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Cenozoic mass extinctions in the deep sea: What perturbs the largest habitat on Earth?

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ABSTRACT

Deep-sea benthic foraminifera live in the largest habitat on Earth, constitute an important part of its benthic biomass, and form diverse assemblages with common cosmopolitan species. Modern deep-sea benthic foraminiferal assemblages are strongly influenced by events affecting their main food source, phytoplankton (a relationship known as benthic-pelagic coupling). Surprisingly, benthic foraminifera did not suffer significant extinction at the end of the Cretaceous, when phytoplankton communities underwent severe extinction. Possibly, benthic-pelagic coupling was less strong than today in the warm oceans of the Cretaceous–Paleogene, because of differences in the process of food transfer from surface to bottom, or because more food was produced chemosynthetically on the seafloor. Alternatively, after the end-Cretaceous extinction the food supply from the photic zone recovered in less time than previously thought. In contrast, deep-sea benthic foraminifera did undergo severe extinction (30%–50% of species) at the end of the Paleocene, when planktic organisms show rapid evolutionary turnover, but no major extinction. Causes of this benthic extinction are not clear: net extinction rates were similar globally, but there is no independent evidence for global anoxia or dysoxia, nor of globally consistent increase or decrease in productivity or carbonate dissolution. The extinction might be linked to a global feature of the end-Paleocene environmental change, i.e., rapid global warming. Cenozoic deep-sea benthic faunas show gradual faunal turnover during periods of pronounced cooling and increase in polar ice volume: the late Eocene–early Oligocene, the middle Miocene, and the middle Pleistocene. During the latter turnover, taxa that decreased in abundance during the earlier two turnovers became extinct, possibly because of increased oxygenation of the oceans, or because of increased seasonality in food delivery. The Eocene–Oligocene was the most extensive of these turnovers, and benthic-pelagic coupling may have become established at that time.

Keywords: deep-sea benthic foraminifera, extinction, K/Pg boundary, P/E boundary, E/O boundary, global warming, global cooling.

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INTRODUCTION

The deep-sea floor (bathyal and abyssal depths, i.e., depths >200 m) constitutes the largest habitat on Earth (e.g., Norse, 1994; Verity et al., 2002). The deep-ocean floor had long been thought to be devoid of life (Wyville Thomson, 1873), but in the early 1840s the Antarctic expedition of James Clarke Ross on the *Erebus* found indications that life existed there. Convincing evidence emerged during the *Lightning* and *Porcupine* expeditions in the late 1860s (Wyville Thomson, 1873), which led to the organization of the *Challenger* Expedition (1872–1876; Murray, 1895). This expedition abundantly documented that the deep-ocean floor was inhabited by many forms of life, and one of the zoological volumes in the expedition reports describes deep-sea foraminifera (Brady, 1884). Until the 1960s, deep-sea faunas were considered to have relatively low diversities, but studies in the second half of the twentieth century established that deep-sea ecosystems are characterized by low density of individuals at high species diversities (e.g., Sanders et al., 1965; Grassle and Maciolek, 1992; Gage, 1996, 1997; Rex et al., 1997; Levin et al., 2001; Snelgrove and Smith, 2002). The deep sea is still one of the least known ecosystems on Earth, however, and even general features of its high diversity, comparable to that in tropical rain forests and coral reefs, are not well known or understood, e.g., whether there are diversity gradients between high and low latitudes (e.g., Gage, 1996; Culver and Buzas, 2000; Rex et al., 2000; Levin et al., 2001), and how to explain diversity gradients with depth (see discussion in Rex et al., 2005). In addition, we do not know how much of the organic matter in the oceanic carbon cycle is contributed by photosynthesizing eukaryotes, how much by photosynthesizing prokaryotes (e.g., Kolber et al., 2000), or how much by lithoautotrophic prokaryotes (e.g., Herndl et al., 2005; Bach et al., 2006).

Present deep-ocean biota live perpetually in the dark, over most of the present ocean floor at temperatures close to freezing, under high pressures, at constant salinities, and in a world where very little food arrives, mainly derived from surface primary productivity hundreds to thousand of meters higher in the water column (e.g., Tappan, 1986; Gooday, 2003). Deep-sea biota outside hydrothermal vent regions and cold seep areas are thus surviving in an extremely low food environment, and are generally slow-growing and small. The seemingly monotonous environment is patchy on varying time-space scales, with skeletons of agglutinated, tree-shaped unicellular organisms (Xenophyophorans) serving as substrate for smaller unicellular biota (Hughes and Gooday, 2004), and with arrival of phyto-detritus patches (algal debris aggregated by mucus from various organisms) in regions of seasonal blooms (e.g., Rice et al., 1994), as well as such unpredictable events as whale-falls (e.g., Gooday and Rathburn, 1999; Gooday, 2002; Smith and Baco, 2003; Rathburn et al., 2005). Environmental heterogeneity is enhanced because the lack of physical disturbance of the environment allows small morphological features of the seafloor to persist for long periods (e.g., Gage, 1996).

In this oligotrophic world small organisms far outnumber larger ones (e.g., Gage and Tyler, 1991; Gage, 1996). Abundant among the small life forms are the eukaryotic, unicellular foraminifera, many of which form a shell or test from organic matter, secreted calcium carbonate, or agglutinated sedimentary particles. Foraminifera are one of the most ecologically important groups of marine heterotrophic protists. Their history goes back to the Early Cambrian (Pawlowski et al., 2003), and they occur throughout the oceans, even in the deepest trenches (Todo et al., 2005). Species abundant in the fossil record are characterized by robust calcium carbonate or agglutinated tests, and are dominantly between 0.1 and 1 mm in size, with most forms in the meiofauna (0.1–0.3 mm). Some delicate agglutinated taxa, the komokiaceans, form a branching, tubular system, typically 1–5 mm across (Gooday et al., 1997), and are classified among the macrofauna of the deep sea.

At depths greater than ~1000 m, foraminifera constitute more than 50% of the total eukaryotic biomass, with estimates of >90% at depths >2000 m in some regions (Gooday et al., 1992, 1998). Their assemblages are highly diverse: ~9000–10,000 living species have been described, with species determinations based on test morphology and composition (e.g., Goldstein, 1999). The shelled species are much better known than the naked (Pawlowski et al., 1999) or organic-walled (soft-shelled) species, most of which have not yet received formal species names (e.g., Cedhagen et al., 2002). Studies of genetic material (e.g., Pawlowski and Holzmann, 2002) suggest that biological species may be more numerous than morphological species, with—as in other marine invertebrates—the few studied groups of foraminifera containing cryptospecies (e.g., Gage, 1996).

