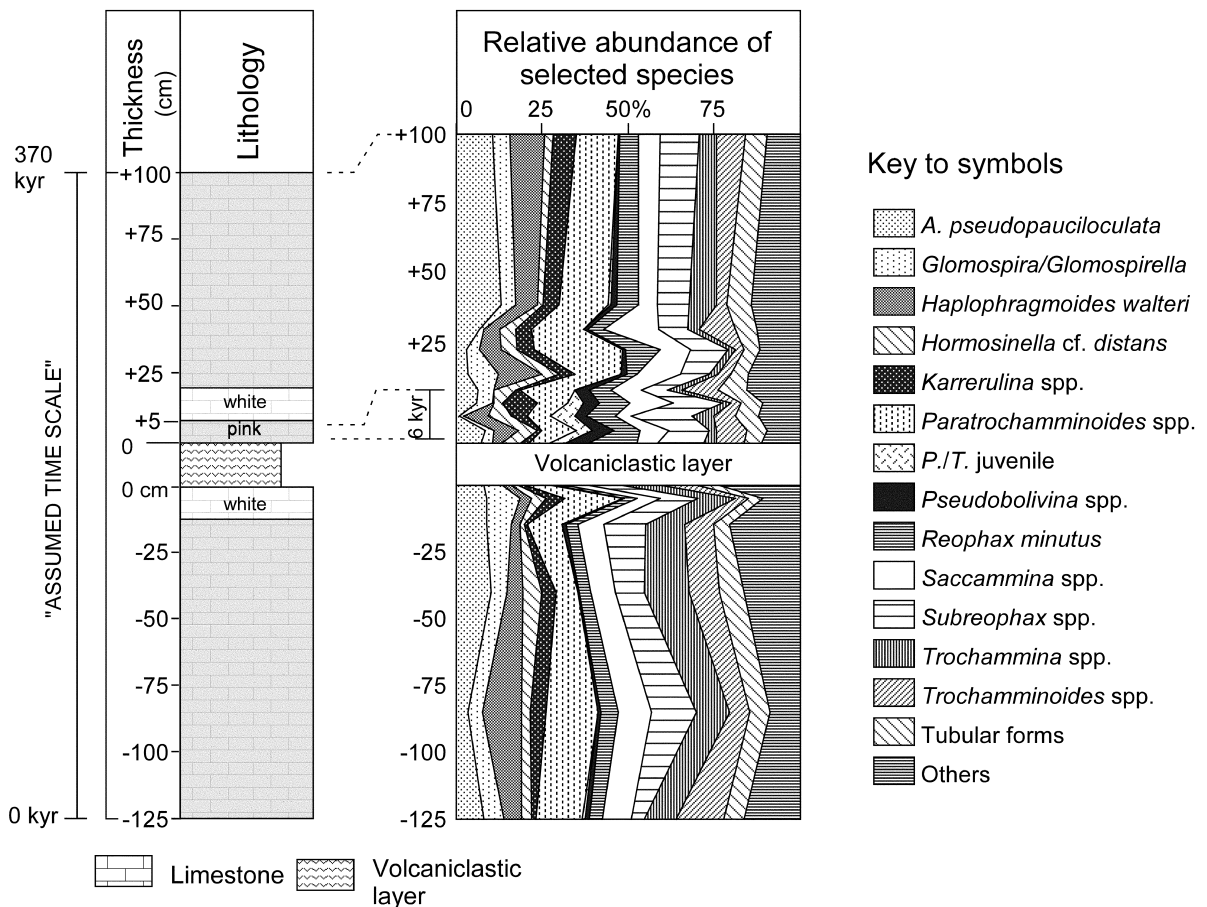
Fig. 2. Vertical distribution of selected DWAF taxa across the volcaniclastic layer at Furlo. Notice the scale break between 0 and 5 cm above the volcaniclastic layer.

division of the second cluster enables us to distinguish samples FB12–FB16.

The first and second axes of the PCA accounted for 78% and 6% of total variance, respectively. Loading scores for the first two axes are reported in Table 3. Based on PCA scores, we identified five assemblages denominated by the dominant taxa (Fig. 4). These display a distinctive distribution across the volcaniclastic layer. A comparison of the relative abundance of faunal groups identified by the PCA in the pre-ashfall, 'recolonisation', and post-recovery intervals is given in Fig. 5.

Pre-ashfall and post-ashfall assemblages are quite similar, despite displaying some minor differences in the species composition of the DWAF. In particular, the post-ashfall assemblages show slightly higher proportions of the *Subreophax* and *Reophax minutus* assemblage, and lower relative abundance of the *Paratrochamminoides–Trochamminoides–Trochammina* assemblage. *Reophax minutus*, which forms a separate assemblage, is a relatively common taxon throughout the studied interval, but shows a peak in relative abundance just above the volcaniclastic layer. The *Pseudobolivina* cf. *munda* assemblage, which consists of *P. munda* and small specimens of *Paratrochamminoides* and *Trochamminoides*, is found almost exclusively in the 'recolonisation interval'. A third PCA assemblage comprised of *Subreophax scalaris*, *Subreophax splendidus*, *Karrerulina* spp., and *Hormosinella* cf. *distans* shows highest relative abundance in the 'recolonisation interval',

although not immediately above the volcaniclastic layer.

