Benthic Foraminiferal Biogeography: Controls on Global Distribution Patterns in Deep-Water Settings

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Abstract

Benthic foraminifera, shell-bearing protists, are familiar from geological studies. Although many species are well known, undescribed single-chambered forms are common in the deep sea. Coastal and sublittoral species often have restricted distributions, but wide ranges are more frequent among deep-water species, particularly at abyssal depths. This probably reflects the transport of tiny propagules by currents across ocean basins that present few insurmountable barriers to dispersal, combined with slow rates of evolution. Undersampling of the vast deep-sea habitat, however, makes it very difficult to establish the ranges of less common foraminiferal species, and endemism may be more prevalent than currently realized. On continental slopes, some species have restricted distributions, but wide-ranging bathyal species that exhibit considerable morphological variation are more common. This may be linked to the greater heterogeneity of continental slopes compared with oceans basins. Improved knowledge of deep-sea foraminiferal biogeography requires sound morphology-based taxonomy combined with molecular genetic studies.
1. INTRODUCTION

Foraminifera, heterotrophic protists classified within the protistan supergroup Rhizaria (Adl et al. 2005), are ubiquitous organisms in marine (Murray 2006) as well as freshwater (Holzmann & Pawlowski 2002) and terrestrial (Lejzerowicz et al. 2010) environments. Although some marine species are important constituents of the plankton, most are benthic. Foraminifera have an outstanding fossil record, and much of the research on them has been conducted by geologists who have described most of the known species. Estimates of the number of extant species range from $\sim$4,100 (Murray 2007) to 10,000–12,000 (Boltovskoy & Wright 1976). Many of the described benthic species have robust shells (“tests”) composed of calcareous material and fossilize readily. Others have agglutinated tests composed of mineral or biogenic particles acquired from the surrounding sediment and are less likely to fossilize. In addition to these well-known taxa, recent studies have revealed a profusion of species with flexible, single-chambered (monothalamous) tests composed of organic or agglutinated material and having very little fossilization potential (Gooday 2002, Habura et al. 2008). In contrast to the hard-shelled species, these soft-shelled monothalamous foraminifera are poorly known and largely undescribed.

Because of their importance in reconstructing ancient marine environments, an enormous literature exists on the relationship between modern foraminiferal species and environmental parameters. However, their use as paleoenvironmental proxies is hampered by the complexity of these distributional controls (Murray 2001, Gooday 2003, Jorissen et al. 2007). In deep water, the organic matter flux to the seafloor is believed to exert a particularly strong influence on benthic foraminiferal ecology. Altenbach et al. (1999) plotted the percentage abundance of some key deep-sea species in samples from the Guinea Basin to the Arctic Ocean against flux estimates. All species were abundant only within certain limits, but they also occurred at lower densities across a wide range of flux values. Thus, species that are considered typical of high productivity areas were also found in oligotrophic regions, and vice versa. As Mackensen et al. (1995) remark, “apparently similar assemblages correspond to very different environmental conditions in different ocean basins.” This represents a major obstacle for the development of transfer functions, aiming to quantitatively reconstruct single environmental parameters on the basis of faunal composition.

A comprehensive treatment of the mass of conflicting information regarding ecological controls on the distribution of modern benthic foraminiferal species is beyond the scope of this short review. Instead, we focus on the distribution and ecology of some key species from different environmental settings, incorporating molecular evidence when available. The study of foraminifera straddles biology and geology. In addition to being important proxies in paleoecological studies, their high density and diversity in various settings make foraminifera ideally suited to address broader questions concerning the distribution of marine species (Ruzas & Culver 1989). Among these is the contentious issue of whether or not protists and small-sized animals exhibit biogeographic patterns. One school of thought maintains that small organisms have ubiquitous distributions and occur around the globe wherever the environmental conditions are suitable (e.g., Finlay & Fenchel 2004). Another view is that some species are cosmopolitan but others exhibit distinct biogeographic patterns that are not dependent on the existence of suitable habitats (the moderate endemcity model) (Jenkins et al. 2007, Foissner 2008). Many foraminifera fall within the transition zone (0.1 to 10 mm) between large and small organisms where distributions switch from ubiquitous to restricted, according to Finlay & Fenchel (2004). Their patterns of distribution are therefore of particular interest in the context of this debate (Gooday 1999).

With these considerations in mind, we address the following questions:

1. Are there “typical” patterns of geographical distribution among deep-water foraminiferal species, and do they differ from those of foraminifera in shelf settings?
2. What are the main factors influencing these distribution patterns, and do they differ in different settings (continental margins, ocean basins, hypoxic habitats)?
3. What is the degree of connectivity between populations in different regions and habitats?
4. Are widely distributed foraminiferal morphospecies genetically coherent, or do they conceal genetically distinct but morphologically very similar cryptic species?
5. To what extent does imperfect taxonomy obscure biogeographic patterns?

We return to these questions in the Summary Points at the end of this review. Although our main focus is on modern deep-water foraminifera, for comparative purposes we also touch on the distribution of those living in shelf and coastal settings.

2. PROBLEMS IN DETERMINING DISTRIBUTION PATTERNS

Many marine foraminifera are well known and widely reported, and their distributions are apparently well established (Murray 1991). However, the description of the same species under different names is a recurrent problem (Boltovskoy 1965); Murray (2007) estimates that 10% to 25% of modern species are synonyms. The opposite tendency, lumping different species under one name, also hampers the study of geographical ranges, especially in the case of agglutinated taxa. Some species names established early in the history of foraminiferal taxonomy have been applied to morphotypes rather than to single species. For example, published images of *Reophax scorpionis* de Montfort 1808, a species reported from coastal to abyssal sites around the world, show a wide range of test morphologies that must encompass a variety of different biological species. Another concern is the existence of cryptic speciation among “species” in which the test morphology is fairly consistent (Tsuchiya et al. 2003, Hayward et al. 2004, Pawlowski et al. 2008). Although most hard-shelled species have been described, a large proportion of monothalamous taxa remain undescribed (Habura et al. 2008), particularly in the deep sea where many species are rare and have been recorded at only one site. The minute proportion (McClain 2007) gives a “very high estimate” of 0.5% of this vast habitat that has ever been sampled makes it impossible to distinguish genuinely endemic species distributions from restricted occurrences that are artifacts of undersampling (Gooday et al. 2004, McClain & Mincks Hardy 2010, Tittensor et al. 2010).

Spatial and temporal patchiness create additional problems (Sen Gupta & Smith 2010). Significant small-scale spatial variability occurs at decametric to decimetric scales (e.g., Griveaud et al. 2010), perhaps reflecting concentrations of labile organic matter and highly localized niches around macrofaunal burrows. Seasonal and interannual studies (Ohga & Kitazato 1997, Fontanier et al. 2006, Langezaal et al. 2006, Gooday et al. 2010b) reveal a similar degree of faunal variability over time, partly attributable to inputs of labile organic matter that trigger bursts of reproduction in opportunistic species. Because most distributional studies are based on single samples, this temporal and spatial variability can strongly influence distributional pattern. Examination of dead (hard-shelled) tests, which represent a time-integrated view of the fauna at a particular locality, can help to alleviate this problem, as long as they have not been subject to significant postmortem transport.

