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BIODIVERSITY OF FORAMINIFERA AND OTHER PROTISTS IN THE DEEP SEA: SCALES AND PATTERNS

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Abstract. Ocean-floor sediments harbour a variety of protistan taxa, including ciliates, flagellates, naked amoebae, testate amoebae, foraminifera and xenophyophores. Only the foraminifera and xenophyohores, however, are reasonably well studied at the species level. Despite being an important component of deep-sea communities, these protists are frequently disregarded in biodiversity studies. This is unfortunate because « live » (rose Bengal stained) foraminifera are rich in species and morphologically very diverse. Individual samples from well-oxygenated bathyal and abyssal settings may contain up to 150 and sometimes more than 200 live species (>63-µm fraction). The local diversity of foraminifera seems broadly comparable to that of nematodes among the meiofauna and polychaetes among the macrofauna. Particularly at abyssal sites, many species are undescribed and belong to poorly-known, soft-shelled taxa. Extrapolating from local to global diversity (a popular activity in biodiversity research) is hampered by lack information about species distribution patterns, particularly for the soft-shelled taxa. However, many deep-sea foraminiferal species in « normal » well-oxygenated deep-sea settings appear to be widely distributed, implying relatively modest levels of global diversity.

Trends in foraminiferal diversity in response to regional gradients of increasing organic enrichment and decreasing oxygen concentrations are fairly well described; species richness decreases, and dominance increases. Changes in foraminiferal diversity with increasing bathymetric depth down the continental slope have also been reported, but latitudinal diversity gradients remain largely undocumented among foraminifera in modern deep-sea settings. Because of their extensive fossil record, calcareous and other hard-shelled species can be used to address the influence of historical processes on large-scale diversity patterns. For example, the establishment of an Antarctic ice sheet 35 million years ago has been linked to the development of an ancient latitudinal diversity gradient among deep-sea foraminifera in the Southern Hemisphere.

Xenophyophores are much less speciose than foraminifera. It has been estimated by TENDAL (1996) that only about one hundred species, described and undescribed, exist in modern oceans. Where the two groups coexist at a single locality, there may be an order of magnitude fewer xenophyophore species than foraminiferal species. The much lower number of xenophyophore species probably reflects their larger size and narrower ecological tolerance compared to foraminifera.

Key words: Foraminifera, protist, diversity, xenophyophore, paleoceanography.

INTRODUCTION

Biodiversity embraces all aspects of biological variety, including variety at the genetic, morphological, species, higher taxon, and community levels (*e.g.* HARPER & HAWKSWORTH, 1994 ; MAY, 1994 ; WILLIAMSON, 1997). Ideas about biodiversity have been developed largely by terrestrial biologists and only fairly recently has attention been directed to marine systems (Committee on Biological Diversity in Marine Systems, 1995 ; Ormond *et al.,* 1997). Yet the seas are inhabited by more major animal groups than the land (MAY, 1994), and macrobenthic soft-bottom deep-sea communities are extremely rich in species, at least at local scales (*e.g.* HESSLER & SANDERS, 1967 ; GRASSLE & MACKIOLEK, 1992 ; GAGE, 1996 ; SMITH *et al.,* 1998). Recently, the diverse nature of the deep-sea meiobenthos, a size fraction which is difficult and laborious to study, has received emphasis (LAMBSHEAD, 1993 ; LAMBSHEAD *et al.,* 1995). The scale of deep-sea diversity is comparable to that found in such obviously heterogeneous environments as coral reefs and tropical rain forests. Given the relatively featureless appearance of much of the ocean floor, explaining this phenomenon has presented ecologists with a major challenge (GAGE, 1996 ; SMITH *et al.,* 1998). Small-scale stochastic processes, for example, species successions in response to patches of labile organic matter (GRASSLE & MORSE-PORTEOUS, 1987 ; GRASSLE & MACKIOLEK, 1992) or to hydrodynamic disturbance (GAGE, 1996, 1997), appear to be important in maintaining local diversity. However, these centimetre to metre-scale processes do not necessarily explain large-scale diversity patterns, for example in relation to bathymetric and latitudinal gradients (REX *et al.,* 1997). In the case of latitudinal diversity gradients, it seems likely that evolutionary or historical processes underlie the patterns observed.

Certain groups of organisms are particularly rich in species and therefore of special importance in biodiversity research (HAMMOND, 1994 ; MAY, 1994). Foraminifera may merit inclusion in this category. However, most foraminiferal workers are geologists, reflecting the fact that these protists are the most common deep-sea benthic organisms preserved in the fossil record. Much of the geologically-orientated research has concerned the search for proxies of parameters which are useful in paleoceanographic reconstructions (*e.g.* MURRAY, 1995), for example, bathymetry (PHLEGER, 1960), near-bottom water masses (SCHNITKER, 1980, 1994) and organic matter fluxes to the seafloor (HERGUERA & BERGER, 1991 ; CORLISS & EMERSON, 1990 ; JORISSEN *et al.,* 1995). With some exceptions (*e.g.* the work of BUZAS *et al.*, 1969, 1994 ; CULVER & BUZAS, 1998, DOUGLAS, 1981 ; DOUGLAS AND WOODRUFF, 1998), the species diversity of deep-sea foraminifera has received relatively little attention. Moreover, those studies that have been undertaken have focused on the hard-shelled component of the fauna, rather than the soft-shelled forms which constitute a major proportion of many assemblages (GOODAY, 1994, 1996 ; GOODAY *et al.,* 1998). This lack of attention contrasts with the efforts devoted by benthic ecologists to establishing patterns and scales of deep-sea metazoan diversity in relation to bathymetric, latitudinal and other environmental gradients (ETTER & GRASSLE, 1992 ; LEVIN & GAGE, 1998 ; REX *et al.,* 1997 ; SMITH *et al.,* 1998).

