plankton and passive dispersal. The latter is made possible by adaptations to suspension feed during an extended period in the plankton. It is likely that most aggregated groups of epifaunal organisms are formed during larval settlement, but the precise behavioral mechanisms also need further study.

Benthic boundary layer adaptations of juvenile and adult life fall into the following groups:

- food collection from seston in sea water;
- resistance to the shear stresses that tend to dislodge macrofauna; and
- the building of epifaunal tubes.

Adaptations for collecting seston may have arisen in a local population to allow them to colonize or adapt to changing flow environments. Estimates of the physiological cost of operating the bivalve ciliary pump to suspension feed have been made and suggest that they are small – less than 2% of the overall energy budget. Nevertheless, the ontogenetic cost of constructing and maintaining the inline ciliary pump in the trophic fluid transport system of a bivalve must be high. To date, there do not appear to be any studies that have investigated this latter possibility.

Shear forces that try to dislodge epifauna are resisted by adaptations that include adhesives, skeletal strengthening, developing an elastic body deformation capability, and behavioral adaptations. The latter often involve changing the orientation of the body to minimize drag and lift forces.

For the few species of tube builders studied, the adaptations found seem linked to optimizing seston feeding where the quality is best. Tube building may be regarded as an extended phenotypic expression from genes that control the complex innate behavior involved in cementing sedimentary particles together. The type of sedimentary particle selected, as well as the shape and size of the tube constructed, can usually be used to identify the organism that created them.

See also

Turbulence in the Benthic Boundary Layer.

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BENTHIC FORAMINIFERA

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Introduction

Foraminifera are enormously successful organisms and a dominant deep-sea life form. These amoeboid protists are characterized by a netlike (granuloreticulate) system of pseudopodia and a life cycle that is often complex but typically involves an alternation of sexual and asexual generations. The most obvious characteristic of foraminifera is the presence of a shell or 'test' that largely encloses the cytoplasmic body and is composed of one or more chambers. In some groups, the test is constructed from foreign particles (e.g., mineral grains, sponge spicules, shells of other foraminifera) stuck together ('agglutinated') by an organic or calcareous/organic cement. In others, it is composed of calcium carbonate (usually calcite, occasionally aragonite) or organic material secreted by the organism itself.

Although the test forms the basis of foraminiferal classification, and is the only structure to survive fossilization, the cell body is equally remarkable and important. It gives rise to the complex, highly mobile, and pervasive network of granuloreticulose pseudopodia. These versatile organelles perform a variety of functions (locomotion, food gathering, test construction, and respiration) that are probably fundamental to the ecological success of foraminifera in marine environments.

As well as being an important component of modern deep-sea communities, foraminifera have an outstandingly good fossil record and are studied intensively by geologists. Much of their research uses knowledge of modern faunas to interpret fossil assemblages. The study of deep-sea benthic foramini-fera, therefore, lies at the interface between biology and geology. This articles addresses both these facets.

History of Study

Benthic foraminifera attracted the attention of some pioneer deep-sea biologists in the late 1860s. The monograph of H.B. Brady, published in 1884 and based on material collected in the *Challenger* round-the-world expedition of 1872–76, still underpins our knowledge of the group. Later biological expeditions added to this knowledge. For much of the 1900s, however, the study of deep-sea foraminifera was conducted largely by geologists, notably J.A. Cushman, F.B. Phleger, and their students, who amassed an extensive literature dealing with the taxonomy and distribution of calcareous and other hard-shelled taxa. In recent decades, the emphasis has shifted toward the use of benthic species in paleoceanographic reconstructions. Interest in deep-sea foraminifera has also increased among biologists since the 1970s, stimulated in part by the description of the Komokiacea, a superfamily of delicate, soft-shelled foraminifera, by O.S. Tendal and R.R. Hessler. This exclusively deep-sea taxon is a dominant component of the macrofauna in some abyssal regions.

Morphological and Taxonomic Diversity

Foraminifera are relatively large protists. Their tests range from simple agglutinated spheres a few tens of micrometers in diameter to those of giant tubular species that reach lengths of 10 cm or more. However, most are a few hundred micrometers in size. They exhibit an extraordinary range of morphologies (**Figures 1** and **2**), including spheres, flasks, various types of branched or unbranched tubes, and chambers arranged in linear, biserial, triserial, or coiled (spiral) patterns. In most species, the test has an aperture that assumes a variety of forms and is sometimes associated with a toothlike structure. The komokiaceans display morphologies not traditionally associated with the foraminifera. The test forms a treelike, bushlike, spherical, or lumpish body that consists of a complex system of fine, branching tubules (**Figure 2A–C**).

The foraminifera (variously regarded as a subphylum, class, or order) are highly diverse with around 900 living genera and an estimated 10 000 described living species, in addition to large numbers of fossil taxa. Foraminiferal taxonomy is based very largely on test characteristics. Organic, agglutinated, and different kinds of calcareous wall structure serve to distinguish the main groupings (orders or suborders). At lower taxonomic levels, the nature and position of the aperture and the number, shape, and arrangement of the chambers are important.

Methodology

Qualitative deep-sea samples for foraminiferal studies are collected using nets (e.g., trawls) that are dragged across the seafloor. Much of the *Challenger* material studied by Brady was collected in this way. Modern quantitative studies, however, require the use of coring devices. The two most popular corers used in the deep sea are the box corer, which obtains a large (e.g., 0.25 m^2) sample, and the multiple corer, which collects simultaneously a battery of up to 12 smaller cores. The main advantage of the multiple corer is that it obtains the sediment–water interface in a virtually undisturbed condition.

Foraminifera are extracted from sieved sediment residues. Studies are often based on dried residues and concern 'total' assemblages (i.e. including both live and dead individuals). To distinguish individuals that were living at the time of collection from dead tests, it is necessary to preserve sediment samples in either alcohol or formalin and then stain them with rose Bengal solution. This colors the cytoplasm red and is most obvious when residues are examined in water. Stained assemblages provide a snapshot of the foraminifera that were living when the samples were collected. Since the live assemblage varies in both time and space, it is also instructive to examine the dead assemblage that provides an averaged view of the foraminiferal fauna. Deep-sea foraminiferal assemblages are typically very diverse and therefore faunal data are often condensed mathematically by using multivariate approaches such as principal components or factor analysis.