3. DISPERSAL IN FORAMINIFERA

The geographical ranges of species are related, at least in some taxa, to their dispersal ability (Gaston 2003). Information on dispersal in marine organisms is limited and biased toward low-dispersing metazoan species in low-latitude settings (Bradbury et al. 2008). Analyses of proxies for dispersal (e.g., genetic differentiation and duration of planktonic larval stages) suggest that marine
metazoans exhibit a wide range of dispersive capabilities (Bradbury et al. 2008), although these are not necessarily linked to species ranges (e.g., Emlet 1995).

Dispersal mechanisms in benthic foraminifera are reviewed by Alve (1999) and Murray (2006). The active movement of free-living species across the seafloor is too slow to account for wide-scale dispersal. Likewise, planktonic life stages, although a potentially efficient means of transport, are reported in only a few species. Most species, therefore, are probably passively entrained into the water column and transported by currents, either as adults or juveniles or as tiny propagules. Small adult and juvenile benthic foraminiferal tests have been caught in plankton-net and sediment-trap samples obtained well above the seafloor (Alve 1999, Brunner & Biscaye 2003, Murray 2006). In a series of elegant experiments, Alve & Goldstein (2010; also see their earlier papers) convincingly demonstrated the transport of propagules small enough to pass through a 32-μm mesh sieve. Large numbers of foraminifera belonging to coastal benthic species appeared and grew when the 32-μm fractions of sediments collected at 320-m water depth were exposed to simulated shallow-water conditions in sealed containers on a window ledge. Similar results were obtained using sediment that had been kept in a dark cold-room for two years, suggesting that propagules can remain viable for at least this period. If foraminiferal propagules have characteristics similar to those of metazoan larvae (Bradbury et al. 2008), they are likely to survive longer at low temperatures, enhancing their potential for wide dispersal in the deep sea.

On geological timescales, benthic foraminifera seem to disperse instantaneously (Buzas & Culver 1991). Mediterranean sapropels provide good evidence of their rapid dispersal. These recurrent anoxic events have repeatedly wiped out benthic faunas across the entire eastern Mediterranean, at least below water depths of 500 to 1,000 m (Jorissen 1999). Each lasted for several thousands of years, after which the seafloor was rapidly repopulated by benthic foraminifera. These species must have either persisted in shallow-water refugia in the eastern Mediterranean or migrated from the western Mediterranean after reoxygenation of the water column. Although recolonization was apparently very rapid (several decades to a few centuries at most), it seems to have taken several millennia to fully restore biodiversity, suggesting that recolonization may be considerably slower for some taxa (Schmiedl et al. 2003).

In addition to natural mechanisms, species can be transported long distances in the ballast tanks of ships (Radziejewska et al. 2006). This mechanism may explain the disjunct distribution of one phylotype of the coastal genus *Ammonia* (Pawlowski & Holzmann 2008), the Japanese species *Trochammina badai* in San Francisco Bay (McGann & Sloan, 1996), and the European and North American species *Haynesina germanica* in an Argentinean estuary (Calvo-Marcilese & Langer 2010).

### 4. ENVIRONMENTAL PARAMETERS INFLUENCING FORAMINIFERAL ASSEMBLAGES

Murray (2006) identified salinity, temperature, oxygen, tides and currents, substrate and food supply, as well as competition and predation, as important factors influencing foraminiferal assemblages (also see sidebar, Benthic Foraminifera as Paleoceanographic and Paleoecological Indicators). Additional factors on the shelf include coverage of the seafloor by seagrasses and macroalgae (e.g., Mateu-Vicens et al. 2010) and light penetration, the latter being crucial for symbiont-bearing species. Salinity plays a role mainly in marginal marine areas subject to freshwater discharges (e.g., Baltic Sea, Black Sea) or to strong evaporation (e.g., Dead Sea, Red Sea). Although temperature is an important factor in coastal environments (Culver & Buzas 1999), it is relatively uniform in most parts of the deep sea and therefore probably not a major parameter for foraminifera, at least in modern oceans. Currents and particularly tides also mainly operate in shallow water, but elevated
BENTHIC FORAMINIFERA AS PALEOCEANOGRAPHIC
AND PALEOECOLOGICAL INDICATORS

Foraminifera are by far the most abundant and widely distributed benthic organisms preserved in the fossil record and are used widely to reconstruct conditions on ancient ocean floors (paleoceanography) as well as in near-shore settings (paleoecology). Faunal characteristics (abundance, diversity, taxonomic composition) have been used to infer, e.g., the food flux to the seafloor (and hence surface primary productivity), bottom-water oxygenation, current activity, and the depth of the carbonate compensation depth. This approach depends on an accurate knowledge of the distribution of species in relation to environmental parameters in modern oceans. Another approach depends on the chemical composition (stable isotope and elemental ratios) of foraminiferal carbonate shells. For instance, the Mg/Ca ratio is used to reconstruct temperature, and stable carbon isotope ratios reflect the organic-matter flux to the seafloor and ocean circulation. Once temperature is known, oxygen isotopes can be used to estimate paleosalinity. In coastal settings, foraminifera have been used to reconstruct past sea levels. Efforts have been made to develop quantitative proxies (transfer functions) for environmental variables on the basis of benthic foraminifera, but these are often fraught with difficulties. In recent years, benthic foraminifera have been used increasingly to monitor the impact of anthropogenic activities in marine ecosystems.

flows are encountered in some deep-sea areas, where they are associated with distinctive epifaunal assemblages (e.g., Schönfeld 1997). Sessile foraminiferal species depend on the availability of firm attachment surfaces. In the predominantly sediment-covered deep ocean, suitable substrates include rocky outcrops, glacial drop stones, manganese nodules, biogenic structures, and larger sessile or even mobile animals. Carbonate dissolution is a major limiting factor for deep-sea calcareous foraminifera. Below the carbonate compensation depth, calcareous species disappear almost entirely and foraminiferal assemblages are composed of agglutinated and organic-walled forms (Saidova 1965). In areas such as oxygen minimum zones (OMZs), low bottom-water dissolved oxygen (DO) concentrations eliminate hypoxia-sensitive species, leading to the formation of low-diversity, high-dominance faunas. However, DO is limiting only when concentrations decline to low levels (∼0.5 ml per liter or less), at least where hypoxia is permanent, as in OMZs (Levin 2003).

In addition to these physical and chemical parameters, recent literature has placed considerable emphasis on food inputs derived from surface primary production as a major influence on the structure and functioning of deep-sea communities in general (Smith et al. 2008), as well as on foraminiferal assemblage composition (e.g., Altenbach et al. 1999, Gooday 2003, Jorissen et al. 2007), diversity (Wollenburg & Mackensen 1998), and faunal patterns with water depth (De Rijk et al. 2000). Distinctive assemblages are also associated with regions that have a pronounced seasonality in the organic-matter flux to the seafloor (Loubere & Fariduddin 1999, Sun et al. 2006).