This paper starts with a brief survey of protistan taxa reported from the deep sea and then reviews the scale of species diversity in foraminifera and xenophyophores (a related group), spatial patterns in foraminiferal diversity, and the importance of the fossil foraminifera in diversity research. Except where stated, data refer to «live» (*i.e.* Rose Bengal stained) faunas.

PROTISTS IN THE DEEP SEA

All the main free-living protozoan groups occur in marine environments and most have been reported from the deep sea. Their size range is enormous, spanning five orders of magnitude from tiny flagellates, a few microns in length (TURLEY *et al.,* 1988; PATTERSON, 1990; ATKINS *et al.*, 1998), to xenophyophores with tests reaching >20cm in size (TENDAL, 1972). Small naked protists in deep-sea sediments (the «nanobiota») are, however, very difficult to study and therefore poorly documented (THIEL, 1983; BURNETT & THIEL, 1988).

SMALL & GROSS (1985) discovered a variety of ciliates (8 classes, 14 families, 15 genera, at least 20 species) in water and hard substrate samples from hydrothermal vents at 21°N on the East Pacific Rise. These included abundant folliculinid heterotrichs attached to artificial surfaces (VAN DOVER *et al.,* 1988). SMALL & GROSS (1985) also reported an amoeboid organism and a colonial flagellate, each possibly representing a new family, in water samples from the same area. In contrast to their abundance on hard substrates near vents, ciliates are generally rare on soft bottoms in the deep sea (BURNETT, 1977, 1979, 1981; ALONGI 1987), probably because they require interstitial space for ciliary movement (BURNETT, 1981). Instead, flagellates and amoebae dominated the eukaryotic nanobiota in the central North Pacific (5498-5800m) (BURNETT 1977; SNIDER *et al.,* 1984) and at depths around 1200m in the San Diego Trough (BURNETT, 1979, 1981) and Coral Sea (ALONGI, 1987). A barophilic bodonid flagellate was associated with phytodetritus in the abyssal NE Atlantic (LOCHTE & TURLEY, 1988; TURLEY *et al.,* 1988) and flagellates which grew faster under pressure than shallow-water strains of the same species have been reported from 2500m from a hydrothermal vent area on the East Pacific Rise (ATKINS *et al.*, 1998). Although testate amoebae are generally restricted to fresh water and nearshore habitats, a very large (up to 34mm diameter) spherical species of the genus *Gromia* (Order Filosea) has recently been discovered in the bathyal (1200-1650m) NW Arabian Sea (GOODAY *et al.,* in revision).

Apart from the observations of SMALL & GROSS (1985), there are virtually no data on the species diversity of deep-sea ciliates, flagellates and amoebae. Xenophyophores and foraminifera, the testate rhizopod taxa which form the main focus of this paper, are much better known. Xenophyophores have some distinctive «soft part» features which distinguish them from foraminifera (TENDAL, 1972). They are generally classified as a distinct higher taxon, usually a class (TENDAL, 1996). Like some foraminifera, xenophyophores have an agglutinated test. Unlike most foraminifera, all xenophyophores are either large (>500µm) or very large (>1cm, sometimes >10cm) and are confined to depths below about 500m. Foraminiferal assemblages are very speciose and often exhibit high densities in the deep sea. The gross taxonomic composition of NE Atlantic faunas has been described in a number of publications (GOODAY, 1986, 1994, 1996; GOODAY *et al.*, 1998). Soft-shelled monothalamous taxa (allogromiids, saccamminids, psammosphaerids), *Lagenammina* species, and hormosinaceans (*Leptohalysis* spp., *Reophax* spp) are important, particularly at abyssal oligotrophic sites. Hyaline calcareous taxa (e.g. rotaliids) are most common in areas (*e.g.* continental margins) with a higher food input. They typically dominate faunas in organically-enriched, oxygen-depleted settings.

THE SCALE OF DEEP-SEA FORAMINIFERAL DIVERSITY

Morphological diversity

Deep-sea foraminifera exhibit an extraordinary morphological diversity (BRADY, 1884 ; CULVER & BUZAS, 1998). At individual abyssal sites they can range from a few tens of microns up to several centimetres in size, and include forms with organic, agglutinated and calcareous tests. Common morphotypes includes spheres, flasks, various types of tube (branched or unbranched, open-ended or with a bulb-shaped initial part) and chambered tests with chambers arranged planispirally, trochospirally, or in biserial, triserial or more complex arrangements. One exclusively deep-sea taxon, the Komokiacea, displays morphologies (elaborate systems of branching tubules) not traditionally associated with foraminifera (TENDAL & HESSLER, 1977 ; SHIRES *et al.,* 1994). If test morphology and function are closely linked, then the great range of foraminiferal sizes and morphologies in the deep sea implies a corresponding diversity of ecological strategies. For example, test morphotypes can be related to preferences for particular microhabitats within the sediment profile (CORLISS, 1985 ; CORLISS & EMERSON, 1990 ; GOODAY, 1994) or to trophic strategies (JONES & CHARNOCK, 1985).