Many of the morphological species are cosmopolitan in the present-day oceans. Benthic foraminifera move at speeds of only micrometers per hour (e.g., Kitazato, 1988; Gross, 1998; 2000), and almost certainly could not move at the speed suggested by the timing of first appearance of some species (e.g., *Cibicidoides wuellerstorfi*) in various oceans (Thomas and Vincent, 1987, 1988). Propagules formed during reproduction may be easily transported by ocean currents (Alve, 1999; Alve and Goldstein, 2003) and assist in the dispersal of species as well as in maintaining gene flow between distant populations.

In such a large habitat, physico-chemical parameters do not change rapidly over the whole habitat, and large-scale, isolating barriers are absent (Gage, 1996). The easily transported propagules ensure that new populations will become established at locations distant from existing ones as soon as environmental conditions are favorable, so that disturbed regions become recolonized quickly (Kuhnt, 1992; Hess and Kuhnt, 1996; Hess et al., 2001; Alve and Goldstein, 2003). Under such circumstances, one would expect morphological species to have relatively long species lives, as indeed observed in deep-sea benthic foraminifera, which have average species lives of ~15 m.y. (Culver, 1993). Some common Recent morphological species, e.g., *Oridorsalis umbonatus*, have persisted since at least the Late Cretaceous (Kaiho, 1998).

Thus a major question is what caused mass extinctions in the deep oceans: What type of environmental disturbance could be so all-encompassing, major, and rapid that cosmopolitan deep-sea species would suffer mass extinction, without the possibility to migrate vertically or horizontally and to repopulate from refugia? In this paper I use deep-sea benthic foraminifera, which of all deep-sea organisms have the most abundant fossil record, to probe this question; emphasis is on assemblages dominated by forms with secreted CaCO_3 tests and agglutinated forms with CaCO_3 cement, which in the present oceans occur at depths between several hundreds and ~4000–4500 m with the exception of the polar oceans (Gooday, 2003). I review our knowledge of present deep-sea benthic foraminiferal ecology, give an overview of deep-sea faunal assemblages through the Cenozoic, and discuss the decoupling between mass extinctions in the pelagic and benthic realms at both the Cretaceous-Paleogene and the Paleocene-Eocene boundaries (Thomas, 1990b; Kaiho, 1994a).

RECENT DEEP-SEA BENTHIC FORAMINIFERA

Historically, benthic foraminifera have been studied more by paleontologists and geologists than by biologists, because of their abundant fossil record and economic use in petroleum exploration (e.g., Cushman, 1940). Paleontological study of deep-sea benthic foraminifera intensified with the beginning of scientific piston coring expeditions after World War II (e.g., Phleger et al., 1953), and of deep-sea drilling in the late 1960s (e.g., Berggren, 1972). At that time, little was known about the biology of foraminifera in general and deep-sea forms specifically, so that early studies consisted mainly of taxonomic descriptions and contained little interpretation of ecological or paleoceanographic information. Only recently, and specifically since such research programs as the Joint Global Ocean Flux Studies in the 1980s, have we learned more about the ecology of living foraminifera (e.g., Murray, 1991; Sen Gupta, 1999a; Smart, 2002; Gooday, 2003) and about the processes through which foraminifera calcify their tests (e.g., Hemleben et al., 1986; Hansen, 1999; Erez, 2003; Toyofuku and Kitazato, 2005). Even now, however, we are still ignorant of much of their biology and ecology, and paleoceanographic interpretation of deep-sea benthic assemblages remains difficult (e.g., van der Zwaan et al., 1999; Murray, 2001; Jorissen et al., 2007).

Benthic foraminifera are abundant deep-sea organisms, one of the principal eukaryote forms of life in the deep ocean, and constitute a large proportion of the eukaryotic deep-sea benthic biomass (e.g., Gooday, 1999, 2003). Like other deep-sea benthic organisms, they are locally highly diverse in normal marine environments, with more than 100 morphological species within relatively small sediment samples (e.g., Gooday, 1999; Gooday et al., 1998), but we do not know how this locally high diversity translates into regional diversity. As for other deep-sea biota, we do not truly understand why there is such high species richness among organisms many of which are deposit feeders that rely on organic detritus, in an environment where structural variety is

apparently lacking in the endless tracts of sediment on the seafloor (Gage, 1996; Levin et al., 2001; Snelgrove and Smith, 2002; Rex et al., 2005). The role of environmental patchiness as described above is not yet well understood, and neither is the contribution of lithoautotrophic prokaryotes to the overall oceanic carbon cycle and environmental patchiness on the seafloor (e.g., Dixon and Turley, 2001; Herndl et al., 2005).

Since the 1970s, benthic foraminiferal assemblages have been used to derive information on the deep-sea environment of the geological past, with early papers interpreting Atlantic foraminiferal assemblages as reflecting the water-mass structure of that ocean (Streeter, 1973; Schnitker, 1974; Lohmann, 1978). Subsequent research looking for such linkages in different oceans and for different times was not entirely successful (e.g., Mackensen et al., 1995); and the development of transfer functions to derive quantitative expressions in which aspects of deep-sea benthic foraminiferal assemblages could be used as proxy for environmental parameters has proven difficult (van der Zwaan et al., 1999). This difficulty is probably explained by the fact that deep-sea benthic foraminiferal assemblages are influenced by a combination of many parameters varying at different temporal and spatial scales and in many cases not independently from each other (e.g., Schnitker, 1994; Levin et al., 2001; Murray, 2001). Benthic foraminiferal proxies, many of which were reviewed by Gooday (2003) and Jorissen et al., 2007, include bathymetry (e.g., Hayward, 2004), organic matter flux, and oxygen concentrations in bottom and pore waters (e.g., Loubere, 1991, 1994, 1996; Kaiho, 1994b, 1999; Schmiedl et al., 1997, 2000); location and motion of redox fronts (with possibly related populations of Archaea and Bacteria) through the sediments (e.g., Fontanier et al., 2002, 2005); sediment type, temperature, bottom water chemistry (e.g., carbonate undersaturation, Bremer and Lohmann, 1982), hydrography (e.g., current flow; Schoenfeld, 2002), and hydrostatic pressure; and difficult-to-quantify parameters such as seasonality of the flux of organic matter, and relative amounts of labile and refractory organic matter (e.g., Gooday, 1988, 2002; Smart et al., 1994; Thomas et al., 1995; Loubere, 1998; Loubere and Fariduddin, 1999; Moodley et al., 2002; Fontanier et al., 2003). A strong correlation between benthic assemblages and one parameter is usually found only in extreme environments where organisms are strongly influenced by one limiting parameter, such as, for instance, severe dysoxia (low oxygen levels) to anoxia (lack of oxygen) (e.g., Bernhard, 1986; Sen Gupta and Machain-Castillo, 1993; Bernhard et al., 1997; Moodley et al., 1998).