5. GEOGRAPHICAL DISTRIBUTIONS OF (MORPHO)SPECIES IN DIFFERENT HABITATS

5.1. Continental Shelf and Slope
Analyses of large data sets suggest that many foraminiferal species have restricted ranges on continental margins. Distributions around the North American continent (intertidal to abyssal depths) have been examined in detail by Stephen Culver and Martin Buzas in a series of publications (e.g., Buzas & Culver 1991, Culver & Buzas 1998) based on literature sources combined with an extensive reexamination of museum material. Within this region, the majority (57%) of the 2,329
species recognized were endemic, in the sense of being confined to one of five regions (Caribbean, Gulf of Mexico, Atlantic, Arctic, and Pacific); only 5% occurred in all regions. However, the majority of endemic species were rare. Similarly, Murray (2007) concluded that a high proportion (83%–90%) of species from marshes, lagoons/estuaries, and shelf seas were restricted to one or two of the six areas spanning either the three major oceans (marshes, lagoons/estuaries) or the eastern and western margins of the Atlantic Ocean (shelf seas). Mikhailевич (2004) estimates that as many as 80% of shallow-shelf (2–50 m) foraminiferal species around the Antarctic continent are endemic.

A different view emerges from a comprehensive survey of foraminifera in the Gulf of Mexico (Sen Gupta & Smith 2010). This may reflect differences in the scale at which endemism and ubiquity were evaluated, either around the North American continent (Buzas & Culver 1991, Culver & Buzas 1998) or globally (Sen Gupta & Smith 2010). Only 4% of the 987 species reported from the Gulf of Mexico (0–3,850 m) are endemic to this region. Of the 557 species confined to depths <1,000 m, 29% are cosmopolitan (occurring in the three major oceans or in both polar oceans and two of the three major oceans), compared with 35% of the 48 species from depths >1,000 m and 47% of the 360 species that straddle this boundary. Evidence for wide species distributions in the Gulf of Mexico also comes from a study of benthic foraminifera associated with hydrocarbon seeps, an important source of heterogeneity on this margin. Lobegeier & Sen Gupta (2008) recognized 183 species in 23 seep samples and 5 nonseep control samples (depth range 245–2,918 m). Although no species was endemic to the seep habitats, some (e.g., Bolivina spp.) were concentrated in seep samples, whereas others (Sacorhiza ramosa, Eponides turgidus, Nuttalilides decorata) were more or less confined to nonseep samples. Other seep sites, notably in Monterey Bay, California, are also reported to lack endemic species (Bernhard et al. 2001, Rathburn et al. 2003). Data from around New Zealand (0–5,000 m), compiled by Hayward et al. (2011), suggest that cosmopolitan distributions are more prevalent (69%) at depths >100 m than at shallower sites (55%).

5.1.1. Species with wide distributions. Uvigerina peregrina, a species reported from all ocean basins (Table 1), encompasses a plexus of morphotypes, mainly differing in their length-width ratio and test ornamentation, which varies from entirely costate to entirely spinose. Two different taxonomic concepts have been applied to this plexus. Some authors proposed new species names for different morphotypes, whereas the existence of many intermediate specimens has led others to apply the name U. peregrina to the entire plexus; in the latter case the various morphotypes are distinguished at a subspecies, variety, or informal level. Lutze (1986) distinguished six morphotypes within this complex on the basis of hundreds of samples from the eastern Atlantic continental slope (10°–50° N). Typical U. peregrina, characterized by very sharp costae and no intervening spines, was found between 900-m and 2,000-m depth. In deeper water, U. peregrina was progressively replaced by a morphotype with spines between the costae, and often an entirely spinose last chamber (Uvigerina bollicki). Below 3,000 m, completely spinose morphotypes, mostly identified (e.g., Van Leeuwen, 1986) as Uvigerina bispida, became increasingly dominant. Toward shallower water, the serrate costae of U. peregrina started to break up into irregular rows of spines. Uvigerina parva, which is smaller than typical U. peregrina, occurred between 300-m and 1,100-m depths. Lutze (1986) found two other morphotypes on the upper slope off northeast Africa. Uvigerina bifurcata (300–450 m depth) has an elongated test with regular costae, whereas Uvigerina sp. 221 (Uvigerina celtica; Schönfeld 2006) resembles U. bifurcata but has numerous small spines between the costae. Lutze (1986) found it between 100-m and 300-m depths.

Lutze (1986) described a complete bathymetric succession of these Uvigerina morphotypes between 10° N and 20° N in the eastern North Atlantic (Figure 1). Further north, U. bollicki and
Figure 1
Bathymetric distribution (red lines) of *Uvigerina* morphotypes on the east Atlantic margin, 10°–20° N. The species names applied by some authors to these forms are given within quotation marks because there is no evidence that they represent distinct species. The map shows the area off northwest Africa within which these morphotypes form a bathymetric succession.

*U. bifurcata* disappear, whereas others persist (Schönfeld, 2006). Unfortunately, only one genetic study partially elucidates the biological status of these various forms. Schweizer et al. (2005) studied small-subunit ribosomal DNA (SSU rDNA) sequences of *U. peregrina* from the Skagerrak. The divergence between the four recognized morphotypes, which belonged to *U. bollicki* and/or *U. celtica*, was rather minimal, leading to the conclusion that, despite substantial morphological variability, the *Uvigerina* assemblages from the Skagerrak were genetically homogenous. Further genetic studies are needed to understand the relationships between the various morphotypes within the *U. peregrina* plexus.

The huge morphological variability encompassed by *U. peregrina* appears to be exceptional, although this may reflect the popularity of this very common species. Some other cosmopolitan taxa, such as the *Gyroidina orbicularis/neosoldanii, Melonis barleeanum/zaandami,* and *Globobulimina affinis/pyrula* groups as well as the biconvex *Cibicoides* (including *C. pseudungerianus*) (*Table 1*), also show substantial morphological variability, which has yet to be examined genetically. In contrast, bathyal species with a wide geographical distribution and a consistent morphology appear to be uncommon. *Hoeglundina elegans* is probably the best example (*Table 1*), although other less frequent but widely distributed taxa also have stable morphologies. *Amphicoryna scalaris* and several miliolids (*Pyrgo subphaerica, Pyrgo depressa, Sigmoilopsis schlumbergeri*) are good examples.

In summary, it appears that most common bathyal species with wide geographical ranges are characterized by substantial morphological variability. The number of genetic studies investigating these morphological complexes is still very limited, and at present, there is no positive evidence that the various morphotypes represent different biological species.

**Bathyal seafloor:**
deep seafloor situated between 300-m and 3,500-m water depths; typically coinciding with the continental slope and continental rise.
### Table 1  Distribution of selected benthic foraminifera in different oceans

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<th>Atlantic Ocean</th>
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*a* Including the Adriatic Sea.

*b* Species considered to be synonyms.

*c* Sea of Marmara.