Local species diversity

Most deep-sea foraminiferal populations consist of a few common species and numerous rare ones. DOUGLAS & WOODRUFF (1981) summarise foraminiferal species richness and diversity data from bathyal and abyssal environments. Most of these earlier data relate to « total » (live plus dead) assemblages.

GOODAY *et al.* (1998) presented a summary of foraminiferal diversity measures from five sites in the bathyal (1340m) and abyssal (4545-4942m) NE Atlantic and the NW Arabian Sea (3350m). In Table 1, I report the same data in condensed form together with similar data from a bathyal site located at 412m in the core of the Arabian Sea oxygen minimum zone (OMZ). Rarefaction curves for the five sites are given in Fig. 1. Foraminiferal species richness and diversity were high in the well-oxygenated bathyal and abyssal NE Atlantic, and at the deep Arabian Sea site where oxygen levels were around 3.0ml.l^{-1}. They were much lower at the 412-m Arabian Sea site where oxygen concentrations were around 0.13ml.l^{-1}. Dominance (R1D) showed the opposite trend. It was low (generally <10%) at the abyssal sites, slightly higher (11-15%) in the bathyal Porcupine Seabight, and higher again (27-44% depending on size fraction) in the core of the Arabian Sea OMZ.

Diversity data for the foraminiferal macrofauna (>300µm) from three sites on the North Carolina Slope are also reported in Table 1 and included in Fig. 1. These sites lie along a gradient of increasing organic matter input but without corresponding oxygen depletion in the bottom water (SCHAFF *et al.*, 1992). Values for species richness and diversity measures were generally higher in both the 0-2cm and 0-15cm layers at Sites I and II compared to the organically-enriched Site III.

TABLE 1

Summary of foraminiferal diversity measures from well-oxygenated sites in the NE Atlantic (GOODAY et al., 1998), the NW Arabian Sea within (412m) and below (3350m) the oxygen minimum zone (GOODAY et al., in revision a), and the North Carolina slope (HUGHES & GOODAY unpublished). Asterisk (*) indicates that the data set consists of median values. Localities: PSB = Porcupine Seabight; PAP = Porcupine Abyssal Plain; MAP = Madeira Abyssal Plain; CVAP = Cape Verde Abyssal Plain. Other abbreviations: OMZ = oxygen minimum zone; TS = topmost sediment; N = number of specimens; S = number of species; R1D = Rank 1 dominance; SW2 = Shanon-Wiener index ($\log_2$)*;* $E(S_{100})$ *= Expected number of species in a sample of 100 specimens*

Locality	*Size fraction (µm)*	*Depth (m)*	*Layer*	*N*	*% Calc*	*S*	*R1D*	*SW2*	*Fishers α*	$E(S_{100})$
Northwest Atlantic										
*PSB	>45	1340	0-5cm	640	20.8	118	11.1	5.7	43.2	46.8
*PSB	>45	1340	0-1cm	335	26.8	89	14.6	5.4	35.4	45.5
*PAP	>63	4850	0-1cm	586	10.1	141	9.5	6.2	58.9	55.0
*PAP	>63	4850	0-10cm	1168.5	9.9	210.5	6.0	6.6	75.0	59.6
*MAP	>63	4940	0-1cm	345	14.2	108	5.2	6.2	62.4	60.0
MAP	>63	4940	0-10cm	575	9.2	158	9.4	6.4	71.9	59.5
CVAP	>63	4545	0-1cm	341	1.75	117	10.0	6.2	62.9	59.1
Northwest Arabian Sea										
Below OMZm	>63	3350	0-1cm	1282	6.2	208	5.3	2.02	67.1	61.4
Below OMZ	>125	3350	0-1cm	893	1.5	158	6.8	1.92	61.0	58.7
Core of OMZ	>63	412	TS	3647	84.9	64	27.0	0.98	8.24	18.6
Core of OMZ	>125	412	0–1cm	6188	70.7	49	44.1	1.23	9.28	23.9
North Carolina Slope										
*Site I	>300	850	0-2cm	231	3.8	53	12.1	1.50	22.14	37.3
Site I	>300	850	0-15cm	301	2.3	59	22.9	1.39	21.93	34.8
Site II	>300	850	0-2cm	286	6.4	64	12.9	1.53	25.61	39.9
Site II	>300	850	0-15cm	486	4.3	71	16.7	1.47	22.90	36.0
*Site III	>300	850	0-2cm	323	68.5	25	65.3	0.65	6.33	15.5
*Site III	>300	850	0-15cm	966	73.8	33	71.7	1.08	6.62	14.3