Oxygen depletion resulting from organic enrichment is much more common along continental margins than on abyssal plains (e.g., Levin, 2003; Helly and Levin, 2004). Continental slopes and rises differ from abyssal plains because they are topographically complex and are more commonly subjected to vigorous currents and mass movements (e.g., turbidity currents, debris flows). Primary productivity along continental margins is higher overall than in open ocean, because of the prevalence of coastal upwelling in addition to nutrient discharges by rivers (e.g., Berger et al., 1988; Levin, 2003). On continental margins sedimentation rates

are higher, sediments are more heterogeneous, and food particles may be supplied not only from primary productivity in the overlying waters but also by lateral transport of usually more refractory organic matter (e.g., Fontanier et al., 2005).

Bottom- and pore-water oxygenation is usually inversely related to the flux of organic matter, because the oxidation of abundant organic matter causes the low oxygen conditions or even absence of oxygen that is common in areas of upwelling (e.g., Bernhard and Sen Gupta, 1999; Levin, 2003; Helly and Levin, 2004). Recent field and laboratory research focuses on these two inversely related parameters, the flux of organic matter (food) to the seafloor and the oxygen concentrations in bottom water and pore waters (e.g., Jorissen et al., 1995, 2007; Ohga and Kitazato, 1997; Schmiedl et al., 2000; Moodley et al., 1998; Gooday and Rathburn, 1999; Loubere and Fariduddin, 1999; van der Zwaan et al., 1999; Jorissen and Rohling, 2000; Moodley et al., 2000). It seems reasonable that food is an important limiting factor for deep-sea benthic foraminifera outside upwelling regions, especially on abyssal plains and along seamounts, because pelagic surface ecosystems are already severely nutrient limited if compared to, for example, terrestrial ecosystems (e.g., Tappan, 1986), and only a very small fraction of primary produced material reaches the bottom of the oceans (e.g., Smith et al., 1997).

The interplay of the two interrelated factors, oxygen availability and food supply, and their effects on the benthic faunal assemblage and its position within the sediments was discussed by Jorissen et al. (1995) in the "TROX-model," and modified and refined by various authors (Jorissen et al., 1998; Jorissen, 1999; Fontanier et al., 2002; and Gooday, 2003). In this model, microhabitat occupancy (the places where foraminifera live within the sediment) is correlated to the availability of food and oxygen: in a continuum of increasing food supply from oligotrophic through mesotrophic to eutrophic, oxygen levels are negatively correlated to food supply. At the oligotrophic extreme, populations are mainly limited by food, with a "critical food level" at shallow depths (a few centimeters). At the eutrophic extreme, populations are limited by oxygen levels, with a critical oxygen level finally reaching the sediment-water interface or even moving into the water column when bottom waters become anoxic.

In oligotrophic settings (e.g., abyssal plains) foraminifera are highly concentrated in the uppermost levels of the sediment: most food particles are used up by organisms dwelling close to the sediment-water interface, very little organic matter is buried in the sediment except for that worked down by bioturbating organisms such as echinurans, and pore waters are well oxygenated. As the food supply increases, epifaunal to shallow infaunal forms use only part of the food. The remainder of the food is buried to greater depths, so that species can live and feed in the sediment, at depths ranging from epifaunal to shallow infaunal (0–1.5 cm), to intermediate infaunal (1.5–5.0 cm), to deep infaunal (5–10 cm). The deepest level of occurrence is limited either by the food available (toward the oligotrophic part of the continuum) or by the low oxygen levels (toward the eutrophic end of the continuum). The highest species diversity occurs in

mesotrophic regions, with co-occurrence of epifaunal through deep infaunal forms (Fig. 1 in Gooday, 2003).

Epifaunal and infaunal groups may differ in, and thus be recognized by, their overall test morphology (e.g., Corliss, 1985; Corliss and Chen, 1988; Thomas, 1990a; Kaiho, 1991), but there is some confusion about the use of the terms "epifaunal" and "infaunal." The above authors used the term "epifaunal" for foraminiferal species living on the surface and in the uppermost 0–1 cm sediment. In soft sediments, the sediment-water interface is not sharply defined, and living exactly at this interface is difficult to impossible. Buzas et al. (1993) pointed out that species within the top 1 cm of sediment are actually living within the sediment because many foraminifera are much smaller than 1 cm, and thus should be called "shallow infaunal." Later publications tend to not use the word "epifaunal," unless indicating species such as *Cibicides wuellerstorfi*, which prefer to live on objects sticking out above the sediment-water interface (e.g., Fig. 3 in Altenbach and Sarnthein, 1989).

In general, benthic foraminifera with plano-convex, biconvex, and rounded trochospiral, tubular, and coiled-flattened tests have been observed to be epifaunal to shallow infaunal. Foraminifera living in the deeper layers of the sediment have cylindrical or flattened tapered, spherical, rounded planispiral, flattened ovoid, globular unilocular, or elongate multilocular tests. For many taxa, however, the relation between test morphology and microhabitat has not been directly observed but is extrapolated from data on other taxa (e.g., Jorissen, 1999). In one of the few studies evaluating the correlation between test morphology and microhabitat statistically, such assignments for modern foraminifera were shown to be accurate only ~75% of the time (Buzas et al., 1993).