*d* *Uvigerina peregrina dirupta.*
5.1.2. Species with restricted distributions. As indicated above, there is conflicting evidence regarding the distribution of foraminiferal species on continental margins (Buzas & Culver 1991, Culver & Buzas 1998, Sen Gupta & Smith 2010). However, there do appear to be relatively few common species with restricted distributions living on bathyal continental slopes not subject to oxygen minima. One example is *Uvigerina mediterranea*, which strongly dominates Mediterranean faunas (>125-μm size fraction) and occurs in the eastern Atlantic between 15° N and 50° N (Lutze 1986), but apparently not in the western Atlantic or in other ocean basins. *Planulina ariminensis* appears to have a very similar distribution, whereas *Uvigerina elongatastriata* is found exclusively in the eastern Atlantic. The deep-water miliolid *Articulina tubulosa* is known only from the eastern Mediterranean, where it has adapted to the extremely oligotrophic conditions of the deep Levantine Basin. These endemic species, restricted to the Mediterranean and east Atlantic, support the concept of the Mediterranean as a hot spot for benthic foraminiferal evolution due to repeated anoxic episodes, at least since the beginning of the Pliocene (Verhallen 1991). According to Mikhailovich (2004), endemism among bathyal foraminiferal faunas in the Southern Ocean is “significant,” as it is for many metazoan taxa (Brandt et al. 2007). Species with apparently restricted geographical distributions also occur at depths between 200 and 2,000 m around New Zealand. Hayward et al. (2011) record 41 such species within this depth range. These include 3 species of *Notorotalia*, a genus restricted to the Southern Hemisphere that probably originated and radiated in the New Zealand region. Of the 41 bathyal (200–2,000 m) endemic species recognized by Hayward et al. (2011), 10 extend below 2,000 m.

5.2. Abyssal Seafloor

Much of the ocean floor is situated at abyssal depths (Smith et al. 2008). In their recent review, McClain & Mincks Hardy (2010) concluded that “many taxa appear broadly distributed across the deep-sea floor.” By contrast, Vinogradova (1997) argued for a high degree of endemism among macro- and mega-faunal animals confined to abyssal depths. In the case of foraminifera, the general perception (e.g., Douglas & Woodruff 1981, Murray 2006) is that many morphospecies occupying this vast habitat are cosmopolitan, a view supported by literature records from different oceans (Table 1). As noted above, however, inconsistencies in the identification of species mean that such records should not be accepted without reference to published photographs, or preferably to original material. Nevertheless, specimens of organic-walled, agglutinated, and calcareous species from widely separated oceanic areas are often remarkably similar in terms of the general appearance and structure of their tests (Figure 2). The existence of cosmopolitan deep-sea foraminiferal species is also indicated by ultradeep sequencing of short, highly variable regions of the SSU rDNA gene in sediment samples from deep-sea sites in the Arctic, North Atlantic, Southern, and Pacific Oceans and the Caribbean Sea (Lecroq et al. 2011). However, most of the operational taxonomic units recognized were confined to one or two sites, and replicates from the same station yielded similar species compositions, suggesting that some species may have restricted distributions (J. Pawlowski, written communication).

5.2.1. Species with wide distributions. We focus on four well-known, predominantly abyssal species, all belonging to the order Rotaliida, for which molecular data are available. *Epistominella exigua* is reported from all oceans (Table 1) and from depths between 500 m and 7,500 m (Murray 1991). However, it is a predominately abyssal species, and the shallower records are questionable. This epifaunal/shallow infaunal species occurs across a wide range of organic-matter flux rates (Altenbach et al. 1999). It appears to feed on algal cells embedded within lumps of phytodetritus derived from surface production. In the northeast Atlantic, *E. exigua* exhibits an
Figure 2
Similar foraminiferal morphospecies from different oceans. Purple outline indicates specimens from the North Atlantic: Porcupine Abyssal Plain, 48°59.4′ N, 16°30′ W, 4,840-m water depth (a,c,e,g) and 57°5.3′ N, 12°24.3′ W, 1,980-m water depth (i). Blue outline indicates a specimen from the North Pacific: 48°59.4′ N, 176°55.06′ W, 5,289-m water depth. Red outline indicates specimens from the central Pacific: 9°14′ N, 146°15′ W, 5,300-m water depth (d) and ~151° N, ~119° W, ~4,100-m water depth (j,b). Green outline indicates specimens from the Weddell Sea: 65°20.09′ S, 54°14.72′ W, 1,108-m water depth. Species identifications are as follows: (a,b) Conicotheca sp.; (c,d) Nodellum-like form 2; (e,f) Lagenammina sp.; (g,h) Adercotryma glomerata; (i,j) Epistominella arctica.
opportunistic, population-level response to pulsed inputs of phytodetritus (Gooday 1988). *Cibicidoides wuellerstorfi* is also reported from all the main oceans. It is often attached to substrates such as stones, sponges, and other biogenic structures and is considered to be a suspension feeder that intercepts fresh phytodetrital aggregates just above the seafloor (Lutze & Thiel 1989). *Oridorsalis umbonatus* is another widely distributed species. *Epistominella arctica* is a tiny species described from the deep Arctic Ocean and subsequently reported from the North Atlantic and Southern Oceans (Figure 2).

Pawlowski et al. (2007b) explored genetic differentiation between Arctic and Antarctic populations of *E. exigua*, *C. wuellerstorfi*, and *O. umbonatus* separated by a distance of 17,000 miles. Analyses of a fragment of the SSU rDNA gene from specimens collected west and north of Svalbard (Arctic Ocean) and in the Weddell Sea (Southern Ocean) revealed no differences between populations of *C. wuellerstorfi* and only minor differences in the case of *E. exigua*. The degree of differentiation was higher in *O. umbonatus*, which exhibited a maximum sequence divergence of 2.9% as well as a substantial degree of genetic polymorphism within an individual. Lecroq et al. (2009) reported a similar lack of differentiation between Arctic and Antarctic populations of *E. arctica*. Analyses of the highly variable internal transcribed spacer (ITS) region of the rDNA gene from the northern and southern polar sites likewise yielded very similar sequences in all three species, with mean divergencies of <1% (Pawlowski et al. 2007b). Some differences were observed between Antarctic and Arctic populations of *O. umbonatus* when ITS sequences were analyzed, but there was no evidence for differentiation in the other two species. However, a population-genetics approach involving an analysis of molecular variance indicated that a deep abyssal (4,650–4,975 m) Antarctic population of *E. exigua* was genetically distinct from shallower abyssal Antarctic (2,600–4,600 m) and bathyal northern (1,352–2,784 m) populations of this species. Arctic and Antarctic populations of *O. umbonatus* were also significantly differentiated, whereas those of *C. wuellerstorfi* were not.

Subsequent analyses by Lecroq et al. (2009) of SSU rDNA sequences of *E. exigua* from deep water off the coast of Japan revealed a striking degree of genetic similarity between these western Pacific populations and those from the Antarctic, Atlantic, and Arctic studied by Pawlowski et al. (2007b). A population-genetics analysis based on ITS rDNA sequences also failed to demonstrate any evidence for cryptic speciation within this species. Instead, much of the genetic variation was attributable to differences between specimens within, rather than between, populations (Lecroq et al. 2009). These results echo those for other protistan taxa, such as heterotrophic flagellates, which include marine species with cosmopolitan distributions (e.g., Scheckenbach et al. 2005).