Below the volcaniclastic layer, DWAF assemblages are characterised by a rather stable epifaunal/infaunal ratio, with an average relative abundance of infaunal forms around 22% (Fig. 6). In this stratigraphic interval, DWAF diversity (Fisher-α) ranges from a minimum value of 10.7 in sample FB2 to a maximum of 16.5 just below the ash layer (FB6), with an average value of 13.3. The changes recorded by the PCA assemblages across the volcaniclastic layer are clearly reflected in the record of faunal parameters (epifaunal vs. infaunal abundance and diversity). The 'bloom' in the elongate morphotypes that dominate the *Reophax minutus*, *Pseudobolivina* cf. *munda*, and *Subreophax* assemblages is reflected in a peak of infaunal forms occurring within the 'recolonisation interval', with a maximum value of 46.2% recorded in the first centimetre above the volcaniclastic layer. Just above the volcaniclastic layer, diversity shows average values slightly lower than those observed in the pre-ashfall interval, dropping to its lowest value in sample FB12, just above the 'recolonisation interval'.

Although based on few samples, a gradual recovery to average values comparable to that of the pre-ash interval can be observed upsection. Unlike the rest of the surveyed interval, a clear covariance between diversity and the proportion of infaunal forms is observed in the 'recolonisation interval'.

5. Discussion

The DWAF assemblages studied at Furlo are generally similar to those reported by Kuhnt (1990) from the Upper Cretaceous Scaglia series of the classic Bottaccione section, near Gubbio. The taxonomic composition of these assemblages is indicative of a lower bathyal depositional setting at a palaeodepth of 1500–2000 m.

Prior to the deposition of the volcaniclastic layer, the DWAF assemblage is indicative of a certain environmental stability as indicated by the relatively minor fluctuations in the measured faunal parameters. This stability was disrupted catastrophically by the deposition of over 15 cm of volcanic ash, an event that would have occurred within a day or two at the lower bathyal water depths represented by the Scaglia Rossa (Wiesner et al., 1995). It is possible that some sediment-dwelling foraminifera reacted to burial by attempting to exhume themselves, and the species found within the basal centimetre of the bentonite, *Glomospira serpens*, does possess the typical morphology of an active burrower. However, the ability of foraminifera to burrow upward through volcanic ash is apparently quite limited (see also Hess and Kuhnt, 1996, figs. 3 and 4).

A remarkable pattern that can be interpreted as evidence of faunal recovery characterised the sea floor following the deposition of the volcanic ash. Species such as *Reophax minutus* and *Pseudobolivina* cf. *munda*, which behaved as opportunists in the recolonisation process, are interpreted as infaunal deposit feeders. Accordingly, a special feature of infaunal elongate/lanceolate morphotypes and, in particular of the genus *Reophax* and its relatives seems to be their high capability for dispersal. Forms belonging to the *Subreophax* assemblage (*Subreophax scalaris*, *Subreophax splendidus*, *Hormosinella* cf. *distans*, and *Karrerulina* sp.), although benefiting from conditions following the deposition of the volcaniclastic layer, apparently represent 'second wave' colonisers.

The stratigraphic distribution of PCA assemblages reveals that the highest abundances of 'recolonisers' is restricted to the first 4 cm above the volcaniclastic layer. This interval corresponds to 4.8 kyr, assuming a constant sedimentation rate of 8.6 m/Myr. However, this value for the time significance of the disturbed fauna is certainly an overestimate, owing to ubiquitous presence of bioturbational mixing in the Scaglia Rossa. The group most adversely affected by the deposition of the volcaniclastic layer appears to be the *Paratrochamminoides–Trochamminoides–Trochammina* assemblage.

5.1. Comparison with Recent analogues

The recovery pattern of the DWAF in the Scaglia Rossa at Furlo displays remarkable simi-
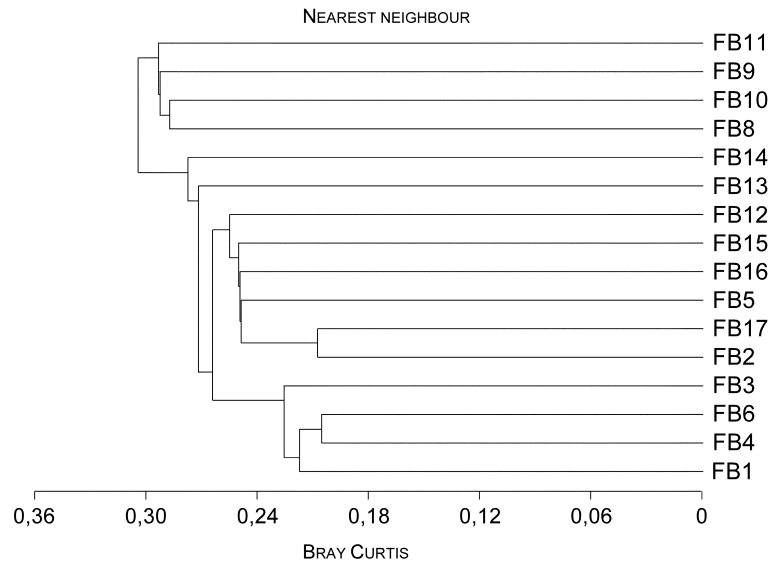
NEAREST NEIGHBOUR