A matter of debate is the importance of the food flux versus that of oxygenation in determining the foraminiferal assemblages, as reviewed most recently by Gooday (2003). Most authors agree that in generally oxygenated conditions (i.e., oxygen concentrations above ~1 mg/L) food is the more important determinant (e.g., Rathburn and Corliss, 1994; Morigi et al., 2001), whereas Kaiho (1994b, 1999) places more importance on oxygen levels in bottom waters. Several authors (as reviewed in Gooday, 2003) agree that the boundary between more oligotrophic and more eutrophic regions is at about a flux level of 2–3 g C_{org} m⁻². The generally more eutrophic continental margins contain assemblages with more abundant infaunal species, including species belonging to the genera *Bolivina*, *Bulimina* and *Uvigerina*, and these species are considered indicative of eutrophic conditions.

In detail, and on short temporal and small spatial scales, the situation is considerably more complex than given in the TROX model (e.g., Linke and Lutze, 1993). Different foraminiferal species have different food preferences (e.g., Lee, 1980; Goldstein and Corliss, 1994; Heinz et al., 2002; Suhr et al., 2003). Species react differently to food pulses, with some species reacting rapidly and opportunistically by fast reproduction (e.g., Altenbach, 1992; Linke et al., 1995; Ohga and Kitazato, 1997; Moodley et al., 2000, 2002), especially species that feed on fresh phytodetritus (Gooday, 1988, 1993; Moodley et al., 2002; Suhr et al., 2003),

whereas other species grow more slowly (Nomaki et al., 2005). Many species do not permanently live at the same depth below the sediment-water interface, but move vertically through the sediments (e.g., Kaminski et al., 1988; Linke and Lutze, 1993; Bornmalm et al., 1997; Ohga and Kitazato, 1997; Gross, 1998; Gooday and Rathburn, 1999; Jorissen, 1999; Gross, 2000; Fontanier et al., 2002; Geslin et al., 2004), either reacting directly to food pulses (Altenbach, 1992; Linke et al., 1995; Heinz et al., 2002), or following pore-water oxygen gradients, which define different redox levels characterized by specific bacterial-archaeal populations (Moodley et al., 1998; Gross, 1998, 2000; Geslin et al., 2004).

Benthic foraminiferal proxies have been used extensively in an attempt to reconstruct export productivity (e.g., Altenbach et al., 1999). Proxies for primary productivity include the Benthic Foraminiferal Accumulation Rate (BFAR; Herguera and Berger, 1991) and the more statistically complex method of Loubere (1994, 1996). The approach appears to give good results mainly in well-oxygenated sediments where no carbonate dissolution occurs, but the validity of the quantitative calculation may be questionable when there is variation in the type of organic matter deposited (e.g., Guichard et al., 1997). The correlation between BFAR and export productivity may not be linear in the presence of opportunistically blooming, phytodetritus-exploiting species (Schmiedl and Mackensen, 1997). The fact that in many regions there is a significant correlation between benthic foraminiferal accumulation rate and primary productivity in surface waters, however, indicates that present deep-sea faunas receive most of their food (directly or indirectly) from photosynthetic primary producers.

Using benthic foraminifera to reconstruct export productivity can be problematic because such a proxy must be calibrated in the present oceans, where the correlation between export productivity and food arriving at the seafloor is not well known quantitatively. The single-celled algae (including prokaryotes, Kolber et al., 2000) at the base of the pelagic food chain are not efficiently deposited to the seafloor as single particles. For efficient transfer, material must be aggregated in larger particles (marine snow; e.g., Turley, 2002), in sticky, seasonally produced phytodetritus (e.g., Jackson, 2001; Beaulieu, 2002) in which the “stickiness” increases by the exudation by phytoplankton of polysaccharides in Transparent Exopolymer Particles (TEP; Engel et al., 2004), in diatom mat aggregates (e.g., Kemp et al., 1995, 2000), in fecal pellets of zooplankton or nekton, ballasted by siliceous and carbonate tests (e.g., François et al., 2002; Klaas and Archer, 2002) or by terrigenous dust (Ittekkot, 1993), or in tunicate feeding structures (Robison et al., 2005). Such aggregated food reaches the deep-sea floor in a few weeks and contains the labile, fresh organic material that is used preferentially by some benthic foraminifera (e.g., Gooday, 1988, 1993, 2002; Ohga and Kitazato, 1997; Suhr et al., 2003). Only a very small fraction of the primary produced biomass reaches the seafloor (0.01%–1.0%; e.g., Murray et al., 1996), and there is no linear correlation between productivity and flux below 2000 m at high productivities ($>200 \text{ gC m}^{-2}\text{yr}^{-1}$) (Lampitt and Antia, 1997). There

is a discrepancy between measured fluxes of sinking particulate organic matter and food demand (sediment community oxygen consumption), with the fauna apparently consuming more food than is supplied, as measured in the Pacific Ocean (Smith and Kaufmann, 1999; Smith et al., 2002) and as averaged over the world’s oceans (Del Giorgio and Duarte, 2006).

Some authors argue that high seasonality results in high efficiency of transport to the seafloor (Berger and Wefer, 1990), whereas others argue the reverse (François et al., 2002). In addition, there is no agreement whether carbonate or siliceous tests are more efficient in ballasting organic matter (compare François et al., 2002, and Klaas and Archer, 2002, with Katz et al., 2005), and whether dust, carbonate, or silica tests function as ballast for organic matter at all (Passow, 2004). Increased supply of calcareous tests intuitively appears to lead to increased ballasting, but investigations of *Emiliania huxleyi* blooms under high atmospheric pCO_2 levels have documented increased transport of organic matter to the seafloor with less calcification, because the production of the sticky TEPs increases under such conditions (Delille et al., 2005). Locally, organic matter may be supplied mainly by lateral transport (e.g., Fontanier et al., 2005). Lithoautotrophic organic matter, which is produced in situ on the seafloor or in overlying waters below the photic zone (e.g., Karner et al., 2001; Herndl et al., 2005; Bach et al., 2006), could add to the overall food supply even outside the direct environment of hydrothermal vents or cold seeps. Bacterial oxidation of methane in hydrothermal plumes in the present oceans contributes an amount of organic carbon up to 150% that of the surface-produced organic matter reaching the depth of the plume (2200 m) in the northeast Pacific (Roth and Dymond, 1989; de Angelis et al., 1993).

In view of these uncertainties about food transfer to the deep-sea in the present oceans, we are uncertain regarding the quantitative correlation between present foraminiferal parameters and primary productivity in the photic zone. Because only such a minute fraction of primary produced organic matter reaches the seafloor, relatively small changes in efficiency of this transfer may have a major impact on the amount of food reaching benthic assemblages, even at constant productivity (see also Katz et al., 2005).