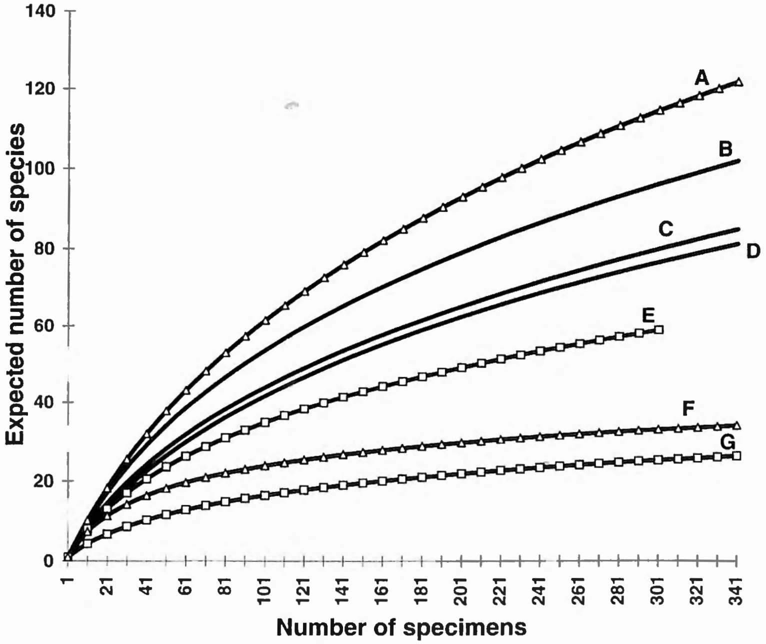

Fig. 1. – Rarefaction curves based on «live» (Rose Bengal stained) foraminifera from individual samples obtained at sites in the N. Atlantic and NW Arabian Sea. A, F are from the NW Arabian Sea, *Discovery* Stations 12687 (3350m depth) and 12692 (412m depth) respectively. B,C,D are from the Porcupine Abyssal Plain, 4840m depth, *Discovery* Station 11908#70, *Challenger* Station 54301#9 and *Discovery* Station 13077#21 respectively. E and G are from the North Carolina continental slope, 850m depth, Site I and Site III respectively of SCHAFF *et al.* (1992). Curves A and F are based on the >125µm fraction, 0–1cm layer; curves B–D on the >63µm fraction, 0–1cm layer; curves E,G on the >300µm fraction, 0–15cm layer.

The percentage of easily fossilizable calcareous foraminifera was inversely related to diversity. It was generally around 10% or less in the abyssal NE Atlantic, increased to 20-27% in the bathyal PSB, and reached 70-85% (depending on size fraction) in the core of the Arabian Sea OMZ. A similar trend was apparent among macrofaunal foraminifera on the North Carolina slope where the percentage of calcareous specimens was much lower at Sites I and II than at Site III.

Species distribution patterns

An extensive literature exists on deep-sea foraminifera and large-scale distribution patterns are well established for the better known hard-shelled species, many of which are calcareous. These sources suggest that common species typically have cosmopolitan distributions on the ocean floor (BRADY, 1884; SCHNITKER, 1980; DOUGLAS & WOODRUFF, 1981; MURRAY, 1991). As long as the environmental conditions are appropriate, the same species tend to occur, irrespective of location. GOODAY *et al.* (1998) analysed the distribution of the more abundant species which could be consistently recognised in samples from three North Atlantic abyssal plains (the Cape Verde, Madeira and Porcupine) and the 35-m Arabian Sea site. Only 17 of the 78 species were restricted to a single site, 17 occurred at all four, 20 at three and 24 at two of the sites, suggesting that many of the species occurring at these well-oxygenated localities were fairly widely distributed.

XENOPHYOPHORE SPECIES DIVERSITY

Xenophyophores are the only deep-sea protistan taxon, apart from the foraminifera, for which reliable data are available at the species level (TENDAL, 1996). This group is much less speciose than the foraminifera. Where faunas are well studied, the number of species present at a particular site is always <20. Seventeen species were recognised among about 200 specimens collected at the DISCOL site in the eastern equatorial Pacific (GOODAY & MAYBURY unpublished). At the well-studied BENGAL site on the Porcupine Abyssal Plain, careful examination of box cores collected over several years has yielded only 8 species among 87 specimens (GOODAY, unpublished). LEVIN & THOMAS (1988) recognised between 2 and 5 distinct xenophyophore morphotypes on seamounts in different areas of the east Pacific (10°-31°N). Many xenophyophore species remain undescribed, for example most of those in the DISCOL area and in the Pacific material of Levin & Thomas (1988).

SPATIAL PATTERNS OF FORAMINIFERAL SPECIES DIVERSITY

Foraminiferal diversity patterns have been described over bathymetric and latitudinal gradients, and in relation to organic enrichment and oxygen depletion. As in the case of local (α) diversity, most studies are based either on total (live + dead) modern assemblages or on fossil faunas, and concern only the hard-shelled taxa. Little is known about patterns of xenophyophore diversity in relation to environmental gradients.