Fig. 3. Results of the Q-mode cluster analysis. The dendrogram is produced using the Bray–Curtis similarity measure on untransformed data in association with the nearest neighbour clustering method. Numbers to the right of the dendrogram are samples.

larities to those observed following disturbance (actual or simulated) in modern deep-sea environments. Several species of the genus *Reophax* have been reported among the early colonisers of current-controlled substrates at the HEBBLE site in the northwestern Atlantic (Kaminski, 1985) as well as in a recolonisation tray experiment carried out in the Panama Basin (Kaminski et al., 1988a,b). According to Kaminski et al. (1988a,b), *Psammosphaera fusca* and *Hormosina ovicula* are among the species that display good dispersal capability. Three years after the deposition of volcanic material from the 1991 Mt Pinatubo eruption, various species of *Reophax* (i.e. *R. scorpiurus*, *R. dentaliniformis*, *R. bilocularis*), a small organically cemented species of *Textularia*, and the calcareous species *Quinqueloculina seminula* and *Bolivina difformis* were reported as the earliest recolonisers on top of the tephra layer at stations collected from lower bathyal depths in the South China Sea (Hess and Kuhnt, 1996). It is noteworthy that this species of *Textularia* shows remarkable morphological similarity to our *Pseudobolivina* cf. *munda*, which recolonised the first 2 cm of sediment above the bentonite in the Scaglia Rossa at Furlo. Both species are characterised by their small size and a lanceolate/ta-

pered morphology with a finely agglutinated wall, and biserial chamber arrangement. Subsequent monitoring studies of the 1991 Mt Pinatubo tephra layer carried out between 1996 and 1999 (Hess, 1998; Hill, 1998; Fisher, 1999; Hess et al., 2002) have documented an increase in foraminiferal diversity and the establishment of additional species that continue to colonise the substrate. The 'second wave' of colonisers in the deep South China Sea includes species of *Subreophax* and tubular forms such as *Rhizammina*, while the abundance of the initial colonists has decreased (Hess et al., 2002). Seven to eight years after the ashfall, the trochamminid group (*Trochammina* ex gr. *globigeriniformis*, *Trochammina* sp., *Adercotryma glomerata*) has increased markedly in abundance, and coiled multichambered forms such as *Recurvoides*, *Eratidus*, *Ammobaculites*, *Haplophragmoides*, and *Karrerulina* are beginning to appear in the samples.

In spite of the large age difference between our locality and the modern faunas, it is remarkable that the recolonisation pattern observed above the volcaniclastic layer at Furlo is entirely comparable (at least on a generic level) with patterns observed on modern deep sea substrates. In line with observations on modern assemblages, the genera

Table 3
Loading scores of identified taxa on the first two axes of the PCA

Taxon		Loadings	
		First axis	Second axis
1	*Ammobaculites* sp.	0.018	0.021
2	*Ammodiscus* spp.	0.135	−0.111
3	*Ammosphaeroidina pseudopauciloculata*	0.333	−0.281
4	*Bulbobaculites problematicus*	0.083	0.037
5	*Glomospira* spp.	0.160	−0.204
6	*Glomospirella gaultina*	0.076	−0.042
7	*Haplophragmoides walteri*	0.263	−0.005
8	*Haplophragmoides* sp.	0.016	0.019
9	*Hormosina* spp.	0.021	−0.076
10	*Hormosinella* cf. *distans*	0.187	0.158
11	*Hyperammina* spp.	0.022	−0.030
12	*Kalamopsis grzybowskii*	0.019	−0.081
13	*Karrerulina* sp.	0.188	0.151
14	*Lituotuba lituiformis*	0.022	−0.033
15	*Paratrochamminoides* sp. 1 (Kuhnt, 1990)	0.337	−0.116
16	*Paratrochamminoides* sp. 2 (Kuhnt, 1990)	0.265	−0.006
17	*Paratrochamminoides/Trochamminoides* juvenile	0.071	0.341
18	*Pseudobolivina* cf. *munda*	0.094	0.288
19	*Recurvoides* spp.	0.045	0.007
20	*Reophax minutus*	0.296	0.523
21	*Reophax subnodulosus*	0.026	−0.015
22	*Reophax* sp. 5 (Kuhnt, 1990)	0.024	0.037
23	*Saccammina placenta*	0.262	−0.037
24	*Saccammina sphaerica*	0.145	0.069
25	*Saccorhiza ramosa*	0.011	−0.041
26	*Spiroplectammina* spp.	0.050	0.025
27	*Subreophax guttifer*	0.113	0.023
28	*Subreophax pseudoscalaris*	0.013	0.013
29	*Subreophax scalaris*	0.111	0.224
30	*Subreophax splendidus*	0.254	0.201
31	*Subreophax* spp.	0.016	−0.020
32	*Trochammina deformis*	0.207	−0.304
33	*Trochammina* spp.	0.101	−0.220
34	*Trochamminoides dubius*	0.270	−0.179
35	*Trochamminoides* spp.	0.087	−0.064
36	Tubular forms	0.285	−0.017
37	*Uvigerinammina jankoi*	0.070	−0.188

The first axis explains 78% of the total variance and the second axis explains 6% of the total variance.