CENOZOIC BENTHIC FORAMINIFERAL FAUNAS

In contrast to planktic foraminifera, deep-sea benthic foraminiferal species have, on average, long species lives, and thus cannot be used for detailed stratigraphic subdivision of geological time: they are not good “guide fossils” (e.g., Boltovskoy, 1980, 1987; van Morkhoven et al., 1986; Tappan and Loeblich, 1988; Thomas, 1992a; Culver, 1993). The majority of modern calcareous smaller benthic foraminifera in the deep oceans belong to the orders Rotalida and Buliminida (Sen Gupta, 1999b), which became common in the deep oceans gradually, after the Cenomanian-Turonian Oceanic Anoxic Event, with many common genera present from the Campanian (Kaiho, 1994a, 1998).

These taxa thus became common in the deep oceans during the later part of the “Mesozoic Marine Revolution,” a time of reorganization of ecosystems and evolution of modern forms of many marine animals and eukaryotic plankton (e.g., Vermeij, 1977; Bambach, 1993; Katz et al., 2005). The deep-sea benthic foraminifera of the later Campanian and the Maastrichtian contain many components that persist in Paleocene faunas, including common species such as *Nuttallides truempyi* and *Stensioeina beccariiiformis* (e.g., Cushman, 1946; van Morkhoven et al., 1986; Thomas, 1990b, 1992a; Kaiho, 1994a, 1998; Alegret and Thomas, 2001). Benthic foraminifera did not suffer significant extinction across the Cretaceous- Paleogene boundary (review by Culver, 2003): their most severe extinction of the Cenozoic occurred at the end of the Paleocene (review by Thomas, 1998).

Assemblage zones for Cenozoic bathyal and abyssal faunas have been recognized for the southern oceans (Thomas, 1990a), for the Indian Ocean (Nomura, 1991, 1995), and for the global oceans (Berggren and Miller, 1989). These zones can be simplified to four Cenozoic faunas (Miller et al., 1992; Thomas, 1992a) (Fig. 1): (1) a “Cretaceous Fauna,” which survived from the Late Cretaceous and suffered abrupt extinction at the end of the Paleocene; (2) an early-middle Eocene “Paleogene fauna,” which underwent a gradual but severe turnover (E/O) through the late Eocene and earliest Oligocene (Corliss, 1981; Thomas, 1992a,

1992b; Thomas and Gooday, 1996); (3) an Oligocene–early Miocene “Transitional Fauna,” which underwent a gradual turnover (mMIO) in the middle Miocene (Woodruff and Douglas, 1981; Thomas, 1986; Woodruff and Savin, 1989); and (4) the “Modern Fauna.” An additional transition (mPL) was recognized in the middle Pleistocene (ca. 1.2–0.6 Ma), with the extinction of many cylindrical species having complex (e.g., dentate, cribrate, lunate) apertural shapes (Weinholz and Lutze, 1989; Schoenfeld, 1996; Hayward, 2001, 2002; Kawagata et al., 2005).

The three gradual benthic foraminiferal faunal turnovers (E/O, mMIO, mPL) are similar in paleoceanographic setting: the first two occurred during periods of global cooling and growth of polar ice sheets (e.g., Zachos et al., 2001), and the last one during the period of intensification of Northern Hemisphere glaciation (Zachos et al., 2001; Tziperman and Gildor, 2003). During all three turnovers there was a loss of “cylindrical” species, mainly uniserial or elongate biserial, belonging to the stilostomellids, pleurostomellids, or uniserial lagenids, some of the latter group surviving to today (e.g., Thomas, 1986; Hayward, 2001, 2002; Kawagata et al., 2005). Many of these cylindrical species (including all stilostomellids) became extinct during the Mid Pleistocene Revolution (so that we have no information on their ecology), after decreasing in abundance during the Eocene-Oligocene and middle Miocene turnovers (Fig. 2). These cylindrical species

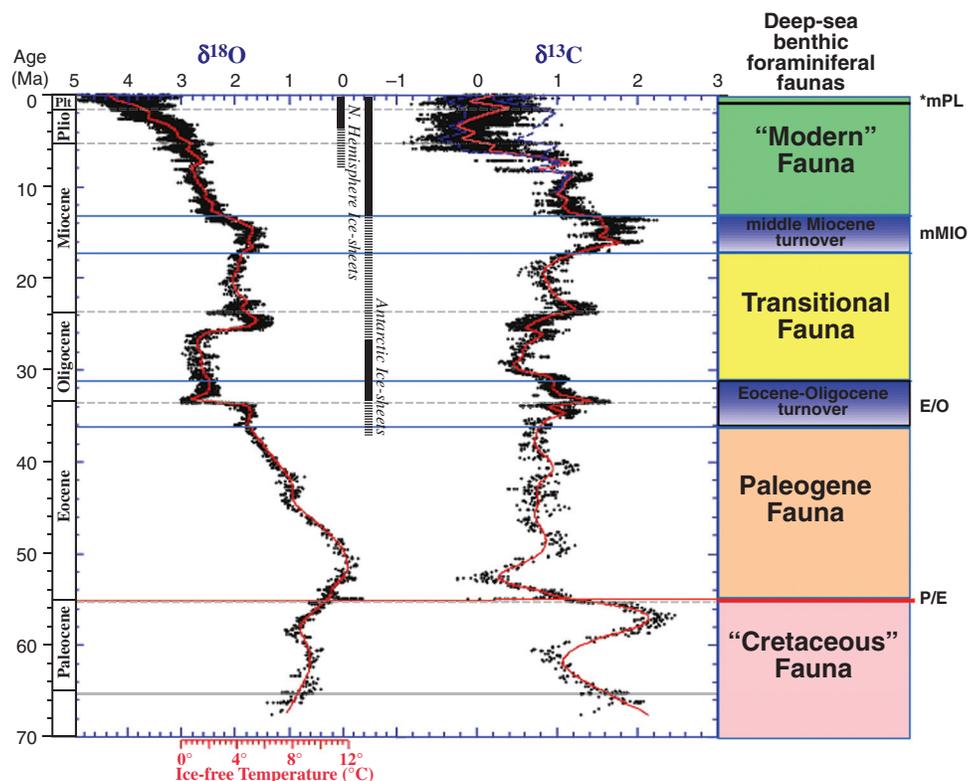


Figure 1. Cenozoic deep-sea benthic foraminiferal faunas (modified after Thomas et al., 2000) as compared with the deep-sea carbon and oxygen isotopic record (Zachos et al., 2001). *mPL—Mid-Pleistocene benthic foraminiferal turnover, also known as the *Stilostomella* extinction (Hayward, 2001). P/E—Paleocene/Eocene benthic foraminiferal extinction.