Large-scale patterns

Bathymetric patterns. In general, total foraminiferal diversity appears to decrease down the continental slope and then increase again on abyssal plains (DOUGLAS & WOODRUFF, 1981). At various sites along the eastern continental margin of North America (from the Canadian Arctic to the Gulf of Mexico) diversity in core top samples reached minimum values on the upper slope and then increased downslope in a non-linear fashion (BUZAS & GIBSON, 1969; GIBSON & BUZAS, 1973; CARTER *et al.,* 1979). In BUZAS & GIBSON's (1969) data from the western North Atlantic (29-5001m), species numbers peaked at 40-50 on the outer shelf (100-200m depth) and then declined on the continental slope before increasing to values of 60-80 or more at abyssal depths (4000-5000m). The pattern was based on total (live + dead) faunas but was also evident in the live assemblage. DOUGLAS & WOODRUFF (1981) also reported that total foraminiferal diversity was higher in the abyssal (80-100 species) than in the bathyal (40-50 species) Pacific.

The opposite trend, an overall decrease in foraminiferal diversity down the continental slope, has also been described. In the NW Gulf of Mexico, species richness and diversity (Shannon-Wiener Index) declined with increasing depth below 100m (BUZAS & GIBSON, 1969), LAGOE (1976) found a depth-related decrease in species richness and Shannon-Wiener values between 1069m and 3709m in the Arctic Ocean, and CUTTER *et al.* (1994) reported no trend in values of the Shannon-Wiener Index (loge) down the continental slope off Cape Hatteras. On the bathyal California borderland, live foraminiferal diversity showed a general, slight decrease with bathymetric depth, but the pattern displayed many complexities related mainly to the distribution of oxygen-depleted basins (DOUGLAS, 1981). Walsh (in DOUGLAS & WOODRUFF, 1981) presented diversity data for live, dead, calcareous live and calcareous dead foraminiferal assemblages in replicated samples from 3200-4600m on the East Pacific Rise. The live component of the fauna showed a much stronger decrease in species richness and Shannon-Wiener Index values than the dead component, which was modified by down-slope transport of foraminiferal tests.

These observations suggest that foraminifera do not conform to the parabolic diversity pattern exhibited by metazoan macrofauna and megafauna (*e.g.*, gastropods, polychaetes and fish) on continental slopes (REX, 1981, 1983 ; REX *et al.,* 1997 ; ETTER & GRASSLE, 1992 ; PATERSON & LAMBSHEAD, 1995). Caution should be exercised, however, when comparing metazoan patterns with foraminiferal patterns based on the hard-shelled component of the fauna. Establishing bathymetric diversity trends among «complete» faunas (*i.e.* live, soft- and hard-shelled foraminifera) might be instructive, although the effort involved in such a study would be considerable.

Latitudinal patterns. The existence of latitudinal diversity patterns in the sea has been the subject of considerable debate (CLARKE, 1992). There does seem, however, to be a decline in diversity towards higher latitudes in the Northern Hemisphere, although perhaps not in the Southern Hemisphere (BREY *et al.,* 1996 ; CLARKE & CRAME, 1997 ; REX *et al.,* 1993 ; 1997).

On the basis of an extensive data set derived from literature and original sources, GIBSON & BUZAS (1973) concluded that modern foraminiferal sample (α) diversity shows a general increase from north (Canadian Arctic) to south (Gulf of Mexico) along the eastern margin of North America (0-100m and 100-1000m depth intervals). The trend, however, was not a smooth one. For example, an area to the south of Nova Scotia (~41-43°N), and sites located on deltas in the Gulf of Mexico were characterised by low diversity within the depth range 0-100m. CULVER & BUZAS (1998) examined the frequency of species occurrence (i.e. the number of localities at which a species occurs) within five regions (Pacific, Arctic, Atlantic, Gulf of Mexico, Caribbean) around North America. They found that this parameter, which is related very closely to species diversity, was higher at low latitudes (Caribbean) than at high latitudes (Arctic).

These trends were described on the continental shelf and slope. No attempt has yet been made to establish whether a latitudinal diversity gradient exists among living benthic foraminifera in truly deep-ocean settings, similar to that suggested by REX *et al.* (1993, 1997) for metazoan macrofauna. However, THOMAS & GOODAY (1996), studying Ocean

Drilling Project (ODP) cores, reported that a deep-water latitudinal gradient in foraminiferal species richness (increasing from high to low latitudes) was initiated about 36 million years ago in the Southern Hemisphere. They speculated that an increase in seasonality at high latitudes, coincident with the build-up of ice on the Antarctic continent, may have depressed foraminiferal diversity, perhaps by encouraging opportunistic species. The ODP cores yielded a few data points which suggested that the diversity gradient may persist in the modern ocean, although this question requires considerable further study. SMART & MURRAY (1995) also described diversity (Fisher α and Shannon-Wiener indices) in fossil (early to middle Miocene) foraminiferal faunas. They found that diversity was lower on Atlantic than Indian Ocean abyssal plains, but, unlike THOMAS & GOODAY (1996), they found no discernible trend in diversity with latitude.