Reophax, *Hormosinella*, and *Pseudobolivina* are indicative of recolonisation following a major substrate disturbance.

An additional indication of stressed environmental conditions following the deposition of the volcaniclastic layer comes from the high proportion of juvenile and/or dwarfed specimens of the *Paratrochamminoides–Trochamminoides* group, which forms part of the *Pseudobolivina* cf. *munda* PCA assemblage and which is observed in the first few centimetres above the bentonitic layer (see Table 2 and Fig. 2). It is possible that these forms, which presumably had an epifaunal to shallow infaunal position in the substrate, were not able to reach the adult stage owing to the lack of food resources on a comparatively sterile volcaniclastic substrate or because of competition for resources from the established opportunists living on the sediment surface. Infaunal foraminifera would in fact have no reason to colonise the ash
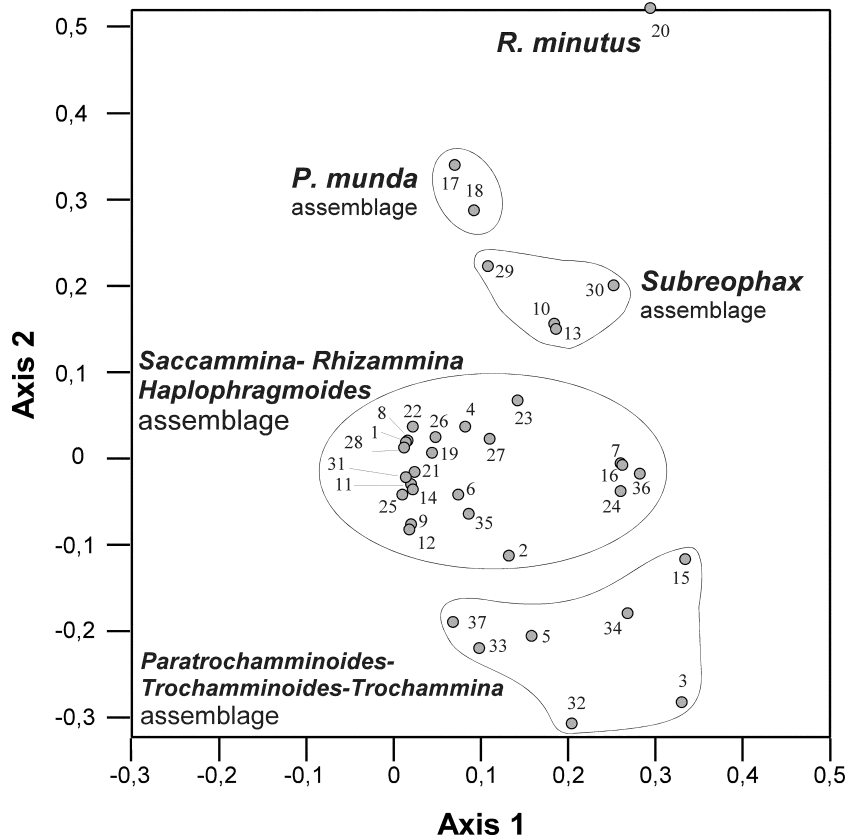
Fig. 4. Plot of taxa scores on the first two axes of the PCA. The first and second axes explain 78% and 6% of total variance, respectively. Numbers refer to taxa as shown in Table 3. Five assemblages (encircled) are identified and denominated by the dominant taxa.

layer itself because of a lack of food (in the form of bacteria).

The unchanged proportion of tubular forms across the volcaniclastic layer seems to be at odds with the findings of Kaminski (1985) and Kaminski et al. (1988a,b), who found that tubular epifaunal forms such as *Dendrophrya* have the lowest dispersal capability. Likewise, these forms are slow at recolonising the 1991 Mt Pinatubo ash layer in the South China Sea (see data tables in Hess, 1998). The proportion of tubular forms in the 'recolonisation interval' (with the exception of sample FB9) is only slightly lower than that observed in the pre-ashfall and post-recovery fauna. However, the relative abundance of tubular foraminifera is certainly overestimated in these samples because of poorer preservation and increased

fragmentation just above the volcaniclastic layer. Fragments of *Rhizammina indivisa* collected in the first few centimetres above the volcaniclastic layer are smaller than those observed in the rest of the studied stratigraphic interval. A possible explanation for the increased fragmentation of *Rhizammina* above the volcaniclastic layer is scavenging by bioturbators, which following the deposition of the sterile volcaniclastic layer must have been concentrated near the sediment–water interface. Tubular foraminifera are also more likely to be scavenged by surface-grazing macrofaunal burrowers than are infaunal species. Burrows filled with tubular foraminifera have been observed in boxcores from the South China Sea (Kaminski and Wetzel, unpublished data).
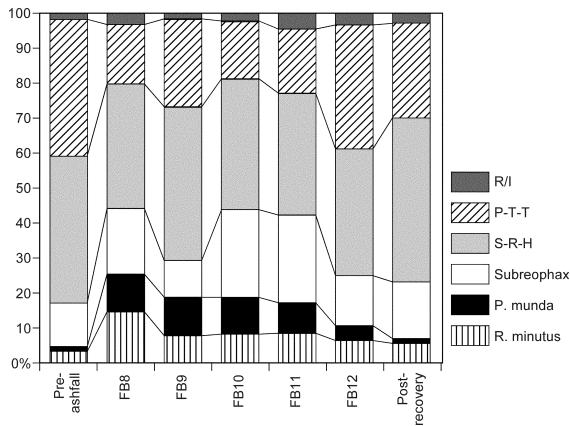
Five centimetres above the volcaniclastic layer