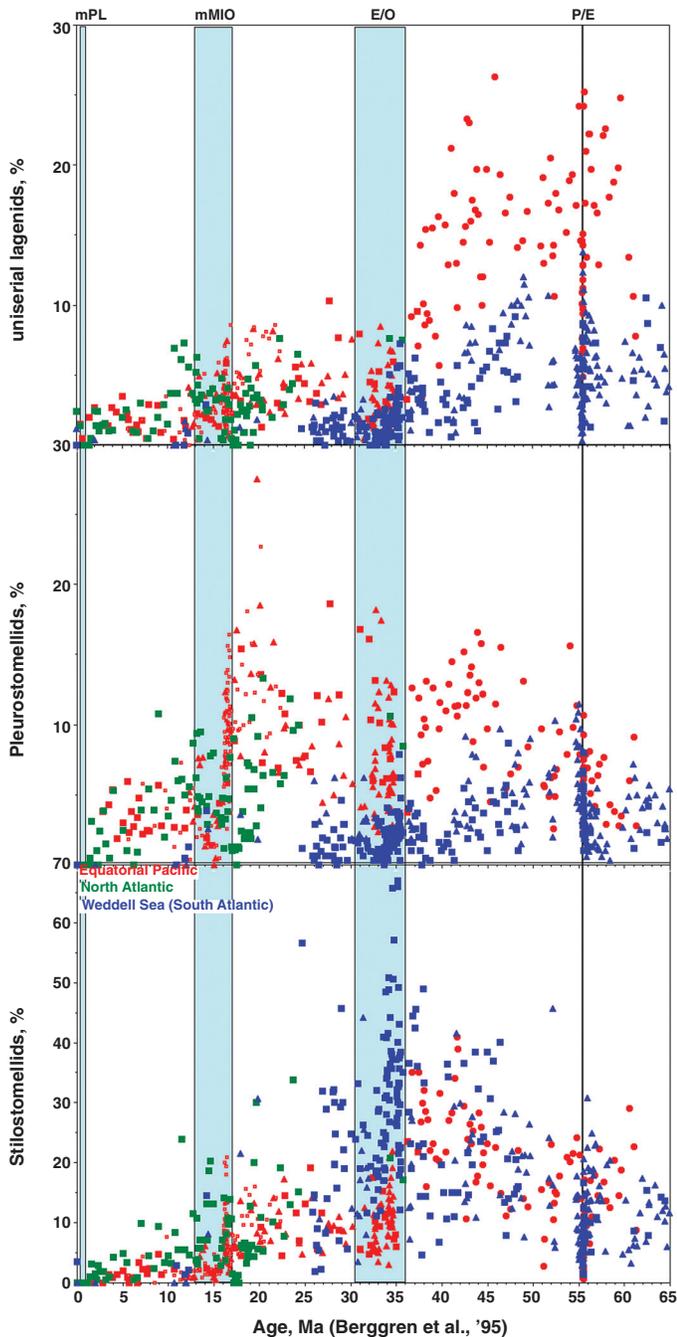


Figure 2. Relative abundance of cylindrical taxa during the Cenozoic. The vertical blue bars indicate the periods of faunal turnover (Fig. 1). P/E—Paleocene/Eocene benthic foraminiferal extinction. E/O—Eocene/Oligocene faunal turnover. mMIO—Middle Miocene faunal turnover. mPL—Middle Pleistocene faunal turnover. Data are compiled from DSDP/ODP Sites in the equatorial Pacific, with ages recalculated according to Berggren et al., 1995. Red—Site 865 (Thomas, 1998, unpublished data); Sites 573, 574, 575 (Thomas, 1985). Blue—Weddell Sea Sites 689, 690 (Thomas, 1990a). Green—North Atlantic Sites 608, 610 (Thomas, 1987; see also Thomas and Gooday, 1996). Note that only some groups of the uniserial lagenids became extinct in the middle Pleistocene, with several surviving until today.

may have lived infaunally and reflect a relatively high food supply: their abundances correlate positively with those of genera that in present oceans are indicative of high food and/or low oxygen (e.g., *Bulimina*, *Uvigerina*, *Bolivina*) in the North Atlantic (Kawagata et al., 2005).

There are biogeographical differences between the various cylindrical taxa (Fig. 2). Uniserial lagenids were more abundant at low latitudes and middle-upper bathyal depths, and decreased in abundance strongly in the late Eocene, whereas the pleurostomellids did so mainly in the middle Miocene. Stillostomellids were more abundant at high latitudes, especially in the late Eocene, and decreased in both the Eocene-Oligocene and the middle Miocene turnovers.

As a result of these three turnovers, Recent open-ocean deep-sea faunas (away from continental margins) differ strongly from middle Eocene and older ones (e.g., Boltovskoy, 1984, 1987; Miller et al., 1992; Thomas et al., 2000), which lived in “greenhouse” oceans that were 10–12 °C warmer than the present oceans (e.g., Zachos et al., 2001). The Eocene and older faunas living remote from the continents resemble present continental-margin faunas in common morphotypes: high percentages of high food/low oxygen indicator genera, cylindrical taxa, and taxa in the Order Buliminida (Thomas et al., 2000). These “greenhouse” faunas contained only very rare phytodetritus-using species (e.g., *Epistominella exigua*), which are common in present open-ocean settings (e.g., Gooday, 2003). Such phytodetritus-using species bloom opportunistically when fresh, labile organic material reaches the seafloor, and they rapidly increased in abundance during the E/O turnover. In the middle Miocene they became common even in the equatorial Pacific (Thomas, 1985; Thomas and Gooday, 1996; Thomas et al., 2000). Miliolid taxa earlier had become common at neritic depths, and migrated into the deep oceans during the middle Miocene turnover (Thomas, 1986; 1992a), when the suspension-feeding *Cibicidoides wuellerstorfi* evolved, with a first appearance slightly earlier in the Pacific than in the Atlantic (Thomas and Vincent, 1987). At greater depth and at high latitudes (close to the lysocline), the relative abundance of *Nuttallides umbonifera* (a species seen as indicative of corrosive bottom waters and/or oligotrophy) strongly increased in abundance during the E/O turnover (Thomas, 1992a; Thomas et al., 2000).