Regional patterns in relation to organic enrichment and oxygen depletion

The interplay between food and oxygen availability is a major factor in both foraminiferal (JORISSEN *et al.,* 1995 ; DE STIGTER, 1996) and metazoan ecology (LEVIN & GAGE, 1998). Organic enrichment is typically associated with oxygen depletion in near-bottom water and sediment pore water (DIAZ & ROSENBERG, 1995). Oxygen depletion is persistent where oxygen minimum zones (OMZs) impinge on the continental slope and in some silled basins and fjords where bottom-water circulation is poor and the system is enriched with organic matter derived from natural sources or pollution (ALVE, 1995a, 1995b). Other basins are periodically flushed, sometimes seasonally, with oxygenated water, leading to cycles of oxygen depletion and renewal (BERNHARD & REIMERS, 1991). These conditions (oxygen depletion combined with organic enrichment) exert a strong influence on the species composition of foraminiferal faunas, leading to the development of distinctive assemblages dominated by taxa such as *Bolivina* d'Orbigny, 1839, *Brizalina* O.G. Costa, 1856, *Bulimina* d'Orbigny, 1826, *Cassidulina* d'Orbigny, 1826, *Epistominella* Husezima and Maruhosi, 1944, *Spiroplectammina* Cushman, 1927 and *Textularia* Defrance, 1824 (SEN GUPTA & MACHAIN-CASTILLO, 1993 ; BERNHARD *et al.,* 1997).

It is well known that these assemblages exhibit low species richness and high dominance (PHLEGER & SOUTAR, 1973 ; VAN DER ZWAAN & JORISSEN, 1991 ; SEN GUPTA & MACHAIN-CASTILLO, 1993). Few studies, however, have documented diversity parameters across gradients of organic enrichment and oxygen depletion in any detail. Data from the two Oman margin sites suggest that species richness ($E(S_{100})$) and diversity (Fisher α and Shannon-Wiener indices) are both much lower, while dominance is higher, in food-rich, low-oxygen settings (Table 1). Similar features characterise foraminiferal assemblages in the severely oxygen-depleted (O_2<0.1ml.l^{-1}) Santa Barbara Basin (BERNHARD *et al.,* 1997). However, dense, low-diversity, high-dominance assemblages are not invariably associated with oxygen-depleted bottom water, and no species is confined to these environments. Faunas from organically-enriched regions where the bottom water is well oxygenated may exhibit similar diversity characteristics and species compositions (SEN GUPTA *et al.,* 1981). This suggests that organic enrichment, rather than oxygen depletion, encourages population growth in opportunistic species, although oxygen depletion may deter less tolerant species and therefore have an impact on the number of species present in such areas (LEVIN & GAGE, 1998).

THE IMPORTANCE OF THE GEOLOGICAL RECORD

Because benthic foraminifera have a rich fossil record, particularly in the Cenozoic, they can be used to investigate historical aspects of diversity, including issues such as evolutionary diversification, ancient diversity patterns, trends in diversity over geological time scales, and changes in the geographical distribution of species. These matters are difficult or impossible to address on the basis of modern samples. This approach has been exploited to considerable effect by M.A Buzas and S.J. Culver. These authors compiled three very extensive data bases on the distribution of modern species around the North American continental margin, the world-wide stratigraphic distribution of a subset of these North American species, and a detailed study of the stratigraphic distribution and first and last occurrences of species in six Cenozoic rock formations located in a restricted area (the Salisbury-Albemarle Embayment) on the United States Atlantic coastal plain (reviewed by CULVER & BUZAS, 1998). Analyses of these data yield results which are highly relevant for studies of modern diversity. These including the following.

1) A number of the modern species which occur in all five regions around North America have no fossil record, implying that they evolved and dispersed around the continent very recently (CULVER & BUZAS, 1998). This suggests that some foraminifera attained cosmopolitan distributions very rapidly, a result with important implications for global diversity estimates (FENCHEL, 1993). Many species, however, are endemic to one particular region. These are much more likely to have no fossil record than the cosmopolitan species, implying that they also evolved very recently, but failed to disperse.

2) Detailed examination of fossil foraminiferal species present in successive Cenozoic formations indicates that local species diversity is maintained through immigration from a regional species pool located on the Atlantic and Gulf coastal plains. However, which species immigrate into an unoccupied neritic area, in this case following a marine transgression, seems to be largely unpredictable and to depend on chance dispersals of individual species from the regional pool rather than the reassembly of a unified community (BUZAS & CULVER, 1994). This geological perspective is relevant to the question of how local and regional species pools interact (CORNELL, 1995).

Buzas and Culver studied shallow-water (neretic) habitats. Their approach may be less applicable in ocean-floor settings where barriers to dispersion, particularly at abyssal depths, are fewer and endemism likely to be less pronounced (GRASSLE & MORSE-PORTEOUS, 1987; GRASSLE & MACKIOLEK, 1992). Studies of foraminiferal and other microfossils through geological time are, however, potentially important for understanding the historical and evolutionary processes that help to shape modern large-scale diversity patterns in the deep sea (REX *et al.,* 1997). For example, they might provide a test of the hypothesis that species tend to evolve in bathyal systems and then invade abyssal environments (ETTER & REX, 1990; REX & ETTER, 1998). In the above-mentioned study of Thomas & Gooday (1996), data from ODP cores revealed that the development of a latitudinal diversity gradient in the Southern Hemisphere was coincident with the onset of Antarctic glaciation. CRONIN & RAYMO (1997) demonstrated a link between regular fluctuations in deep-sea ostracod diversity (Shannon-Wiener Index) and Quaternary glacialinterglacial cycles. These examples demonstrate that the geological record can yield information on deep-sea diversity trends in relation to changing environmental conditions over time scales of thousands of years.