Fig. 5. Distribution of PCA assemblages across the volcani-clastic layer. Pre-ashfall values are calculated as a simple average of data from sample below the volcaniclastic layer. Likewise, post-recovery values represents an average of relative abundances recorded from samples above the 'recolonisation interval' (i.e. the first 5 cm above the volcaniclastic layer). P-T-T = *Paratrochamminoides–Trochamminoides–Trochammina* assemblage. S-R-H = *Saccammina–Rhizammina–Haplophragmoides* assemblage. The relative abundance of rare and indeterminate species (reported as R/I) is also reported.

at Furlo, we observe a return to background values in the relative abundance of the initial recolonisers (i.e. *Reophax minutus*, *Hormosinella* cf. *distans*, and *Pseudobolivina* cf. *munda*), together with the disappearance of juvenile forms of the *Paratrochamminoides–Trochamminoides* group. This change is here interpreted as the final phase of the recolonisation process. Based on an estimation of the average sedimentation rate for Chron 33r in the Scaglia Rossa at Furlo, this return to pre-ashfall comparable assemblages occurred some 5 kyr after the deposition of the volcaniclastic material. This estimate is at odds with the findings of Hess et al. (2002), who document the return of trochamminids to the 1991 Mt Pinatubo tephra layer some 5–8 years after the volcanic eruption. As mentioned above, this estimate of the recovery time at Furlo is certainly affected by relatively intense bioturbation, which would have displaced part of the original recolonisation assemblage upward.

It is most likely that the deposition of a c. 15-cm-thick volcaniclastic layer (whose original thickness prior to compaction was probably much higher) sealed off the entire benthic fauna. Studies of the 1991 Mt Pinatubo ash layer reveals that an ash thickness in excess of about 4 cm results in total mortality of the benthic foraminifera within a few years, as oxygen becomes depleted beneath the ash layer. The bentonite layer at Furlo contains dispersed pyrite crystals, indicating a reducing environment (Mattias et al., 1988). At Furlo, the mechanism responsible for total mass mortality would have been burial and subsequent oxygen depletion of the pore waters, which would have killed off any surviving deep infaunal species.

In terms of the recolonisation mechanism, the lateral migration of initial recolonisers from areas unaffected by the ashfall seems most appropriate. It is interesting to note that the species which recolonised the substrate after the ashfall all belong to the deep infaunal morphogroup, implying that they might not be easily transported by bottom currents or similar mechanisms. However, the elongate/lanceolate morphology might be more an adaptation for mobility in the mixed layer of the sediment. In dysoxic environments, species belonging to the deep infaunal morphogroup are found living at the sediment surface (Kaminski et al., 1995). An obvious mechanism for dispersal would be the drifting of gametes or zygotes during/after reproduction, since numerous species of benthic foraminifera possess flagellated gametes (see table 1 in Lee et al., 1991). Additionally, resuspension and transport of the first recolonisers by bottom currents is another mechanism for dispersion. Living specimens of *Reophax scotti* have been found in plankton tows collected from the North Sea (John, 1987), although these organisms may have gone into suspension in shallow water areas during a major storm.