The mesh size of the sieve strongly influences the species composition of the foraminiferal assemblage retained. Most deep-sea studies have been based on > 63 μm, 125 μm, 150 μm, 250 μm, or even 500 μm meshes. In recent years, the use of a fine 63 μm mesh has become more prevalent with the realization that some small but important species

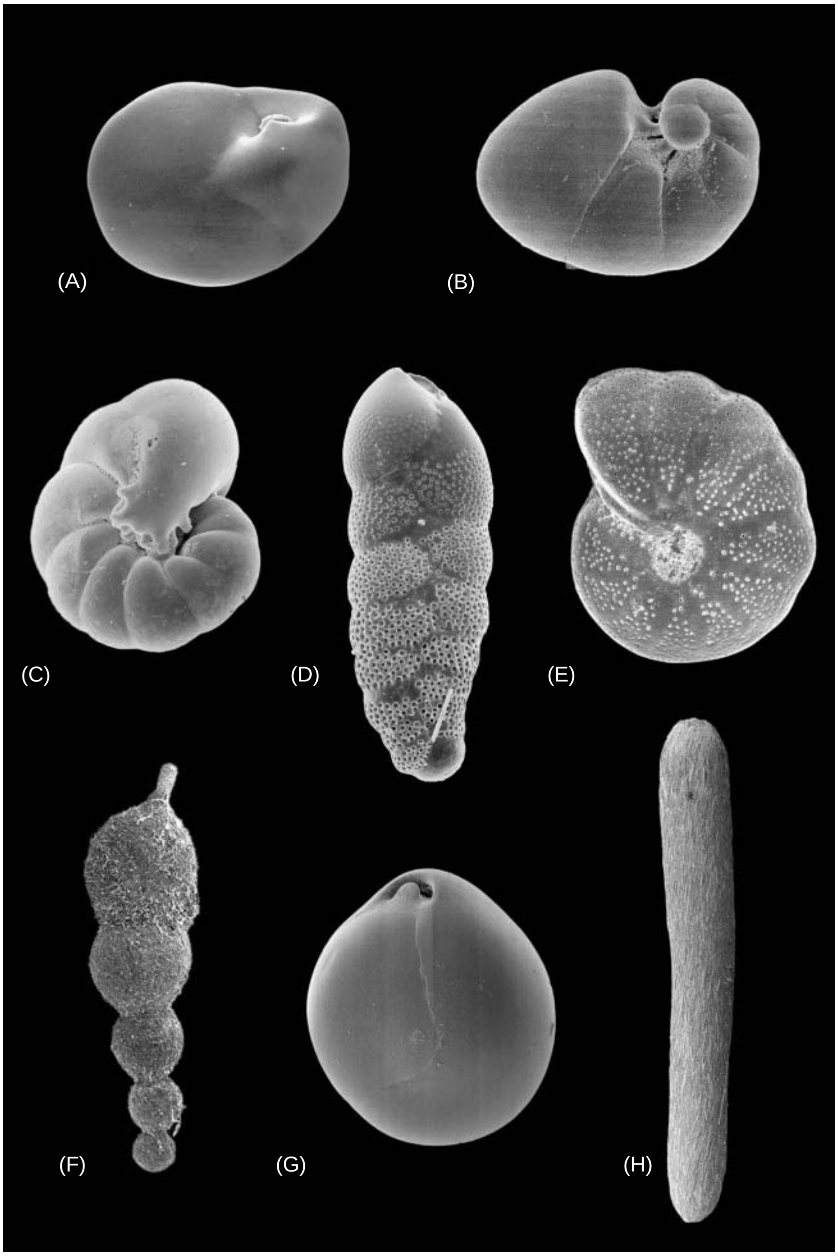

Figure 1 Scanning electron micrographs of selected deep-sea foraminifera (maximum dimensions are given in parentheses). (A) *Epistominella exigua*; 4850 m water depth, Porcupine Abyssal Plain, NE Atlantic (190 μm). (B) *Nonionella iridea*; 1345 m depth, Porcupine Seabight, NE Atlantic (110 μm). (C) *Nonionella stella*; 550 m depth, Santa Barbara Basin, California Borderland (220 μm). (D) *Brizalina tumida*; 550 m depth, Santa Barbara Basin, California Borderland (680 μm). (E) *Melonis barleaanum*; 1345 m depth, Porcupine Seabight, NE Atlantic (450 μm). (F) *Hormosina* sp., 4495 m depth, Porcupine Abyssal Plain (1.5 mm). (G) *Pyrgoella* sp.; 4550 m depth, foothills of Mid-Atlantic Ridge (620 μm). (H) *Technitella legumen;* 997–1037 m depth, NW African margin (8 mm). (A)–(E) and (G) have calcareous tests, (F) and (H) have agglutinated tests. (C) and (D), photographs courtesy of Joan Bernhard.

are not adequately retained by coarser sieves. However, the additional information gained by examining fine fractions must be weighed against the considerable time and effort required to sort foraminifera from them.

Ecology

Abundance and Diversity

Foraminifera typically make up $> 50\%$ of the soft-bottom, deep-sea meiofauna (**Table 1**). They are