The modern assemblages typical for seasonal delivery of fresh phytodetritus to the seafloor had no early Paleogene counterpart: benthic-pelagic coupling, in which labile organic matter is supplied in seasonal pulses, may have originated or intensified with the establishment of the Antarctic ice sheet in the earliest Oligocene (Zachos et al., 2001), when stratification of the oceans increased (e.g., Schmidt et al., 2004), seasonality of productivity increased (e.g., Thomas and Gooday, 1996), the importance of diatoms as primary producers increased (Katz et al., 2004), the size of diatoms increased (Finkel et al., 2005), and fresh phytodetritus (arriving at the seafloor only weeks after having been produced) became an important part of the food delivered to the deep-sea benthos. Early Paleogene deep-sea benthic foraminiferal assemblages may thus have differed from modern ones by not having the niche of

“phytodetritus species” filled. The Paleogene assemblages contained mainly deposit feeders (as defined by Goldstein and Corliss, 1994), with different niches defined by their location with regard to redox fronts, the presence or absence of xenophyophoran tests, and other differences at a small spatial scale. In this view, the E/O turnover represents an important, structural change in deep-sea faunas, with modern-type assemblages becoming established (Boltovskoy, 1984, 1987; Thomas et al., 2000).

The Eocene/Oligocene, middle Miocene, and middle Pleistocene benthic foraminiferal faunal turnovers occurred during periods of global cooling, and represent subsequent but similar steps during which the open-ocean faunas gradually took on their modern composition, losing various groups that we consider to indicate either a high food supply or low oxygenation (Kaiho, 1991; Kawagata et al., 2005), or a less seasonally pulsed overall food supply (Thomas and Gooday, 1996; Thomas et al., 2000; Thomas, 2003). In these speculations it should not be forgotten that morphotype assignments are problematic in the present oceans (Buzas et al., 1993), and thus even more so for extinct species.

The apparent loss of high-food species during global cooling presents a paleoceanographic problem, because cooling, increasingly vigorous ocean circulation, and upwelling, possibly in addition to more vigorous chemical weathering and delivery of nutrients to the oceans, have been thought to induce increased oceanic productivity, (e.g., Brasier, 1995a, 1995b; Katz et al., 2004; Finkel et al., 2005). The problem is exacerbated because in the early Paleogene deep-water temperatures were $\sim 10^\circ\text{C}$ higher than today, so that metabolic rates of foraminifera were higher by as much as a factor of 2 (e.g., Hallock et al., 1991; Gillooly et al., 2001), thus requiring twice as much food in order to keep the same faunal structure. Research on modern faunas does not support the hypothesis (Kaiho, 1991) that the faunal change in the late Eocene–Oligocene resulted mainly from increased oxygenation, because benthic foraminifera do not appear to be influenced by oxygenation at the levels reconstructed for these times (e.g., Gooday, 2003).

It seems improbable that export productivity in the middle Eocene and earlier was more than twice as high as at present (e.g., Brasier, 1995a, 1995b), but the efficiency of food transfer to the seafloor (as discussed above for the present oceans) may very well have differed in the “greenhouse” oceans, as suggested by the proposal that a larger fraction of organic matter was preserved in Paleogene sediments (Kump and Arthur, 1997). In view of our lack of understanding of food transfer in the present oceans, we cannot be certain about such processes in the “greenhouse” oceans. Ecosystem modeling does not clearly answer whether warming would result in higher or lower net global productivity (Sarmiento et al., 2004), or export productivity (Laws et al., 2000). Food-web structure would probably be different in a warmer world (e.g., Petchey et al., 1999) without polar sea ice (Loeb et al., 1997), and the effects of such changes in ecosystems structure are not understood. We can speculate on several, not mutually exclusive, possibilities (see also Thomas et al., 2000; Thomas, 2003):

1. The ocean circulation may have been not just quantitatively but also qualitatively different from that in the present oceans, with ‘greenhouse’ oceans dominated by eddy rather than gyral circulation (Hay et al., 2005), or increased hurricane activity and vertical mixing, resulting in increased poleward heat transport (Emanuel, 2001, 2002). Such different circulation patterns might have resulted in more efficient transfer of food to the seafloor as the result of more extensive vertical water motion and more vigorous deep vertical mixing. Emanuel’s (2001) discussion argues for increased open-ocean upwelling, thus less difference in primary productivity between continental margins and open ocean, as supported by the benthic foraminiferal evidence.
2. Higher temperatures of the oceans could have resulted in lower oxygenation, thus in less degradation of organic matter. This does not appear to be probable because there is no significant correlation between oxygenation and organic matter preservation in the present oceans (e.g., Hedges and Keil, 1995; Kristensen et al., 1995). In addition, present deep-sea faunas in relatively warm oceans (e.g., the Red Sea) are oligotrophic in character (e.g., Thiel et al., 1987; Edelman-Furstenberg et al., 2001).
3. Higher temperatures would result in higher metabolic rates for bacteria, which determine organic matter degradation and transformation, as well as lithoautotrophic production. More active bacteria could have resulted in a more active “bacterial loop,” more conversion of dissolved organic carbon into particulate organic carbon, thus enhanced food supply for zooplankton, delivering more food (fecal pellets) to the seafloor (e.g., Jannasch, 1994; Verity et al., 2002). Alternatively, higher bacterial activity could mean higher use of refractory carbon, and increase in bacterial biomass that can be taken in by benthic foraminifera. In addition, increasing temperatures lead to the dominance of different bacterial groups, producing different organic compounds (Weston and Joye, 2005), for which different groups of foraminifera might have a preference.
4. Dominant “greenhouse” ocean primary producers differed from those in the present “icehouse” ocean: diatoms strongly increased in importance and size after the end of the Eocene (e.g., Katz et al., 2004; Finkel et al., 2005). Many diatoms produce mucus that causes coagulation of organic matter; thus one would expect more diatom productivity to result in more rapid transfer of organic matter to the seafloor. François et al. (2002) and Klaas and Archer (2002), however, argue that transfer is less efficient in diatom-dominated systems than in carbonate (calcareous nannofossil) dominated systems. If this was true for the early Paleogene, food transfer could have been more efficient due the greater prevalence of calcareous primary producers.
5. Under the higher $p\text{CO}_2$ levels that may have been present in the atmosphere in the Paleogene (Zachos et al., 2001; Pagani et al., 2005) calcareous nannoplankton may have calcified less in the more acid oceans (Feely et al., 2004; Orr et al., 2005), unexpectedly leading not to decreased deposition of organic

matter because of decreased carbonate ballasting, but to increased exudation of sticky polysaccharides and increased deposition of organic carbon (Delille et al., 2005).