DISCUSSION

Species concepts in foraminifera

Almost all foraminiferal species and genera are recognised on the basis of test morphology, structure and composition. Analysis of ribosomal DNA sequences has recently made it possible to separate some morphologically very similar species (Pawlowski *et al.*, 1995), but this approach is not generally applicable, and particularly not to deep-sea foraminifera. Thus, most foraminiferal species are, in effect, morphospecies. Many of those recognised in deep-sea samples are undescribed «working» morphospecies. Foraminifera are able to reproduce asexually, and Murray (1991) has suggested that this mode of reproduction is particularly prevalent among deep-sea species. Thus, as in the case of many inbreeding or asexual, free-living ciliates (Findlay *et al.*, 1996a), it may be inappropriate (as well as practically impossible) to apply biological species concepts to deep-sea foraminifera.

Why are foraminifera much more diverse than xenophyophores?

Foraminiferal species are much more numerous than xenophyophore species at both local and global scales. On the Porcupine Abyssal Plain, only eight xenophyophore species have been recognised in numerous box cores compared to as many as 150 foraminiferal species present in a single sample. Since there are rarely more than ten xenophyophore species at any single locality (an area which may cover $10 km^2$ or more), this level of disparity in species numbers is probably fairly typical. Tendal (1996) estimated the total number of xenophyophore species, described and undescribed, at around 100. It is difficult to even guess at the corresponding number of deep-sea foraminiferal species, but the figure is likely to be at least two orders of magnitude higher (note that >200 foraminiferal species >63μm were present in $25.5 cm^3$ of sediment from one of the sites studied by Gooday *et al.*, 1998).

The relatively small number of xenophyophore species compared to foraminiferal species present at any particular locality must reflect the much greater test size of most xenophyophores. May (1988) showed that, within a particular taxonomic group, smaller size classes contain more species than larger size classes. As Fenchel (1993) and Findlay *et al.* (1996b) argue, however, this is not necessarily true at global scales since small species (e.g. ciliates and other protozoa) are more likely to be cosmopolitan than large species. Although some xenophyophores such as *Syringammina fragilis* (which occurs in New Zealand and Scottish waters; Tendal, 1972, 1981) are widely distributed, there does appear to be a tendency towards endemicity within the group. For example, the Atlantic and Pacific faunas are rather distinct (Gooday & Tendal, 1988). One xenophyophore order (Stannomida) is abundant in parts of the Pacific but virtually absent in the Atlantic

(TENDAL, 1972, 1980, 1996). Many deep-sea foraminifera, on the other hand, occur widely at abyssal depths (GOODAY *et al.,* 1998). There may therefore be some additional factors which account for the low number of xenophyophore species compared to the undoubtedly much larger, but unquantified, total for deep-sea foraminifera.

In addition to occupying a much larger size range, foraminifera possess a greater variety of wall types (organic, agglutinated, calcareous) than xenophyophores which, with a few exceptions, construct agglutinated tests. Xenophyophores also have a peculiar but very consistent internal organisation consisting of a branching protoplasmic strand, enclosed within an organic tube system and closely associated with branching, string-like stercomata masses. This may impose ecological constraints on, for example, trophic mechanisms. Xenophyophores are most common in relatively food-rich regions, although they do occur in more oligotrophic areas as well (TENDAL, 1972 ; LEVIN & GOODAY, 1992). They seem to have narrower ecological tolerances than foraminifera and have not been reported in highly energetic (GAGE, 1997) or low-oxygen (O_2<0.2ml/l) areas (LEVIN & GOODAY, 1992). Together with factors associated with size differences, these structural and ecological factors may explain why foraminifera are more diverse than xenophyophores at global as well as at local scales.

How does protistan diversity compare with metazoan diversity in the deep sea?

Megafauna. As indicated above, the number of xenophyophore species present at any one locality ranges from 1 to <20. This is similar to the numbers of species belonging to deep-sea megafaunal groups such as the holothurians. At the PAP site, 16 holothurian species have been recorded (BILLETT pers. comm.) compared to 8 xenophyophore species. According to HANSEN (1975), the total number of described holothurian species in the deep sea is 380, and the total number belonging to the Order Elasipoda is about 171, compared to TENDAL's (1972) estimate of 100 described and undescribed xenophyophore species.

Macrofauna. GOODAY *et al.* (1998, p. 192) suggested that macrofaunal foraminifera (>500-µm size fraction) « are as speciose as metazoan taxa such as polychaetes, bivalves and isopods, but that, as a result of their much greater abundance, they may be less diverse when numbers are normalised by rarefaction ». Recently, PATERSON *et al.* (1998) recognised 101 polychaete species among 427 specimens recovered from 5 box-core samples (>300-µm fraction, 0-5cm depth) obtained at the BENGAL Porcupine Abyssal Plain (PAP) site in the NE Atlantic. By comparison, 100 and 123 large foraminiferal species were found among, respectively, 1501 and 4061 complete specimens sorted from two box-core samples (>500-µm fraction, 0-1cm depth) taken at the same site (GOODAY *et al.,* 1998). Values of $E(S_{100})$ for the polychaetes are around 44 (from PATERSON *et al.,* 1998, fig. 5a) compared to 35.5 and 29.3 for the foraminifera. These data therefore tend to support the conclusions of Gooday *et al.* (1998), although the comparison is blurred by the lack of comparability between size fractions and depth horizons. Thus, partly as a result of their sheer numerical abundance, foraminifera make a substantial contribution to macrofaunal species richness at this site and probably elsewhere in the deep sea (TENDAL & HESSLER, 1977).