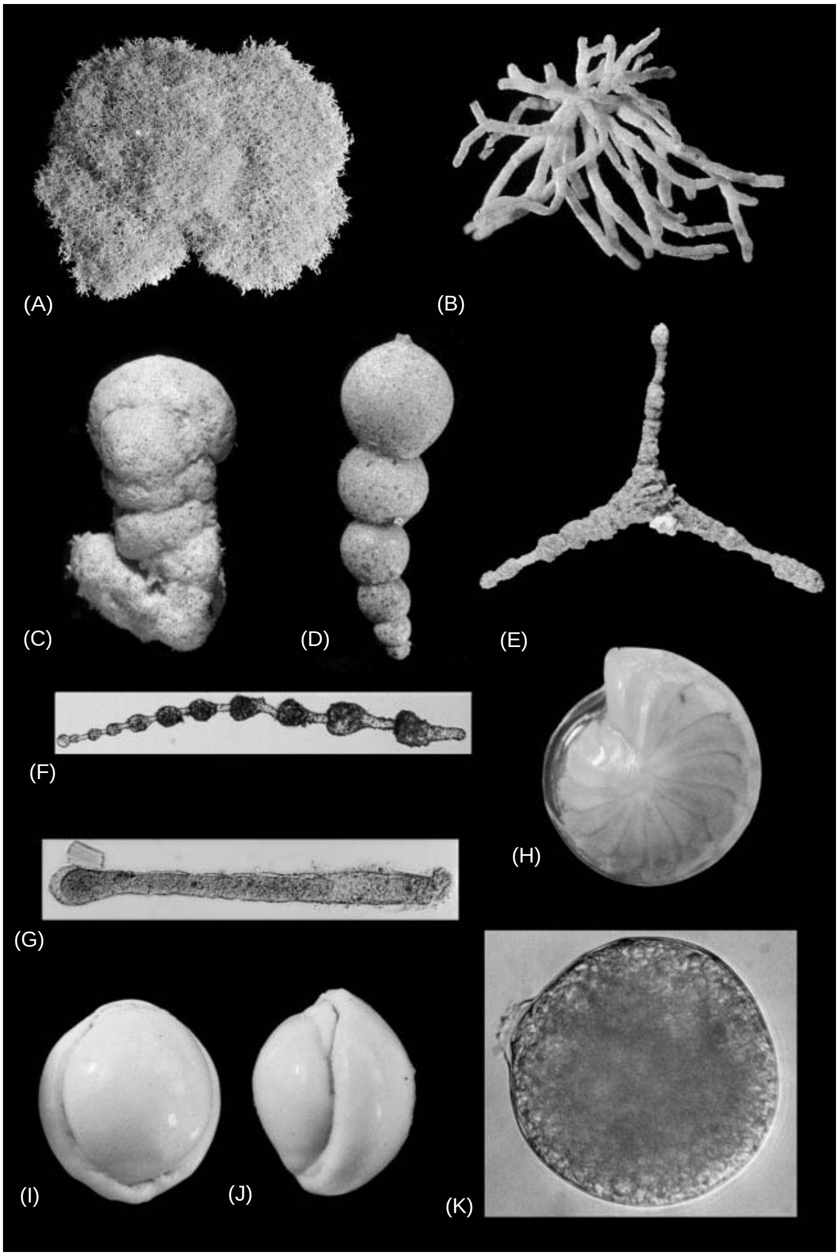

Figure 2 Light micrographs of deep-sea foraminifera (maximum dimensions are given in parentheses). (A) Species of *Lana* in which pad-like test consists of tightly meshed system of fine tubules; 5432 m water depth, Great Meteor East region, NE Atlantic (7.4 mm). (B) *Septuma* sp.; same locality (2 mm). (C) *Edgertonia* mudball; same locality (3.8 mm). (D) *Hormosina globulifera*; 4004 m depth, NW African margin (6.4 mm). (E) *Rhabdammina parabyssorum*; 3392 m depth, Oman margin, NW Arabian Sea (18 mm). (F) *Leptohalysis* sp.; 3400 m depth, Oman margin, NW Arabian Sea (520 μm). (G) Minute species of *Hyperammina*; 3400 m depth, Oman margin, NW Arabian Sea (400 μm). (H) *Lenticularia* sp.; 997–1037 m depth, NW African margin (2.5 mm). (I, J) *Biloculinella* sp.; 4004 m depth, NW African margin (3 mm). (K) Spherical allogromiid; 3400 m depth, Oman margin, NW Arabian Sea (105 μm). Specimens illustrated in (A)–(G) have agglutinated tests, in (H)–(J) calcareous tests and in (K) an organic test. (A)–(C) belong to the superfamily Komokiacea.

Table 1 The percentage contribution of foraminifera to the deep-sea meiofauna at sites where bottom water is well oxygenated

Area	*Depth (m)*	*Percentage of foraminifera*	*Number of samples*
NW Atlantic			
Off North Carolina	500–2500	11.0–90.4	14
Off North Carolina	400–4000	7.6–85.9	28
Off Martha's Vineyard	146–567	3.4–10.6	4
NE Atlantic			
Porcupine Seabight	1345	47.0–59.2	8
Porcupine Abyssal Plain[a]	4850	61.8–76.3	3
Madeira Abyssal Plain[a]	4950	61.4–76.1	3
Cape Verde Abyssal Plain[a]	4550	70.2	1
Off Mauretania	250–4250	4–27	26
46°N, 16–17°W	4000–4800	0.5–8.3	9
Indian Ocean			
NW Arabian Sea[b]	3350	54.4	1
Pacific			
Western Pacific	2000–6000	36.0–69.3	11
Central North Pacific	5821–5874	49.5	2
Arctic	1000–2600	14.5–84.1	74
Southern Ocean	1661–1680	2.2–23.7	2

[a] Data from Gooday AJ (1996) Epifaunal and shallow infaunal foraminiferal communities at three abyssal NE Atlantic sites subject to differing phytodetritus input regimes. *Deep-Sea Research I* 43: 1395–1421.

[b] Data from Gooday AJ, Bernhard JM, Levin LA and Suhr SB (2000) Foraminifera in the Arabian Sea oxygen minimum zone and other oxygen-deficient settings: taxonomic composition, diversity, and relation to metazoan faunas. *Deep-Sea Research II* 47: 25–54.

Based on Gooday AJ (1986) Meiofaunal foraminiferans from the bathyal Porcupine Seabight (northeast Atlantic): size structure, standing stock, taxonomic composition, species diversity and vertical distribution in the sediment. *Deep-Sea Research* 35: 1345–1373; with permission from Elsevier Science.

also often a major component of the macrofauna. In the central North Pacific, for example, foraminifera (mainly komokiaceans) outnumber all metazoans combined by at least an order of magnitude. A few species are large enough to be easily visible to the unaided eye and constitute part of the megafauna. These include the tubular species *Bathysiphon filiformis*, which is sometimes abundant on continental slopes (**Figure 3**). Some xenophyophores, agglutinated protists that are probably closely related to the foraminifera, are even larger (up to 24 cm maximum dimension!). These giant protists may dominate the megafauna in regions of sloped topography (e.g., seamounts) or high surface productivity. In well-oxygenated areas of the deep-seafloor, foraminiferal assemblages are very species rich, with well over 100 species occurring in relatively small volumes of surface sediment (**Figure 4**). Many are undescribed delicate, soft-shelled forms. There is an urgent need to describe at least some of these species as a step toward estimating global levels of deep-sea species diversity. The common species are often widely distributed, particularly at abyssal depths, although endemic species undoubtedly also occur.

Foraminifera are also a dominant constituent of deep-sea hard-substrate communities. Dense populations encrust the surfaces of manganese nodules as well as experimental settlement plates deployed on the sea floor for periods of months. They include various undescribed matlike taxa and branched tubular forms, as well as a variety of small coiled agglutinated species (many in the superfamily Trochamminacea), and calcareous forms.

Role in Benthic Communities

The abundance of foraminifera suggests that they play an important ecological role in deep-sea communities, although many aspects of this role remain poorly understood. One of the defining features of these protists, their highly mobile and pervasive pseudopodial net, enables them to gather food particles very efficiently. As a group, foraminifera exhibit a wide variety of trophic mechanisms (e.g.,

Figure 3 *Bathysiphon filiformis,* a large tubular agglutinated foraminifer, photographed from the Johnson Sealink submersible on the North Carolina continental slope (850 m water depth). The tubes reach a maximum length of about 10 cm. (Photograph courtesy of Lisa Levin.)

suspension feeding, deposit feeding, parasitism, symbiosis) and diets (herbivory, carnivory, detritus feeding, use of dissolved organic matter). Many deep-sea species appear to feed at a low trophic level on organic detritus, sediment particles, and bacteria. Foraminifera are prey, in turn, for specialist deep-sea predators (scaphopod mollusks and certain asellote isopods), and also ingested (probably incidentally) in large numbers by surface deposit feeders such as holothurians. They may therefore provide a link between lower and higher levels of deep-sea food webs.