### 5.2.2. Species with restricted distributions

The dual problems of rarity and undersampling are particularly acute in deep-ocean basins, making it difficult to establish the existence of endemism. In the abyssal equatorial Pacific, there are some obvious faunal differences between the Kaplan East (Nozawa et al. 2006) and Kaplan Central (N. Ohkawara & A.J. Gooday, unpublished results) sites. In particular, *Saccommina minimus*, the overwhelmingly dominant species at the Central site (5,042-m water depth) (Ohkawara et al. 2009), is absent at the shallower (4,100 m) East site. However, because this minute species has an extremely patchy distribution at small spatial scales and is easily overlooked, no conclusions can be drawn about its wider distribution.

At regional and global scales, some deep-sea foraminifera appear to be restricted to particular basins or oceans. Despite close faunal links between the Southern Ocean and North Atlantic abyssal faunas (Cornelius & Gooday 2004), certain species may be confined to deep Antarctic waters. These include a distinctive form of the cosmopolitan deep-sea genus *Vanhoeffenella*, characterized by a broad agglutinated rim and a three-dimensional morphology. Another possible example is *Haplophragmoides umbilicatum*, a species known only from the abyssal Southern Ocean (N. Cornelius, personal communication). There are also faunal differences between the Pacific
and Atlantic Oceans. Among large and distinctive foraminifera that are unlikely to be overlooked, stannomoid xenophyophores and the tubular species *Fugimurammina stellaperuta* are largely or entirely confined to the Pacific (Gooday et al. 2004). Conversely, the discoidal miliolid *Discospirina tenuissima* is currently reported only from the Atlantic and Indian Oceans. Similar examples probably exist among the smaller foraminifera. Given the different geological ages and environmental characteristics (bottom-water oxygenation and corrosivity, sediment types, sedimentary processes, timing and magnitude of primary production) of the Pacific and Atlantic Oceans (Levin & Gooday 2003), it seems highly unlikely that all deep-water foraminiferal species occur in both oceans.

5.3. Hypoxic Environments

Deep-water hypoxia (*O₂ < 0.5 ml per liter*) has persisted over millennial-scale time periods at bathyal depths in stratified basins and OMZs, where it is associated with upwelling combined with reduced circulation, water column stratification, and oxygen-depleted source waters (Levin 2003). OMZs are developed intensely in the eastern Pacific and in the northern Indian Ocean (Arabian Sea and Bay of Bengal), and somewhat less so in the eastern Atlantic (Diaz & Rosenberg 1995, Levin 2003, Helly & Levin 2004). Where they impinge on the seafloor, OMZs create strong bottom-water oxygen gradients. In addition to oxygen depletion, these regions are characterized by high sediment organic carbon content, lowered pH, and soft, unconsolidated sediments with a high water content (Gooday et al. 2010a).

Bathyal hypoxic environments are usually inhabited by low-diversity, high-dominance assemblages of foraminiferal species. Despite the depressed pH, calcareous taxa typically dominate these faunas. Many species exhibit at least some morphological, physiological, or ultrastructural adaptations to hypoxia (Bernhard & Sen Gupta 1999). These include an ability to accumulate and respire nitrate, as demonstrated initially in *Globobulimina* (Risgaard-Petersen et al. 2006) and subsequently in numerous other taxa (Piña-Ochoa et al. 2010). Deep-infaunal species, which occupy habitats deeper in the sediment in well-oxygenated benthic environments, replace species that are less resistant to hypoxia in low-oxygen settings. Specialized shallow-infaunal taxa may also appear. Whereas the deep-infaunal taxa are mostly cosmopolitan, the hypoxia-resistant surface dwellers often show more regional distributions. OMZs undoubtedly limit species ranges by excluding hypoxia-sensitive species (Gooday 2003). They may also act as a strong barrier to the spread of species between upper and lower slope environments (Rogers 2000).

There is mounting evidence that the extent and thickness of OMZs in tropical and subtropical regions of the oceans have increased since the 1960s (Stramma et al. 2008, 2010). Continued expansion of OMZs (Hofmann & Schellnhuber 2009) is likely to have profound consequences for marine life (Stramma et al. 2010, Gruber 2011). These effects will probably include an increased dominance of carbon processing by hypoxia-tolerant foraminiferal species (Wouds et al. 2007) and an expansion of their geographical ranges.

5.3.1. Species with wide distributions. The best example is *Virgulinella fragilis*, reported at depths between 16 m and >100 m from off west Africa, the eastern Arabian Sea, the Japanese islands, the Australian and New Zealand margins, the Peru margin, the Gulf of Mexico, and the Venezuelan shelf (Tsuchiya et al. 2008, Leiter & Altenbach 2010). This species appears to be a habitat endemic (Anderson 1994) that is confined to sulfidic/hypoxic environments; it occupies a deep-infaunal microhabitat where the bottom-water oxygen content is <0.3 ml per liter (Leiter & Altenbach 2010). Molecular analyses of individuals from three widely separated and isolated populations off Japan, New Zealand, and Namibia demonstrated a remarkable degree of genetic homogeneity with no hint of cryptic speciation (Tsuchiya et al. 2008). Because gene flow between
Cosmopolitan species: a widely distributed species that is found in many parts of the world.

the populations and recent dispersal are very unlikely, Tsuchiya et al. (2008) suggested that *V. fragilis* exhibits evolutionary stasis (both genetic and morphological), perhaps enhanced by persistent asexual reproduction.

Some other deep-infaunal, hypoxia-tolerant species have wide distributions. *Chilostomella oovidea/oolina* (the names are probably synonyms) is a particularly interesting example (Table 1). An analysis of partial SSU rDNA sequences of specimens from disjunct, bathyal (611–1,449 m), moderately hypoxic sites in the Pacific and Atlantic Oceans and Mediterranean Sea yielded three distinct genetic types that could not be distinguished morphologically. These types, which were supported by ITS data, occurred in (a) the Bay of Biscay and Mediterranean (AtlMed), (b) Sagami Bay (Japan) and the Oregon slope (NPac), and (c) Sagami Bay and the Costa Rica slope (CPac) (Grimm et al. 2007). The NPac and CPac types occurred on both sides of the Pacific Ocean, probably reflecting recent or ongoing genetic exchange across the Pacific mediated by the passive dispersal of propagules (Grimm et al. 2007).

**Globobulimina** is another important deep-infaunal genus that is widely distributed in hypoxic settings. It includes a number of species with only minor and rather subtle morphological differences, in some cases supported by molecular data (Ertan et al. 2004). One such species, *Globobulimina affinis*, is reported from the Atlantic, Indian, and Pacific Oceans as well as the Sea of Marmara (Table 1).