Meiofauna. Nematodes dominate the deep-sea metazoan meiofauna numerically (VINCX *et al.,* 1994) and are a highly diverse taxon (LAMBSHEAD, 1993). Single samples may contain over 100 species with the most abundant species usually representing <10% of the population (Tietjen, 1989). Dinet & Viviers (1979) recognised 50, 115 and 84 species at 4216m, 4220-4225m and 4700-4725m in the Bay of Biscay; corresponding specimen numbers were 105, 190 and 190 respectively. At the PAP site, numbers of nematode species in multicore samples (25.5cm^2 area, 0-1cm depth; >45-µm fraction) varied from 35 (59 specimens) to 71 (338 specimens) per core compared to 131-153 (499-651 specimens) foraminiferal species per core (>63-µm fraction) (Gooday *et al.,* 1998). On the Madeira Abyssal Plain, nematode species numbers varied from 25 (53 specimens) to 49 (187 specimens) compared to 100 (290 specimens) to 149 (405 specimens) foraminiferal species.

To summarise, the very limited available data (most of it from the PAP), suggest that foraminiferal species richness is comparable to that of polychaetes in the macrofaunal size range and comparable to or rather greater than that of nematode in the meiofaunal size range.

Is diversity related to phylogeny?

Recent molecular evidence suggests that foraminifera branch close to the plasmodial and cellular slime moulds near the middle of the eukaryotic tree (Pawlowski *et al.,* 1994). Foraminifera and metazoans are therefore phylogenetically distant as well as being structurally very different (unicellular vs multicellular). Nevertheless, locally (for example, in samples taken at one site), foraminifera and metazoan taxa such as polychaetes and nematodes, exhibit similar levels of species richness and diversity in the deep sea. They also display similar population responses to organic-enrichment and oxygen-depletion gradients (albeit possibly not bathymetric gradients). As far as local (α) diversity is concerned, the answer to the question posed above appears to be « no ».

There are, however, some important differences between foraminifera and metazoans. As mentioned above, foraminifera, unlike most metazoans (but like other protistan groups such as ciliates), can reproduce asexually and this may allow rare species to persist. It may also explain the extraordinary geological longevity of some foraminiferal species; for example, >35 million years in the case of *Epistominella exigua* (Brady, 1884) and *Alabaminella weddellensis* (Earland, 1936) (Thomas & Gooday, 1996), compared to an estimated average lifespan of 5-10 million years for most marine invertebrates (May *et al.,* 1995). Another important consideration is that many deep-sea foraminifera are widely distributed (Gooday *et al.*, 1998) and occur wherever conditions are suitable. In this respect, they again resemble ciliates and other protistan groups (Fenchel, 1993; Findlay, 1998; Findlay *et al.*, 1996b; 1998). Thus, the total number of foraminiferal species in the deep sea is likely to be much lower than recent estimates of the global numbers of macroinfaunal ($1x10^7$) and nematode species ($1x10^8$) in ocean-floor sediments (Grassle & Mackiolek, 1992; Lambshead, 1993).

SOME QUESTIONS AND FUTURE DIRECTIONS

Foraminifera are commonly disregarded by biologists investigating deep-sea biodiversity (species diversity). At the same time, geologists, who are at the forefront of research into deep-sea foraminiferal ecology, are (understandably, and with some notable exceptions) more concerned with developing proxies for use in palaeoceanographic reconstructions than in determining scales and patterns of foraminiferal diversity. Nevertheless, foraminifera clearly represent an important and highly diverse component of the deep-sea benthos and one which should be incorporated into assessments of biodiversity on the ocean floor.

The following problems and questions are among those that need to be addressed in order to improve understanding of the scale and pattern of foraminiferal diversity in ocean-floor sediments.

1) Deep-sea foraminiferal assemblages incorporate a substantial pool of undescribed species, many of them belonging to poorly-known, soft-walled taxa. A wider recognition of these organisms will only come about if effort is devoted to the description of new species.

2) In order to estimate the global scale of foraminiferal diversity, it is important to establish the distributional ranges of species. Are cosmopolitan distributions really more prevalent among deep-sea species than they are in shallow water? Calcareous foraminifera, which are better known taxonomically than other meiofaunal groups in the deep sea, are well suited to an analysis of these patterns.

3) Information is required about large-scale trends in foraminiferal diversity. Does a latitudinal gradient exist among modern deep-sea foraminifera, similar to that reported for fossil foraminifera and modern macrofauna? Do bathymetric trends in foraminiferal diversity down the continental slope differ fundamentally from the parabolic patterns exhibited by metazoan taxa, and if so why?

4) Are the patterns and scales of foraminiferal diversity (both local and global) similar to those reported for metazoans? Or are they more similar to those of other protists such as free-living ciliates?

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