Some deep-sea foraminifera exhibit opportunistic characteristics – rapid reproduction and population growth responses to episodic food inputs. Well-known examples are *Epistominella exigua, Alabaminella weddellensis* and *Eponides pusillus*. These small (generally $< 200\ \mu m$), calcareous species feed on fresh algal detritus ('phytodetritus') that sinks through the water column to the deep-ocean floor after the spring bloom (a seasonal burst of phytoplankton primary production that occurs most strongly in temperate latitudes). Utilizing energy from this labile food source, they reproduce rapidly to build up large populations that then decline when their ephemeral food source has been consumed. Moreover, certain large foraminifera can reduce their metabolism or consume cytoplasmic reserves when food is scarce, and then rapidly increase their metabolic rate when food again becomes available. These characteristics, together with the sheer abundance of foraminifera, suggest that their role in the cycling of organic carbon on the deep-seafloor is very significant.

The tests of large foraminifera are an important source of environmental heterogeneity in the deep sea, providing habitats and attachment substrates for other foraminifera and metazoans. Mobile infaunal species bioturbate the sediment as they move through it. Conversely, the pseudopodial systems of foraminifera may help to bind together and stabilize deep-sea sediments, although this has not yet been clearly demonstrated.

Microhabitats and Temporal Variability

Like many smaller organisms, foraminifera reside above, on and within deep-sea sediments. Various factors influence their overall distribution pattern within the sediment profile, but food availability and geochemical (redox) gradients are probably the most important. In oligotrophic regions, the flux of organic matter (food) to the seafloor is low and most foraminifera live on or near the sediment surface where food is concentrated. At the other extreme, in eutrophic regions, the high organic-matter flux causes pore water oxygen concentrations to decrease rapidly with depth into the sediment,

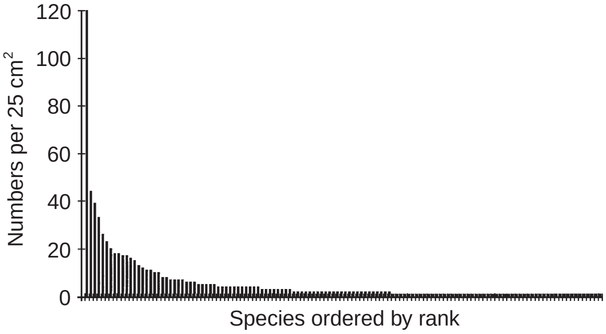

Figure 4 Deep-sea foraminiferal diversity: all species from a single multiple corer sample collected at the Porcupine Abyssal Plain, NE Atlantic (4850 m water depth), ranked by abundance. Each bar represents one 'live' (rose Bengal-stained) species. The sample was 25.5 cm^2 surface area, 0–1 cm depth, and sieved on a 63 μm mesh sieve. It contained 705 'live' specimens and 130 species.

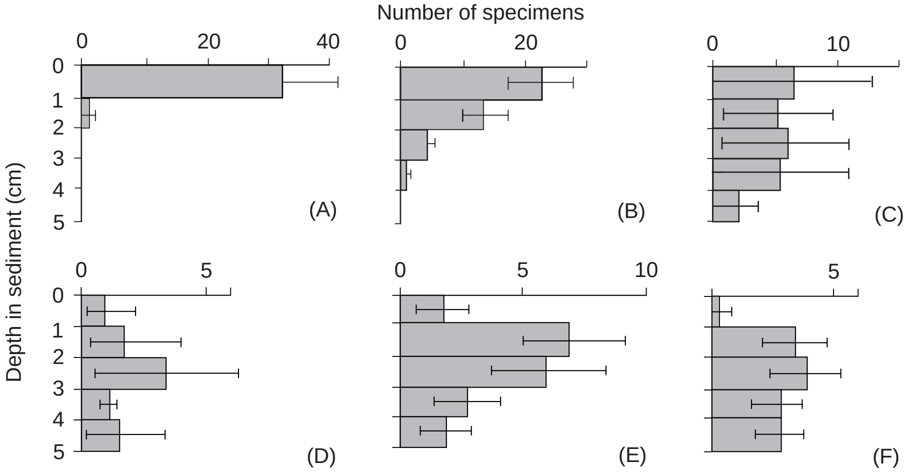

Figure 5 Vertical distribution patterns within the top 5 cm of sediment of common foraminiferal species ('live', rose Bengal-stained specimens) in the Porcupine Seabight, NW Atlantic (51°36′N, 13°00′W; 1345 m water depth). Based on >63 μm sieve fraction. (A) *Ovammina* sp. (mean of 20 samples). (B) *Nonionella iridea* (20 samples). (C) *Leptohalysis* aff. *catenata* (7 samples). (D) *Melonis barleeanum* (9 samples). (E) *Haplophragmoides bradyi* (19 samples). (F) '*Turritellella' laevigata* (21 samples). (Amended and reprinted from Gooday AJ (1986) Meiofaunal foraminiferans from the bathyal Porcupine Seabight (northeast Atlantic): size structure, standing stock, taxonomic composition, species diversity and vertical distribution in the sediment. *Deep-Sea Research* 35: 1345–1373; permission from Elsevier Science.)

restricting access to the deeper layers to those species that can tolerate low oxygen levels. Foraminifera penetrate most deeply into the sediment where organic inputs are of intermediate intensity and the availability of food and oxygen within the sediment is well balanced.