5.3.2. Species with restricted distributions. Different species are found at different localities within the same general area, such as the California borderland (e.g., Bernhard & Sen Gupta 1999). Different oxygen concentrations probably explain much of this variation (Bernhard et al. 1997), but it could also reflect restricted distributions. In the Arabian Sea, *Uvigerina ex gr. U. semiornata* and *Bolivina aff. B. dilatata* dominate the core region of the Pakistan margin OMZ, where bottom-water oxygen levels drop to ~0.1 ml per liter (Schumacher et al. 2007, Larkin & Gooday 2009). Similar forms occur on the Oman margin (Gooday et al. 2000). Following an exhaustive effort to identify them, Schumacher et al. (2007) concluded that both were undescribed species confined to the Arabian Sea. They contrasted the endemic character of foraminiferal species inhabiting the OMZ core with assemblages of more cosmopolitan species (e.g., *Globobulimina* spp. and *Chilostomella* spp.) found in the lower part of the zone.

6. CRYPTIC SPECIATION

There is good evidence among planktonic foraminiferal species for cryptic speciation, associated with slight morphological as well as biological, ecological, and physiological differences (e.g., Huber et al. 1997, de Vargas et al. 2002, Darling et al. 2004). However, cryptic speciation is less evident among benthic foraminifera, which evolve at a slower rate than their planktonic counterparts (Pawlowski et al. 1997). The best evidence comes from shallow-water taxa. Analyses of ITS rDNA sequences in *Planogloboratella opercularis* (Tsuchiya et al. 2003) from intertidal locations around Japan demonstrates the existence of two cryptic species, Type A and Type B, the sequences of which diverge by 7.0% to 8.5%. Type B is genetically closer (3.9% to 4.8% divergence) to another species, *P. nakamurai*, than it is to Type A. Careful examination revealed subtle morphological differences between the two phylotypes of *P. opercularis*, with Type B exhibiting some test features in common with *P. nakamurai*. Cryptic speciation has also been described within *Ammonia*, a highly variable coastal genus often regarded as comprising a few species with many different ecophenotypes (Hayward et al. 2004, Pawlowski & Holzmann 2008). Partial, large-subunit rDNA sequences revealed 13 phylotypes (T1 to T13), each sufficiently distinct to be regarded as a species and exhibiting a variety of biogeographic patterns. Phylotype T1 is distributed around the world in both hemispheres, T2 and T5 occur on either side of the North Atlantic and South Pacific, respectively,
whereas T3 is widely distributed around European coastlines. T6 has been found in Japanese and European waters and may be an invasive species dispersed by shipping. The other 8 phylotypes have restricted distributions. Some shallow-water morphospecies with bipolar distributions also encompass cryptic species (Mikhalevich 2004, Brandt et al. 2007, Pawlowski et al. 2008).

Although genetic studies have revealed complexes of cryptic species among some animal groups in the deep sea (e.g., isopods; Raupach et al. 2007), there is currently little unequivocal evidence for cryptic speciation among bathyal or abyssal benthic foraminifera. The only real example is Conqueria laevis, a monothalamous species of which Arctic and Antarctic individuals were genetically distinct (Brandt et al. 2007). The three genetic types of Chilostomella mentioned above are less differentiated than the five planktonic forms of Neogloboquadrina pachyderma recognized by Darling et al. (2004) and apparently lack any clear morphological expression, leaving their taxonomic status uncertain (Grimm et al. 2007). Likewise, the genetic differences observed among Arctic and Antarctic populations of O. umbonatus, and to a lesser extent in E. exigua, do not amount to cryptic speciation (Pawlowski et al. 2007b). Some species (e.g., Adercotryma glomerata) are reported from shelf to abyssal depths (Murray 1991); inaccurate taxonomy is possibly responsible for these vast bathymetric ranges, but cryptic species occupying progressively deeper depth zones could also be involved. Although this latter suggestion is purely speculative, it would be consistent with the considerable degree of depth-related genetic differentiation observed among some animal morphospecies (e.g., Zardus et al. 2006). By contrast, there is good molecular evidence that the monothalamous species Bathyallogromia weddellensis is genetically coherent across a depth range of 1,100–6,300 m in the Southern Ocean (Gooday et al. 2004). Populations of the calcareous species Epistominella vitrea from 15 to 30 m in McMurdo Sound and bathyal depths (>1,000 m) in the Weddell Sea on the opposite side of the Antarctic continent are genetically almost identical (Pawlowski et al. 2007a). These wide bathymetric ranges are possibly related to the essentially isothermal water column around Antarctica.

7. CONTROLS ON DISTRIBUTION PATTERNS

7.1. Evolutionary Factors

Coastal and shelf environments have been subject to repeated modification, for example, as a result of sea-level changes, leading to the continual destruction and reformation of shallow-water marine habitats. Geological and oceanographic fluctuations have also impacted bathyal continental margins, particularly at upper-slope depths. Environmental instability of this sort is likely to enhance genetic differentiation (Katz et al. 2005) as well as create barriers to gene flow, resulting in a greater degree of endemism compared with deeper-water settings, which have been generally more stable over geological timescales (Buzas & Culver 1984, 1989; Rogers 2000).

Caron (2009) suggested that different modes of reproduction (sexual versus asexual) may influence distribution patterns in protists. Foraminifera can reproduce sexually or asexually. Most of the species that have been studied undergo an alternation of generations. However, because population densities are generally lower in the deep sea, asexual reproduction is more likely to occur here than in shelf settings (Murray 1991, p. 301). If this is true, then rates of genetic differentiation and speciation are also likely to be slower, promoting the development of larger geographical ranges, particularly at abyssal depths (Pawlowski et al. 2007b). A slower rate of evolution would be consistent with the greater geological longevity that seems to be typical of deep-water species (Buzas & Culver 1984). As mentioned above, evolutionary stasis, rather than gene flow, is one possible explanation for the remarkable genetic homogeneity between widely separated and isolated populations of the hypoxia-tolerant species Virgulinella fragilis.
7.2. Barriers to Dispersal

Grasse & Morse-Porteous (1987) noted the “lack of barriers to dispersal over very large areas” as one of the main influences on deep-sea benthic community structure. Certainly, the generally open nature of abyssal plains is consistent with the widespread distribution of many abyssal foraminiferal species. Nevertheless, barriers to dispersal do exist in the deep sea. Hydrographic features, such as strong current systems, create barriers that potentially limit the ranges of deep-sea animals (e.g., Won et al. 2003). However, the most obvious are topographic features such as major ridges (Vinogradova 1997). Preliminary analysis of foraminiferal assemblages on either side of the Mid-Atlantic Ridge (49°–54° N, 2,500-m depth) did not reveal any clear faunal differences (N. Rothe & A.J. Gooday, unpublished data). Similar abyssal foraminiferal assemblages occupy areas to the north and south of the Walvis Ridge, a feature that rises 4,000 m above the adjacent basins (Schmiedl et al. 1997). The bathymetric distributions of many deep-sea foraminiferal species, and presumably of their propagules, are sufficiently broad to span these kinds of topographic obstacles (Pawlowski et al. 2007b). Given the ability for propagules to survive inhospitable conditions for periods of years (Alve & Goldstein 2010), the potential for the wide dispersal of foraminifera by currents at abyssal depths is considerable. Passive transport by bottom currents across topographic barriers has been invoked to explain the cosmopolitan distributions of abyssal harpacticoid copepod species in the genus *Mesoectodes* (Menzel et al. 2011).