6. Conclusions

Significant differences in diversity, community structure, feeding and habitat preferences are observed among benthic foraminiferal assemblages below and above the volcaniclastic layer, which is virtually barren of foraminifera.
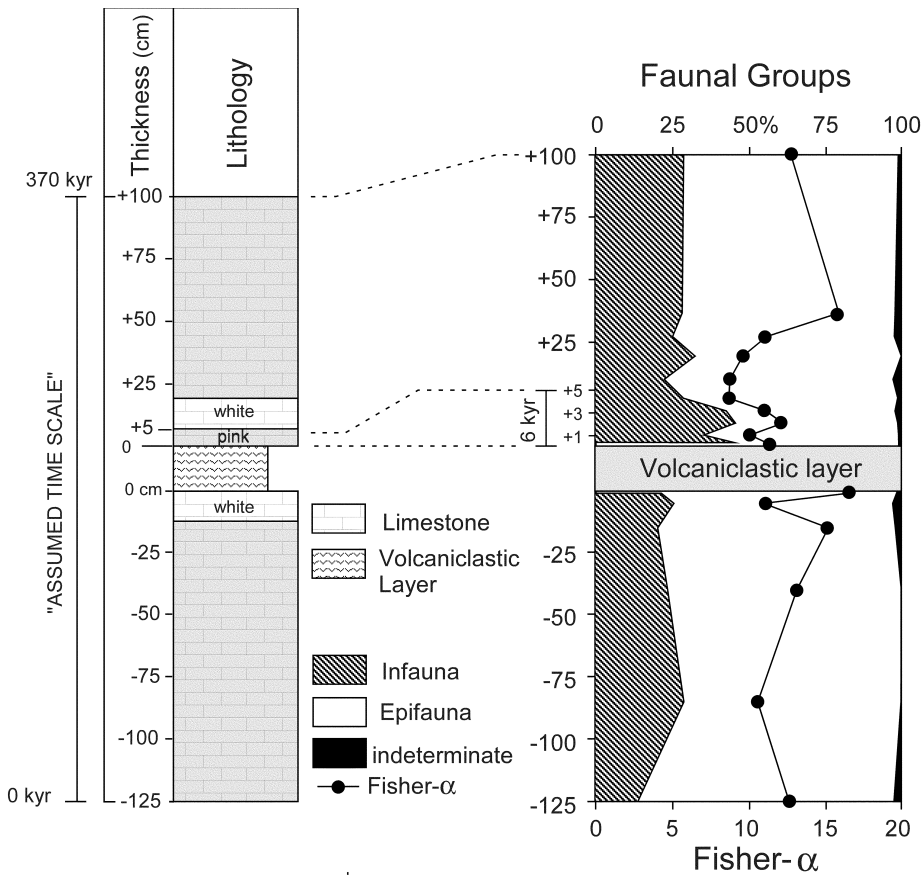
Fig. 6. Relative abundance of inferred infaunal and epifaunal taxa, and DWAF diversity (Fisher-α index) across the volcaniclastic layer at Furlo. The proportion of indeterminate species is also reported. Notice the scale break between 0 and 5 cm above the volcaniclastic layer.

Below the volcaniclastic layer, DWAF assemblages are diverse with 28–34 species, and only minor fluctuations in the relative abundance of taxonomic groups and faunal parameters are observed. Common taxa are *Paratrochamminoides* spp., *Trochamminoides dubius*, *Trochammina* spp., *Subreophax* spp., *Saccammina* spp. and tubular forms.

The recolonising assemblage above the bentonitic layer is significantly different in terms of both diversity and relative abundances of taxa and faunal parameters, showing reduced diversity and an increased proportion of infaunal forms. High relative abundances of *Reophax minutus* and *Pseudobolivina* cf. *munda* (the latter being almost exclusively represented just above the volcaniclastic layer) are observed in the first centimetre

above the bentonitic layer, in association with juvenile/dwarfed specimens of *Paratrochamminoides* and *Trochamminoides*. *Reophax minutus* and *P. munda* probably represent the initial recolonisers that appeared following the deposition of the volcaniclastic material. Between 2 and 4 cm above the volcaniclastic layer, the highest relative abundances of *Subreophax scalaris*, *Subreophax splendidus*, *Hormosinella* cf. *distans*, and *Karrerulina* sp. are observed. These taxa represent the next stage in the recolonisation process, and although exploiting niches opened up by the mass mortality of the original fauna, are not as opportunistic as *R. minutus* and *P. munda*. The recolonisation fauna is comprised mainly of morphologies belonging to the infaunal morphogroup (Plate I), which
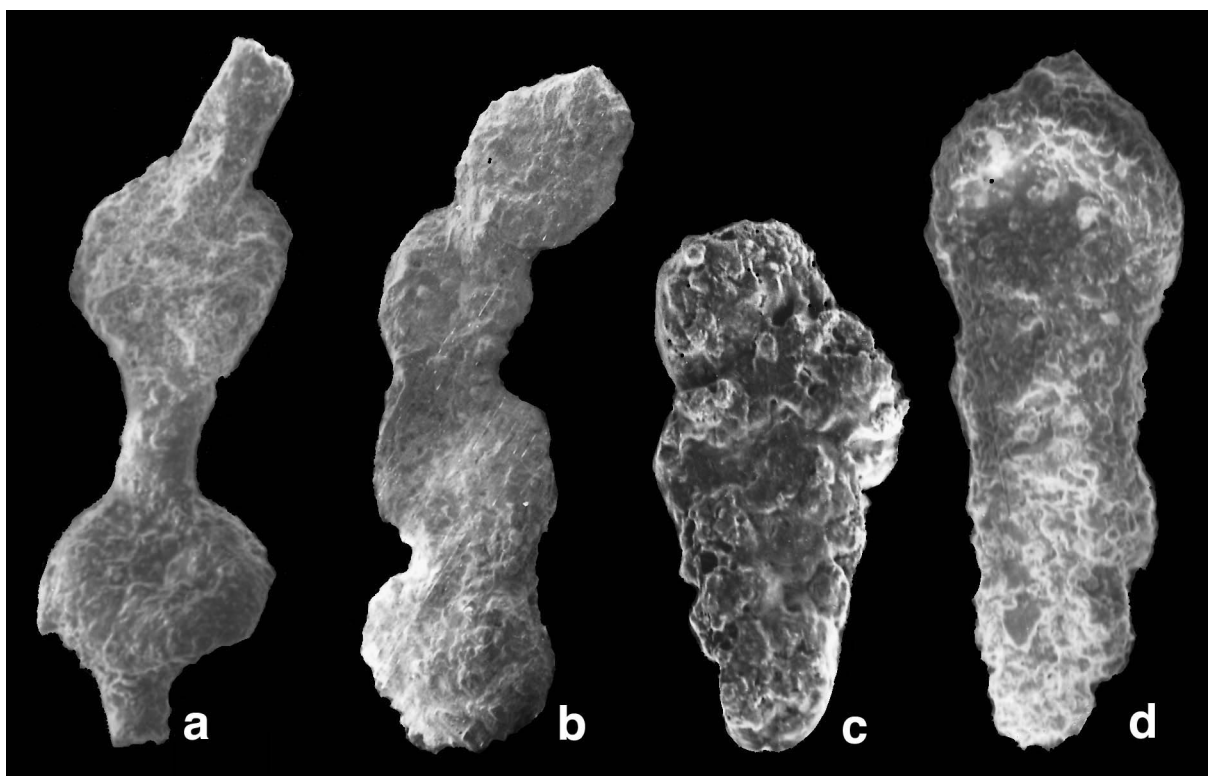
Plate I. Typical specimens of the recolonisation fauna above the volcaniclastic layer.