Underlying these patterns are the distributions of individual species. Foraminifera occupy more or less distinct zones or microenvironments ('microhabitats'). For descriptive purposes, it is useful to recognize a number of different microhabitats: epifaunal and shallow infaunal for species living close to the sediment surface (upper 2 cm); intermediate infaunal for species living between about 1 cm and 4 cm (**Figure 5**); and deep infaunal for species that occur at depths down to 10 cm or more (**Figure 6**). A few deep-water foraminifera, including the well-known calcareous species *Cibicidoides wuellerstorfi*, occur on hard substrates (e.g., stones) that are raised above the sediment–water interface (elevated epi-

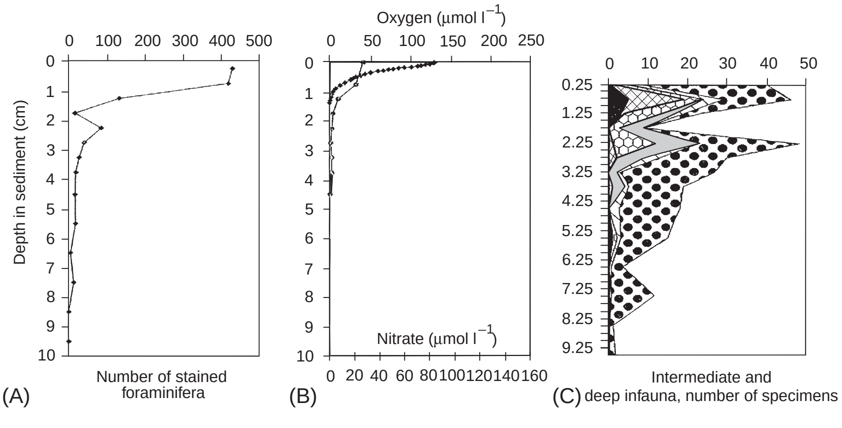

Figure 6 Vertical distribution of (A) total 'live' (rose Bengal-stained) foraminifera), (B) pore water oxygen and nitrate concentrations, and (C) intermediate and deep infaunal foraminiferal species within the top 10 cm of sediment on the north-west African margin (21°28.8′N, 17°57.2′W, 1195 m). All foraminiferal counts based on >150 μm sieve fraction, standardized to a 34 cm^3 volume. Species are indicated as follows: *Pullenia salisburyi* (black), *Melonis barleeanum* (crossed pattern), *Chilostomella oolina* (honeycomb pattern), *Fursenkoina mexicana* (grey), *Globobulimina pyrula* (diagonal lines), *Bulimina marginata* (large dotted pattern). (Adopted and reprinted from Jorissen FJ, Wittling I, Peypouquet JP, Rabouille C and Relexans JC (1998) Live benthic foraminiferal faunas off Cape Blanc, northwest Africa: community structure and microhabitats. *Deep-Sea Research I* 45: 2157–2158; with permission from Elsevier Science.)

faunal microhabitat). There is a general relation between test morphotypes and microhabitat preferences. Epifaunal and shallow infaunal species are often trochospiral with large pores opening on the spiral side of the test; infaunal species tend to be planispiral, spherical, or ovate with small, evenly distributed pores. It is important to appreciate that foraminiferal microhabitats are by no means fixed. They may vary between sites and over time and are modified by the burrowing activities of macrofauna. Foraminiferal microhabitats should therefore be regarded as dynamic rather than static. This tendency is most pronounced in shallow-water settings where environmental conditions are more changeable and macrofaunal activity is more intense than in the deep sea.

The microhabitats occupied by species reflect the same factors that constrain the overall distribution patterns of foraminifera within the sediment. Epifaunal and shallow infaunal species cannot tolerate low oxygen concentrations and also require a diet of relatively fresh organic matter. Deep infaunal foraminifera are less opportunistic but are more tolerant of oxygen depletion than are species living close to the sediment–water interface (**Figure 6**). It has been suggested that species of genera such as *Globobulimina* may consume either sulfate-reducing bacteria or labile organic matter released by the metabolic activities of these bacteria. These species move closer to the sediment surface as redox zones shift upward in the sediment under conditions of extreme oxygen depletion. Although deep-infaunal

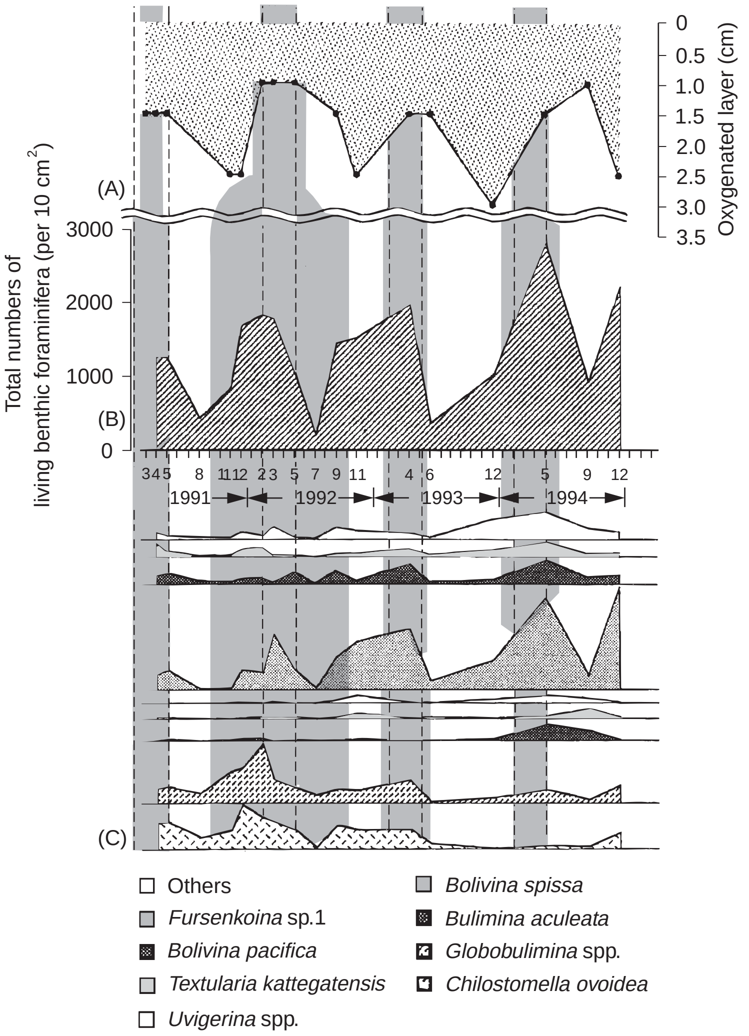

Figure 7 Seasonal changes over a 4-year period (March 1991 to December 1994) in (A) the thickness of the oxygenated layer, (B) the total population density of live benthic foraminifera, and (C) the abundances of the most common species at a 1450 m deep site in Sagami Bay, Japan. (Reprinted from Ohga T and Kitazato H (1997) Seasonal changes in bathyal foraminiferal populations in response to the flux of organic matter (Sagami Bay, Japan). *Terra Nova* 9: 33–37; with permission from Blackwell Science Ltd.)

foraminifera must endure a harsh microenvironment, they are exposed to less pressure from predators and competitors than those occupying the more densely populated surface sediments.