Additional topographic barriers exist on continental margins, which are generally much more heterogeneous than the abyssal plains (Levin & Dayton 2009). This heterogeneity has been implicated in the greater degree of morphological (Etter & Rex 1990) and genetic (Etter et al. 2005) variability on bathyal continental slopes compared with abyssal plains. Submarine canyons, features that often extend from near the coastline to abyssal depths, constitute one obvious source of heterogeneity. Distinctive foraminiferal species are sometimes common within canyons but are not present on adjacent slopes (Hess & Jorissen 2009). However, these species appear to be adapted to special conditions inside the canyons, such as sediment instability and/or organic matter focusing. There is no evidence that canyons, or other physical obstacles, limit the geographical distribution of any species at bathyal depths on continental margins.

Shallow sills create major barriers to the influx of species into partially land-locked basins. The most obvious example is the Mediterranean, where the Straits of Gibraltar has limited the exchange of species with the North Atlantic since the basin refilled following the Late Miocene Messinian salinity crisis. As a result, the deep fauna is impoverished compared with that in the Atlantic (Murray 1991). However, the low diversity of these faunas, especially in the eastern Mediterranean, may also reflect the extreme oligotrophy of the deep Levantine basin (De Rijk et al. 2000). As explained above, several species (e.g., *Articulina tubulosa*, *Rotamorphina involuta*) appear to be limited to the Mediterranean, whereas others (e.g., *U. mediterranea*, *Planulina ariminensis*, *Paranomalina coronata*) may have evolved in the Mediterranean and then invaded the eastern Atlantic.

7.3. Environmental Parameters

Irrespective of the overall geographical range of a particular species, environmental factors will determine where that species actually occurs (Finlay & Fenchel 2004, Tsuchiya et al. 2008). As indicated above, the abundance, diversity, and composition of foraminiferal assemblages in coastal and sublittoral environments are controlled largely by a combination of physical and chemical parameters (temperature, salinity, currents, substrate, vegetation cover), food resources, and biotic interactions (Culver & Buzas 1999, Murray 2006). In deep water, early studies related the occurrence of foraminiferal species to the physical and chemical properties of bottom-water masses (Schnitker 1980). These ideas are no longer considered tenable (Jorissen et al. 2007), although...
some water-mass properties, notably current flow (Schönfeld 1997) and bottom-water corrosiveness (Schniedt et al. 1997), may be important. Levin et al. (2001) concluded that food inputs, bottom flow, bottom-water oxygenation, sediment heterogeneity, and ecological disturbance are the five main influences on deep-sea diversity patterns. Mackensen et al. (1995) identified a similar set of parameters that they considered to underlie the distribution of foraminiferal assemblages in the South Atlantic Ocean. Jorissen et al. (2007) reformulated these as follows: (a) organic matter exported to the seafloor and organic carbon content of the sediment, (b) bottom-water hydrodynamics and related sediment grain-size properties, (c) bottom-water oxygenation, and (d) bottom-water carbonate saturation. Hayward et al. (2011) reached similar conclusions based on their analysis of foraminiferal assemblages around New Zealand. Organic-matter flux and carbonate dissolution are probably the dominant ecological parameters across the vast abyssal areas, particularly in the Pacific Ocean (Saidova 2000), whereas hydrodynamics, oxygen, and sediment grain size are more influential at bathyal depths. Carbonate dissolution, together with sediment characteristics, is believed to exert an important influence on foraminiferal distributions down to abyssal depths around the Antarctic continent (e.g., Echols 1971, Anderson 1975).

Particularly in oligotrophic abyssal settings, the supply of organic matter to the seafloor, which is related to phytoplankton primary production, profoundly influences the structure, composition, and functioning of deep-sea benthic communities (Smith et al. 2008). The scale of the flux (Altenbach et al. 1999) and its seasonality (Gooday 1988, Loubère & Fariduddin 1999, Sun et al. 2006) are both important for foraminifera. In the North Atlantic (2,178–4,673-m water depth), an assemblage dominated by two phytodetritus species (Alabaminella weddellensis and Epistominella exigua) is associated with a highly seasonal organic carbon flux, whereas a Globocassidulina subglobosa–Nuttallides umbonifera assemblage is negatively correlated with a seasonal flux (Sun et al. 2006). The surface-ocean biogeochemical provinces recognized by Longhurst (1998) provide a comprehensive overview of the contrasting productivity regimes that undoubtedly underlie global macroecological patterns among benthic foraminifera. However, the main impact of food availability is likely to be on the ability of some species to outcompete others, as indicated by increases in their absolute and relative abundance (e.g., Koho et al. 2009). Whether fluxes of labile organic matter to the seafloor also limit species ranges is debatable. In contrast, physical and chemical parameters such as temperature, salinity, and oxygen concentrations act as limiting factors where they approach the tolerance level of the species under consideration (Murray 2001, 2006). At lower levels, variations in the magnitude of these parameters probably have no effect on species distribution patterns. Thus, given sufficient ability to disperse, species will probably occur everywhere, at higher or lower densities according to available food resources, except in areas where physical and chemical parameters (e.g., temperature, salinity, DO concentrations) place them under intolerable stress.

8. CONCLUSIONS

Like those of other organisms, biogeographic studies of deep-sea benthic foraminifera are hampered by imperfect taxonomy, the relative rarity of many species, and undersampling of the vast ocean-floor environment. Nevertheless, there is more information about foraminifera than many other deep-sea taxa. In contrast to the apparent prevalence of endemic distributions among coastal and sublittoral species, many common, well-characterized hard-shelled species appear to be distributed widely at bathyal and abyssal depths. This is consistent with the pattern of moderate cosmopolitanism and low endemism among species in the Gulf of Mexico (Sen Gupta & Smith 2010). However, this generalization must be tempered with some important caveats. Broad ranges are supported by genetic data in only a few cases, and widespread bathyal species often exhibit considerable morphological variation. It is possible that endemism is more prevalent among rare
species than currently realized, although conclusive evidence for restricted distributions will be difficult to obtain.

**SUMMARY POINTS**

Here, we return to the questions posed in the Introduction (see section above).

1. Do deep-water foraminiferal species have typical distribution patterns? Many common bathyal and abyssal morphospecies appear to have broad ranges (in few cases, supported by genetic analyses), while relatively few have restricted distributions. This contrasts with the frequency of apparent endemic distributions among shallow-water species. However, many deep-sea foraminiferal species are rare, often undescribed in the case of monothalamous taxa, and known only from one or a few samples. This makes it impossible to draw sensible conclusions about their geographical ranges.