a.   *Hormosinella* cf. *distans* Brady; sample FB8, ×250
b.   *Subreophax splendidus* Grzybowski; sample FB8, ×250
c.   *Pseudobolivina* cf. *munda* Krasheninnikov; sample FB10, ×350
d.   *Reophax minutus* Tappan; sample FB8, ×226

apparently live at the sediment surface in disturbed conditions, and are dispersed by deep-sea currents. The succession of species above the volcaniclastic layer at Furlo displays interesting similarities to the succession of species found colonising the 1991 Mt Pinatubo tephra layer in the abyssal South China Sea. Profound differences between the calculated duration of the recolonisation process at Furlo and that observed in the South China Sea are attributed to bioturbational mixing in the Scaglia Rossa, which resulted in an expanded record of the fossil 'recolonisation assemblage'. Despite the passage of 80 million years of Earth History, broad similarities at the generic level between modern and fossil analogues

strengthens the reliability of environmental reconstructions based on DWAF.

Appendix A. Taxonomic reference list

All DWAF species identified in the samples of

this study are alphabetically arranged with reference to their original description.

Ammobaculites sp.

Test consisting of 3–4 chambers in the coiled stage later uncoiling to form a rectilinear stage composed of 2–3 chambers. The wall is composed of medium to fine grain-sized particles resulting in a somewhat smooth aspect. Aperture is a round, simple opening at the end of the last chamber.

Ammodiscus cretaceus (Reuss)

Operculina cretacea Reuss, 1845, pl. 13, figs. 64, 65.

Ammodiscus glabratus Cushman and Jarvis, 1928 pl. 12, figs. 6, 6a.

Ammodiscus peruvianus Berry, 1928, pl. 27.

Ammodiscus planus Loeblich, 1946, pl. 22, fig. 2.

Loeblich, 1946. Foraminifera from the type Pepper shale of Texas. J. Paleontol., 20, 130–139.

Ammodiscus sp.

We place in this species specimens showing a slightly irregular planispiral coiling. Our specimens are, therefore, comparable to those reported as *Ammodiscus* sp. 1 from the Campanian and Maastrichtian Scaglia Rossa of the Gubbio section by Kuhnt (1990), who regarded them as intermediate forms between the genera *Ammodiscus* and *Trochamminoides*.

Ammosphaeroidina pseudopaciloculata (Mjatliuk)

Cystamminella pseudopaciloculata, Mjatliuk, 1966, pl. 1, figs. 5–8; pl. 2, fig. 6; pl. 3, fig. 3.

Aschemocella sp.

This species resembles *A. carpathica* (Neagu) in possessing large chambers with a relatively coarsely agglutinated wall. However, in our material we found only large fragments, which prevented us from classifying it at the species level.

Bulbobaculites problematicus (Neagu)

Ammobaculites agglutinans sp. *problematicus* Neagu, 1962.

Dorothia sp.

Test finely agglutinated, consisting of subrounded, inflated chambers arranged in trocochospiral coil, later becoming biserial. The aperture is a low interiomarginal arch, at the base of the last chamber.

Glomospira charoides (Jones and Parker)

Trochammina squamata var. *charoides* Jones and Parker, 1860, p. 304.

Glomospira glomerata (Grzybowski)

Ammodiscus glomeratus Grzybowski, 1898, pl.11, fig. 4.

Glomospira gordialis (Jones and Parker)

Trochammina squamata var. *gordialis* Jones and Parker, 1860, p. 304.

Glomospira serpens (Grzybowskii)

Ammodiscus serpens Grzybowski, 1898, pl. 11, figs. 2, 3.

Glomospirella gaultina (Berthelin)

Ammodiscus gaultinus Berthelin, 1880, pl. 1, figs. 3a,b.

Haplophragmoides suborbicularis (Grzybowski)

Cyclammina suborbicularis Grzybowski, 1896, pl. 9, figs. 5–6.

Haplophragmoides walteri (Grzybowski)

Trochammina walteri Grzybowski, 1898, pl. 11, fig. 31.

Hippocrepina depressa Vasicek, 1947, pl. 11, figs. 1, 2.

Hormosina excelsa (Dylazanka)

Hyperammina excelsa Dylazanka, 1923, pl. 1, fig. 3.