Deep-sea foraminifera may undergo temporal fluctuations that reflect cycles of food and oxygen availability. Changes over seasonal timescales in the abundance of species and entire assemblages have been described in continental slope settings (**Figure** 7). These changes are related to fluctuations in pore water oxygen concentrations resulting from episodic (seasonal) organic matter inputs to the seafloor. In some cases, the foraminifera migrate up and down in the sediment, tracking critical oxygen levels or redox fronts. Population fluctuations also occur in abyssal settings where food is a limiting ecological factor. In these cases, foraminiferal population dynamics reflect the seasonal availability of phytodetritus ('food'). As a result of these temporal processes, living foraminifera sampled during one season often provide an incomplete view of the live fauna as a whole.

Environmental Controls on Foraminiferal Distributions

Our understanding of the factors that control the distribution of foraminifera on the deep-ocean floor is very incomplete, yet lack of knowledge has not prevented the development of ideas. It is likely that foraminiferal distribution patterns reflect a combination of influences. The most important first-order factor is calcium carbonate dissolution. Above the carbonate compensation depth (CCD), faunas include calcareous, agglutinated, and allogromiid taxa. Below the CCD, calcareous species are almost entirely absent. At oceanwide or basinwide scales, the organic carbon flux to the seafloor (and its seasonality) and bottom-water hydrography appear to be particularly important, both above and below the CCD.

Studies conducted in the 1950s and 1960s emphasized bathymetry (water depth) as an important controlling factor. However, it soon became apparent that the bathymetric distribution of foraminiferal species beyond the shelf break is not consistent geographically. Analyses of modern assemblages in the North Atlantic, carried out in the 1970s, revealed a much closer correlation between the distribution of foraminiferal species and bottom-water masses. For example, *Cibicidoides wuellerstorfi* was linked to North Atlantic Deep Water (NADW) and *Nuttallides umbonifera* to Antarctic Bottom Water (AABW). At this time, it was difficult to explain how slight physical and chemical differences between water masses could influence foraminiferal distributions. However, recent work in the south-east Atlantic, where hydrographic contrasts are strongly developed, suggests that the distributions of certain foraminiferal species are controlled in part by the lateral advection of water masses. In the case of *N. umboniferus* there is good evidence that the main factor is the degree of undersaturation of the bottom water in calcium carbonate. This abyssal species is found typically in the carbonate-corrosive (and highly oligotrophic) environment between the calcite lysocline and the CCD, a zone that may coincide approximately with AABW. Where water masses are more poorly delineated, as in the Indian and Pacific Oceans, links with faunal distributions are less clear.

During the past 15 years, attention has focused on the impact on foraminiferal ecology of organic matter fluxes to the seafloor. The abundance of dead foraminiferal shells $> 150\ \mu m$ in size correlates well with flux values. There is also compelling evidence that the distributions of species and species associations are linked to flux intensity. Infaunal species, such as *Melonis barleeanum, Uvigerina peregrina, Chilostomella ovoidea* and *Globobulimina affinis,* predominate in organically enriched areas, e.g. beneath upwelling zones. Epifaunal species such as *Cibicidoides wuellerstorfi* and *Nuttallides umbonifera* are common in oligotrophic areas, e.g. the central oceanic abyss. In addition to flux intensity, the degree of seasonality of the food supply (i.e., whether it is pulsed or continuous) is a significant factor. *Epistominella exigua,* one of the opportunists that exploit phytodetritus, occurs in relatively oligotrophic areas where phytodetritus is deposited seasonally.

Recent analysis of a large dataset relating the relative abundance of 'live' (stained) foraminiferal assemblages in the north-east Atlantic and Arctic Oceans to flux rates to the seafloor has provided a quantitative framework for these observations. Although species are associated with a wide flux range, this range diminishes as a species become relatively more abundant and conditions become increasingly optimum for it. When dominant occurrences (i.e., where species represent a high percentages of the fauna) are plotted against flux and water depth, species fall into fields bounded by particular flux and depth values (**Figure** 8). Despite a good deal of overlap, it is possible to distinguish a series of dominant species that succeed each other bathymetrically on relatively eutrophic continental slopes and other species that dominate on the more oligotrophic abyssal plains.

Other environmental attributes undoubtedly modify the species composition of foraminiferal

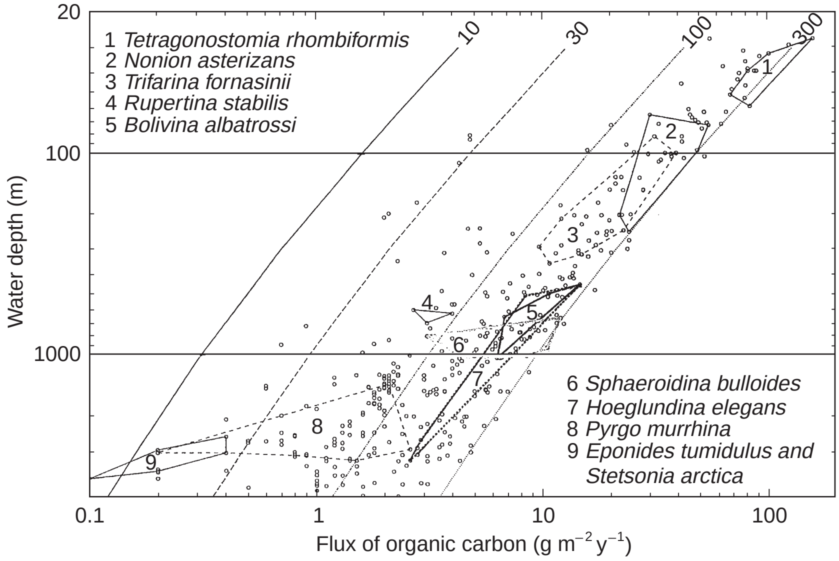

Figure 8 Dominant 'live' (rose Bengal-stained) occurrences of foraminiferal species in relation to water depth and flux or organic carbon to seafloor in the North Atlantic from the Guinea Basin to the Arctic Ocean. Each open circle corresponds to a data point. The polygonal areas indicate the combination of water depth and flux conditions under which nine different species are a dominant faunal component. The diagonal lines indicate levels of primary production (10, 30, 100, 300 g m^{-2} y^{-1}) that result in observed flux rates. Based on $>$ 250 μm sieve fraction plus 63–250 μm fraction from Guinea Basin and Arctic Ocean. (Reprinted from Altenbach AV, Pflaumann U, Schiebel R *et al.* (1999) Scaling percentages and distribution patterns of benthic foraminifera with flux rates of organic carbon. *Journal of Foraminiferal Research* 29: 173–185; with permission from The Cushman Foundation.)

assemblages in the deep sea. Agglutinated species with tubular or spherical tests are found in areas where the seafloor is periodically disturbed by strong currents capable of eroding sediments. Forms projecting into the water column may be abundant where steady flow rates convey a continuous supply of suspended food particles. Other species associations may be linked to sedimentary characteristics.