2. What are the main factors influencing distribution patterns? Foraminiferal species distributions are influenced by their evolutionary history and environmental controls. In shallow-water settings, species ranges are limited by temperature and salinity close to the shore as well as by sediment characteristics, vegetation cover, and light penetration on the shelf. On the continental slope, distributions are influenced by food quantity and quality, sediment characteristics, topographic features (e.g., canyons), and, in places, bottom-water DO concentrations and current flow. On the environmentally more uniform abyssal plains, the main factors are the quantity and quality of organic matter reaching the seafloor, its seasonality, and the carbonate corrosion of the bottom water.

3. What is the degree of connectivity between populations? Most foraminifera appear to have excellent dispersive capabilities, mediated mainly by microbe-sized propagules, which can remain viable for several years. Transport of propagules by thermohaline and other currents has the potential to link distant populations genetically, either directly or via intermediate populations. However, slow evolution may also account for a lack of genetic differentiation, as is likely in the case of isolated populations of *Virgulinella fragilis*, a species confined to hypoxic/sulfidic habitats.

4. Are widely distributed benthic foraminiferal morphospecies genetically coherent or do they conceal cryptic species? There is good evidence for cryptic speciation (combined with slight morphological differences) in a few coastal benthic foraminifera as well as in planktonic species. Distant populations of certain bathyal and abyssal species have diverged genetically but probably not enough to regard them as cryptic species. Some morphologically simple monothalamous species, which possess few taxonomically useful characters, may encompass cryptic species. It is also possible that morphospecies with wide bathymetric ranges are genetically differentiated, although evidence is lacking.

5. To what extent does imperfect taxonomy obscure biogeographic patterns? Establishing species ranges depends crucially on the consistent use of species names. Synonyms appear to be quite prevalent among shelf-dwelling species and may lead to the inappropriate splitting of widely distributed species (pseudoendemism). The opposite problem, that of including disparate forms within one species name, seems to be quite common in some monothalamous and agglutinated taxa. This can artificially inflate species ranges.
FUTURE ISSUES

1. **Taxonomy:** Determining biogeographic patterns among foraminifera requires accurate taxonomy. A major effort is needed to revise difficult species groups (e.g., *Uvigerina* and *Globobulimina* spp.) and to describe novel species, particularly those belonging to the monothalamous taxa that abound in deep-sea sediments.

2. **Endemism:** How can endemic distributions be recognized, given the difficulty in establishing the presence of rare species in a particular area? The problem of undersampling is particularly acute in the deep sea, where only a tiny proportion of the vast benthic habitat has ever been sampled and the proportion of rare species, many of them undescribed, is particularly high.

3. **Cosmopolitanism:** Conversely, claims for ubiquitous species distributions based on literature sources from different regions depend crucially on the assumption that the species are accurately identified. Imperfect taxonomy means that, unless species are clearly illustrated, or the original material reexamined, reliance on faunal lists for distributional records is risky.

4. **Molecular genetics:** Only a handful of deep-sea species has been studied genetically. More analyses based on the SSU and ITS regions of the rDNA gene would reveal the degree of genetic differentiation between geographically and bathymetrically dispersed populations of the same morphospecies, as well as the possible existence of cryptic species. New generation sequencing will provide a rapid way to identify species in sediment samples as well as reveal species that cannot easily be detected visually.

5. **Climate change:** The consequences of ocean warming will create multiple challenges for benthic foraminifera. Many species feed at the base of the food chain on detrital material and will be impacted by warming-related changes in the quantity and quality of surface-derived organic matter reaching the seafloor. This is likely to lead to shifts in the diversity and dominance of foraminiferal assemblages, as well as species ranges, particularly at abyssal depths. In bathyal settings, hypoxia-tolerant species will become more widely distributed as OMZs expand and intensify.

6. **Reproduction:** Foraminifera can reproduce both sexually and asexually. Species that reproduce asexually may evolve more slowly and hence establish wider geographical ranges. Very little is known about which mode is typical for deep-sea foraminifera, although asexual reproduction seems more likely in the case of rare species, particularly at abyssal depths. This question could be investigated by studying the prevalence of microspheric and megalospheric forms in deep-sea samples.

**DISCLOSURE STATEMENT**

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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Contents

A Conversation with Karl K. Turekian
Karl K. Turekian and J. Kirk Cochran ......................................................... 1

Climate Change Impacts on Marine Ecosystems
Scott C. Doney, Mary Ruckelshaus, J. Emmett Duffy, James P. Barry, Francis Chan,
Chad A. English, Heather M. Galindo, Jacqueline M. Grebmeier, Anne B. Hollowed,
Nancy Knowlton, Jeffrey Polovina, Nancy N. Rabalais, William J. Sydeman,
and Lynne D. Talley .......................................................... 11

The Physiology of Global Change: Linking Patterns to Mechanisms
George N. Somero ....................................................................................... 39

Shifting Patterns of Life in the Pacific Arctic and Sub-Arctic Seas
Jacqueline M. Grebmeier ........................................................................... 63

Understanding Continental Margin Biodiversity: A New Imperative
Lisa A. Levin and Myriam Sibuet ............................................................... 79

Nutrient Ratios as a Tracer and Driver of Ocean Biogeochemistry
Curtis Deutsch and Thomas Weber .......................................................... 113

Progress in Understanding Harmful Algal Blooms: Paradigm Shifts
and New Technologies for Research, Monitoring, and Management
Donald M. Anderson, Allan D. Cembella, and Gustaaf M. Hallegraeff .......... 143

Thin Phytoplankton Layers: Characteristics, Mechanisms,
and Consequences
William M. Durham and Roman Stocker .................................................. 177

Jellyfish and Ctenophore Blooms Coincide with Human Proliferations
and Environmental Perturbations
Jennifer E. Purcell ...................................................................................... 209

Benthic Foraminiferal Biogeography: Controls on Global Distribution
Patterns in Deep-Water Settings
Andrew J. Gooday and Frans J. Jorissen .................................................. 237
Plankton and Particle Size and Packaging: From Determining Optical Properties to Driving the Biological Pump

L. Stemmann and E. Boss ................................................................. 263

Overturning in the North Atlantic

M. Susan Lozier ................................................................. 291

The Wind- and Wave-Driven Inner-Shelf Circulation

Steven J. Lentz and Melanie R. Fewings .................................................. 317

Serpentinite Mud Volcanism: Observations, Processes, and Implications

Patricia Fryer ................................................................. 345

Marine Microgels

Pedro Verdugo ................................................................. 375

The Fate of Terrestrial Organic Carbon in the Marine Environment

Neal E. Blair and Robert C. Aller ............................................................. 401

Marine Viruses: Truth or Dare

Mya Breitbart ................................................................. 425

The Rare Bacterial Biosphere

Carlos Pedrós-Alió ............................................................. 449

Marine Protistan Diversity

David A. Caron, Peter D. Countway, Adriane C. Jones, Diane Y. Kim, and Astrid Schnetzer ................................................................. 467

Marine Fungi: Their Ecology and Molecular Diversity

Thomas A. Richards, Meredith D.M. Jones, Guy Leonard, and David Bass ................................................................. 495

Genomic Insights into Bacterial DMSP Transformations

Mary Ann Moran, Chris R. Reisch, Ronald P. Kiene, and William B. Whitman .... 523

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