Hormosina velascoensis (Cushman)

Nodosinella velasconsis Cushman, 1926, pl. 20, fig. 9.

Hormosina sp.

Test coarsely agglutinated, composed of large subrounded chambers linked by thick connections.

Hormosinella cf. *distans* (Brady)

cf. Reophax distans Brady, 1881, p. 50.

Specimens in our material differ from typical *H. distans* in having a smaller test and finer agglutination.

Hyperammina dilatata Grzybowski, 1896, pl. 8, fig. 17.

Hyperammina sp.

Large subrounded chambers composed of a finely agglutinated, thick wall. Differs from *H. dilatata* in possessing less elongate, more regularly subrounded, instead of sack-like chambers.

Kalamopsis grzybowskii (Dylazanka)

Hyperammina grzybowskii Dylazanka, 1923, p. 65–66.

Karreriella conversa (Grzybowski)

Gaudryina conversa Grzybowski, 1901, pl. 7, figs. 15, 16.

Karrerulina sp.

A small-sized species with a variably elongate,

tapered test. The aperture is slightly produced on a short neck.

Lituotuba lituiformis (Brady)

Trochammina lituiformis Brady, 1879, pl. 5, fig. 16.

Lituotuba sp.

Test finely agglutinated with an irregularly coiled initial portion. This form resembles *Glomospira irregularis* (Grzybowski) from which it is differs in having the tendency to uncoil in the final part of the test.

Paratrochamminoides heteromorphus (Grzybowski)

Trochamminoides heteromorphus Grzybowski, 1898, pl. 11, fig. 16.

Paratrochamminoides sp.1 Kuhnt, 1990, pl. 5, figs. 12–13.

Paratrochamminoides sp.2 Kuhnt, 1990, pl. 5, figs. 14–16.

Paratrochamminoides/Trochamminoides juvenile

We place in this group small-sized specimens showing an irregular coiling of a few rounded to subrounded chambers resembling the initial portion of the test in *Trochamminoides* and *Paratrochamminoides*.

Pseudobolivina lagenaria Krasheninnikov, 1974, pl. 5, figs. 1a,b, 2c.

Pseudobolivina munda Krasheninnikov, 1973, pl. 2, figs. 10–11.

Pseudobolivina variabilis Vasicek, 1947, pl. 1, figs. 10–12.

Recurvoides nucleosus (Grzybowski)

Trochammina nucleosus Grzybowski, 1898, pl. 11, figs. 28–29.

Recurvoides sp.

Test small, streptospiral. The 5–6 visible chambers are difficult to distinguish. Specimens in our material are often deformed.

Reophax minutus Tappan, 1940, pl. 14, figs. 4a,b.

Reophax subnodulosus Grzybowski, 1898, pl. 10, figs. 17–18.

Reophax sp. 5 Kuhnt, 1990, pl. 3, fig. 11.

Rzehakina epigona (Rzehak)

Silicina epigona Rzehak, 1895, pl. 6, fig. 1.

Saccammina grzybowskii (Schubert)

Reophax grzybowskii Schubert, 1902, pl. 1, fig. 13.

Saccammina placenta (Grzybowski)

Reophax placenta Grzybowski, 1898, pl. 10, figs. 9–10.

Saccammina sphaerica Sars, 1872, p. 250.

Saccorhiza ramosa (Brady)

Hyperammina ramosa Brady, 1879, pl. 3, figs. 14–15.

Spiroplectammina dentata (Alth)

Textularia dentata Alth, 1850, pl. 13, fig. 13.

Spiroplectammina laevis (Roemer)

Textularia laevis Roemer, 1841, pl. 15, fig. 17.

Spiroplectammina spp.

We place in this group all specimens that, due to relatively bad preservation of *Spiroplectammina* in the HCl residues, could not be classified at species level.

Subreophax guttifer (Brady)

Reophax guttifer Brady, 1881, p. 49.

Subreophax pseudoscalaris (Samuel)

Reophax pseudoscalaria Samuel, 1977, pl. 3, figs. 4a,b.

Subreophax scalaris (Grzybowski)

Reophax guttifer var. *scalaria* Grzybowski, 1896, pl. 8, fig. 26.

Subreophax splendidus (Grzybowski) 1898

Reophax splendida Grzybowski, 1898, pl. 10, fig. 16.

Trochammina deformis Grzybowski, 1898, pl. 11, figs. 20–22.

Trochammina gyroidinaeformis Krasheninnikov, 1974, pl. 5, figs. 7a–c, 8a–c, 9c.

Trochamminoides dubius (Grzybowski)

Ammodiscus dubius Grzybowski, 1898, pl. 8, figs. 12, 14.

Trochamminoides septatus (Grzybowski)

Ammodiscus spetatus Grzybowski, 1898, pl. 11, fig. 1.

Trochamminoides subcoronatus (Grzybowski)

Trochammina subcoronata Grzybowski, 1896, pl. 9, figs. 3a–c.

Turritellella sp.

A tubular form characterised by a series of close convolutions whose diameter slightly increases in size giving the test a somewhat conical shape. Aperture terminal, rounded.

Uvigerinammina jankoi Majzon, 1943, pl. 2, figs. 15a,b.

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