Low-Oxygen Environments

Oxygen availability is a particularly important ecological parameter. Since oxygen is consumed during the degradation of organic matter, concentrations of oxygen in bottom water and sediment pore water are inversely related to the organic flux derived from surface production. In the deep sea, persistent oxygen depletion ($O_2 < 1$ ml l^{-1}) occurs at bathyal depths ($<$ 1000 m) in basins (e.g., on the California Borderland) where circulation is restricted by a sill and in areas where high primary productivity resulting from the upwelling of nutrient-rich water leads to the development of an oxygen minimum zone (OMZ; e.g., north-west Arabian Sea and the Peru margin). Subsurface sediments also represent an oxygen-limited setting, although oxygen penetration is generally greater in oligotrophic deep-sea sediments than in fine-grained sediments on continental shelves.

On the whole, foraminifera exhibit greater tolerance of oxygen deficiency than most metazoan taxa, although the degree of tolerance varies among species. Oxygen probably only becomes an important limiting factor for foraminifera at concentrations well below 1 ml l^{-1}. Some species are abundant at levels of 0.1 ml l^{-1} or less. A few apparently live in permanently anoxic sediments, although anoxia sooner or later results in death when accompanied by high concentrations of hydrogen sulfide. Oxygen-deficient areas are characterized by high foraminiferal densities but low, sometimes very low ($<$ 10), species numbers. This assemblage structure (high dominance, low species richness) arises because (i) low oxygen concentration acts as a filter that excludes non-tolerant species and (ii) the tolerant species that do survive are able to flourish because food is abundant and predation is reduced. Utrastructural studies of some species have revealed features, e.g., bacterial symbionts and unusually high abundances of peroxisomes, that may be adaptations to extreme oxygen depletion. In addition, mitachondria-laden pseudopodia have the potential to extend into overlying sediment layers where some oxygen may be present.

Many low-oxygen-tolerant foraminifera belong to the Orders Rotaliida and Buliminida. They often have thin-walled, calcareous tests with either flattened, elongate biserial or triserial morphologies (e.g., *Bolivina, Bulimina, Globobulimina, Fursenkoina, Loxotomum, Uvigerina*) or planispiral/lenticular morphologies (e.g., *Cassidulina, Chilostomella, Epistominella, Loxotomum, Nonion, Nonionella*). Some agglutinated foraminifera, e.g., *Textularia, Trochammina* (both multilocular), *Bathysiphon*, and *Psammosphaera* (both unilocular), are also abundant. However, miliolids, allogromiids, and other soft-shelled foraminifera are generally rare in low-oxygen environments. It is important to note that no foraminiferal taxon is currently known to be confined entirely to oxygen-depleted environments.

Deep-Sea Foraminifera in Paleo-Oceanography

Geologists require proxy indicators of important environmental variables in order to reconstruct ancient oceans. Benthic foraminifera provide good proxies for seafloor parameters because they are widely distributed, highly sensitive to environmental conditions, and abundant in Cenozoic and Cretaceous deep-sea sediments (note that deep-sea sediments older than the middle Jurassic age have been destroyed by subduction, except where preserved in ophiolite complexes).

Foraminiferal faunas, and the chemical tracers preserved in the tests of calcitic species, can be used to reconstruct a variety of paleoenvironmental parameters and attributes. The main emphasis has been on organic matter fluxes and bottom-water/pore water oxygen concentrations (inversely related parameters), the distribution of bottom-water masses, and the development of thermohaline circulation (**Table 2**). Modern deep-sea faunas became established during the Middle Miocene (10–15 million years ago), and these assemblages can often be interpreted in terms of modern analogues. This approach is difficult or impossible to apply to sediments from the Cretaceous and earlier Cenozoic, which contain many foraminiferal species that are now extinct. In these cases, it can be useful to work with test morphotypes (e.g., trochospiral, cylindrical, biserial/triserial) rather than species. The relative abundance of infaunal morphotypes, for example, has been used as an index of bottom-water oxygenation or relative intensities of organic matter inputs. The trace element (e.g., cadmium) content and stable isotope (δ^{13}C; i.e., the deviation from a standard

Table 2 Benthic foraminiferal proxies or indicators (both faunal and chemical) useful in paleo-oceanographic reconstruction

Environmental parameter/property	*Proxy or indicator*	*Remarks*
Water depth	Bathymetric ranges of abundant species in modern oceans	Depth zonation largely local although broad distinction between shelf, slope and abyssal depth zones possible
Distribution of bottom water masses	Characteristic associations of epifaunal species	Relations between species and water masses may reflect lateral advection
Carbonate corrosiveness of bottom water	Abundance of *Nuttallides umbonifera*	Corrosive bottom water often broadly corresponds to Antarctic Bottom Water
Deep-ocean thermohaline circulation	Cd/Ca ratios and δ^{13}C values for calcareous tests	Proxies reflect ‘age’ of bottom water masses; i.e., period of time elapsed since formation at ocean surface
Oxygen-deficient bottom-water and pore water	Characteristic species associations; high-dominance, low-diversity assemblages	Species not consistently associated with particular range of oxygen concentrations and also found in high-productivity areas
Primary productivity	Abundance of foraminiferal tests $> 150\ \mu$m	Transfer function links productivity to test abundance (corrected for differences in sedimentation rates between sites) in oxygenated sediments
Organic matter flux to seafloor	(i) Assemblages of high productivity taxa (e.g. *Globobulimina*, *Melonis barleeanum*) (ii) Ratio between infaunal and epifaunal morphotypes (iii) Ratio between planktonic and benthic tests	Assemblages indicate high organic matter flux to seafloor, with or without corresponding decrease in oxygen concentrations
Seasonality in organic matter flux	Relative abundance of ‘phytodetritus species’	Reflects seasonally pulsed inputs of labile organic matter to seafloor
Methane release	Large decrease (2–3‰) in δ^{13}C values of benthic and planktonic tests	Inferred sudden release of ^{12}C enriched methane from clathrate deposits following temperature rise

^{12}C:^{13}C ratio) chemistry of the calcium carbonate shells of benthic foraminifera provide powerful tools for making paleo-oceanographic reconstructions, particularly during the climatically unstable Quaternary period. The cadmium/calcium ratio is a proxy for the nutrient (phosphate) content of sea water that reflects abyssal circulation patterns. Carbon isotope ratios also reflect deep-ocean circulation and the strength of organic matter fluxes to the seafloor.

It is important to appreciate that the accuracy with which fossil foraminifera can be used to reconstruct ancient deep-sea environments is often limited. These limitations reflect the complexities of deep-sea foraminiferal biology, many aspects of which remain poorly understood. Moreover, simple relationships between the composition of foraminiferal assemblages and environmental variables are elusive, and it is often difficult to identify faunal characteristics that can be used as precise proxies for paleo-oceanographic parameters. For example, geologists often wish to establish paleobathymetry. However, the bathymetric distributions of foraminiferal species are inconsistent and depend largely on the organic flux to the seafloor, which decreases with increasing depth (**Figure 8**) and is strongly influenced by surface productivity. Thus, foraminifera can be used only to discriminate in a general way between shelf, slope, and abyssal faunas, but not to estimate precise paleodepths. Oxygen concentrations and organic matter inputs are particularly problematic. Certain species and morphotypes dominate in low-oxygen habitats that also are usually characterized by high organic loadings. However, the same foraminifera may occur in organically enriched settings where oxygen levels are not severely depressed, making it difficult for paleo-oceanographers to disentangle the influence of these two variables. Finally, biological factors such as microhabitat preferences and the exploitation of phytodetrital aggregates ('floc') influence the stable isotope chemistry of foraminiferal tests.

There are many examples of the use of benthic foraminiferal faunas to interpret the geological history of the oceans. Only one is given here. Cores collected at 50°41′N, 21°52′W (3547 m water depth) and 58°37′N, 19°26′W (1756 m water depth) were used by E. Thomas and colleagues to study changes in the North Atlantic over the past 45 000 years. The cores yielded fossil specimens of two foraminiferal species, *Epistominella exigua* and *Alabaminella weddellensis,* both of which are associated with seasonal inputs of organic matter (phytodetritus) in modern oceans. In the core from 51°N, these 'phytodetritus species' were uncommon during the last glacial maximum but increased sharply in absolute and relative abundance during the period of deglaciation 15 000–16 000 years ago (**Figure 9**). At the same time there was a decrease in the abundance of *Neogloboquadrina pachyderma*, a planktonic foraminifer found in polar regions, and an increase in the abundance of *Globigerina bulloides,* a planktonic species characteristic of

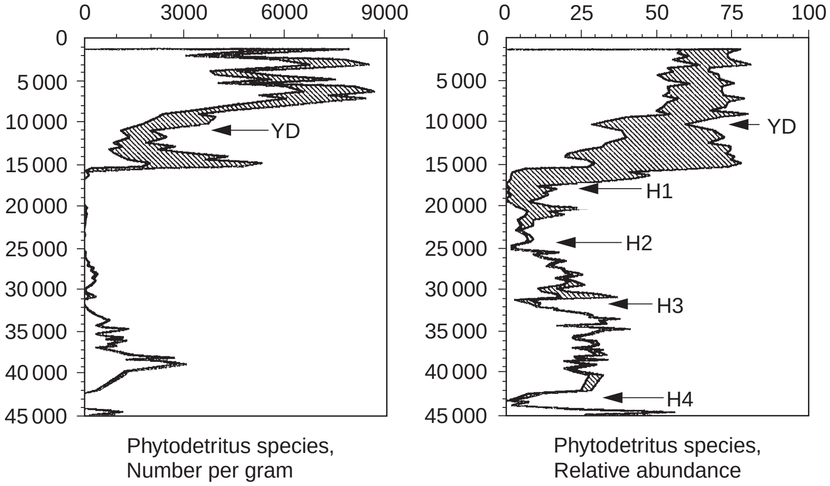

Figure 9 (A) Absolute (specimens per gram of dry sediment) and (B) relative (percentage) abundances of *Alabaminella weddellensis* and *Epistominella exigua* ($>$ 63 μm fraction) in a long-sediment core from the North Atlantic (50°41.3′N, 21°51.9′W, 3547 m water depth). In modern oceans, these two species respond to pulsed inputs of organic matter ('phytodetritus') derived from surface primary production. Note that they increased in abundance around 15 000 years ago, corresponding to the main Northern Hemisphere deglaciation and the retreat of the Polar Front. Short period climatic fluctuations (YD = Younger Dryas; H1–4 = Heinrich events, periods of very high meltwater production) are also evident in the record of these two species. (Reprinted from Thomas E, Booth L, Maslin M and Shackleton NJ (1995). Northeast Atlantic benthic foraminifera during the last 45 000 years: change in productivity seen from the bottom up. *Paleoceanography* 10: 545–562; with permission from the American Geophysical Union.)

warmer water. These changes were interpreted as follows. Surface primary productivity was low at high latitudes in the glacial North Atlantic, but was much higher to the south of the Polar Front. At the end of the glacial period, the ice sheet shrank and the Polar Front retreated northwards. The 51°N site was now overlain by more productive surface water characterized by a strong spring bloom and a seasonal flux of phytodetritus to the seafloor. This episodic food source favored opportunistic species, particularly *E. exigua* and *A. weddellensis*, which became much more abundant both in absolute terms and as a proportion of the entire foraminiferal assemblage.

Conclusions

Benthic foraminifera are a major component of deep-sea communities, play an important role in ecosystem functioning and biogeochemical cycling, and are enormously diverse in terms of species numbers and test morphology. These testate (shell-bearing) protists are also the most abundant benthic organisms preserved in the deep-sea fossil record and provide powerful tools for making paleo-oceanographic reconstructions. Our understanding of their biology has advanced considerably during the last two decades, although much remains to be learnt.

See also

Abrupt Climate Change. Anthropogenic Trace Elements in the Ocean. Benthic Foraminifera. Benthic Organisms Overview. Cenozoic Oceans – Carbon Cycle Models. Deep-sea Fauna. Floc Layers. Macrobenthos. Meiobenthos. Microphytobenthos. Ocean Carbon System, Modelling of. Phytoplankton Blooms. Primary Production Processes. Radiocarbon. Stable Carbon Isotope Variations in the Ocean. Tracers of Ocean Productivity.

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BENTHIC ORGANISMS OVERVIEW

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Introduction

The term benthos is derived from the Greek word *βαθος* (vathos, meaning depth) and refers to those organisms that live on the seabed and the bottom of rivers and lakes. In the oceans the benthos extends from the deepest oceanic trench to the intertidal spray zone. It includes those organisms that live in and on sediments, those that inhabit rocky substrata and those that make up the biodiversity of coral reefs.

The benthic environment, sometimes referred to as the benthal, may be divided up into various well defined zones that seem to be distinguished by depth (**Figure 1**).

Physical Conditions Affecting the Benthos

In most parts of the world the water level of the upper region of the benthal fluctuates, so that the animals and plants are subjected to the influence of the water only at certain times. At the highest level, only spray is involved; in the remainder of the region, the covering of water fluctuates as a result of tides and wind and other atmospheric factors. Below the level of extreme low water, the seafloor is permanently covered in water.