6. In the Paleogene, the contribution to the seafloor food supply by in situ lithoautotrophic productivity was larger (Thomas, 2003). Benthic foraminifera living in cold-seep areas are not taxonomically different from high-food/low oxygen species (Rathburn et al., 2000; Bernhard et al., 2000, 2001; Barbieri and Panieri, 2004), and we thus cannot distinguish overall high food supply from supply by chemosynthesis. The higher temperatures could have speeded up metabolism of bacteria, resulting in increased methane production at the lower oxygenation, possibly in combination with higher delivery of organic matter to the seafloor. They could also have led to production of more labile compounds by bacteria, which foraminifera can take up more easily (Weston and Joye, 2005).
7. The hypothesis that benthic foraminiferal assemblages indicate a higher overall food supply to the seafloor is incorrect: what is really indicated is a less seasonal delivery of organic material in the early Paleogene (e.g., Thomas and Gooday, 1996; Ohkushi et al., 1999). The abundant occurrence of phytodetritus species apparently does not indicate overall levels of primary productivity, but rather a strongly seasonal delivery of food (e.g., Gooday, 2003). Such a strongly seasonal food supply can be used only by species that can rapidly and opportunistically react, possibly causing the gradual demise of species that may have been specialized detritus feeders, with their complex apertural structures directing pseudopodial flow.

BENTHIC FORAMINIFERA AT THE CRETACEOUS-PALEOGENE BOUNDARY

Most earth scientists accept that the end-Cretaceous mass extinction was caused at least in part by the impact of a meteorite with a diameter of ~10 km (Alvarez et al., 1980) on the northern Yucatán peninsula (Hildebrand et al., 1991). Deep-sea benthic foraminifera are among the survivors. Until recently, net extinction of benthic foraminifera was alleged to have been more severe in shallower waters (e.g., Thomas, 1990b; Kaiho, 1992, 1994a; Coccioni and Galeotti, 1998), but the excellent review by Culver (2003) documents that shallow-dwelling species were not more severely affected than deeper-dwelling ones. Benthic foraminiferal assemblages underwent temporary changes in community structure in calcareous species (Culver, 2003) as well as in agglutinated taxa (e.g., Kuhnt and Kaminski, 1996; Culver, 2003; Bak, 2005; Kaminski and Gradstein, 2005). These changes in community structure varied geographically and bathymetrically (e.g., Coccioni and Galeotti, 1998; Alegret and Thomas, 2005) but did not result in significant net extinction.

At locations relatively close to the impact location, e.g., in Mexican sections (Alegret and Thomas, 2001; Alegret et al., 2001) and in the northwestern Atlantic (Alegret and Thomas, 2004), the record is interrupted by slump-beds containing alloch-

thonous neritic foraminifera, so that detailed faunal records across the boundary cannot be obtained. At other locations, e.g., in the Caravaca and Agost sections in Spain (Coccioni et al., 1993; Coccioni and Galeotti, 1994; Kaiho et al., 1999; Alegret et al., 2003), dark clay layers contain low-diversity, high food/low oxygen assemblages, indicative of low oxygen conditions. In the equatorial Pacific, assemblages and benthic foraminiferal accumulation rates indicate a short-time increase in food delivery, but evidence for low oxygen conditions is weak (Alegret and Thomas, 2005). Recovery of faunas, i.e., of diversity and abundance of infaunal taxa, varied at different locations, from 100 to 300 k.y. (Alegret and Thomas, 2005). This paper will not address the regionally variable patterns of assemblage composition after the Cretaceous-Paleogene boundary, except to mention that there is no agreement on the detailed environmental interpretation of the generally low-diversity assemblages occurring just after that boundary (see, e.g., discussions on the El Kef section by Speijer and van der Zwaan, 1996, and by Culver, 2003).

Most authors agree that the temporary faunal restructuring of benthic foraminifera was caused by the collapse of the pelagic food web (e.g., Thomas, 1990a, 1990b; Widmark and Malmgren, 1992; Coccioni et al., 1993; Kuhnt and Kaminski, 1996; Speijer and van der Zwaan, 1996; Peryt et al., 1997, 2002; Culver, 2003; Alegret et al., 2001, 2003, 2004; Alegret and Thomas, 2001, 2004, 2005). It is difficult to understand, however, how such relatively minor and reversible changes in benthic faunal assemblages could have been the response to a major, long-term collapse of oceanic productivity, with biological productivity low for hundreds of thousands to several millions of years after the asteroid impact, and the slow-down or even stop of the “biological pump” of organic matter to the seafloor (“Strangelove Ocean”). Evidence for such a “Strangelove Ocean” consists of the collapse of the gradient between benthic and planktic (foraminiferal and/or bulk carbonate) carbon isotope values (e.g., Arthur et al., 1979; Hsü et al., 1982; Hsü and McKenzie, 1985; Zachos and Arthur, 1986; Zachos et al., 1989).

The end-Cretaceous benthic foraminiferal assemblages may have been characterized by less intense benthic-pelagic coupling than present faunas (as argued above; Thomas et al., 2000), but even under such conditions they should have shown a more severe change in community structure than observed, if food supplies remained so extremely low for millions of years. At times of less intense benthic-pelagic coupling, most benthic foraminifera probably adopted some form of deposit-feeding lifestyle, and such a lifestyle has been argued to be a possible exaptation to survive an impact-driven productivity crash. Recent evidence does not support this hypothesis, however (Levinton, 1996; Jablonski, 2005), even though the wide geographic range of benthic foraminiferal genera might have predisposed them for survival (Jablonski, 2005).

More recently, it was proposed that productivity (in terms of biomass) recovered as soon as light returned after the impact, although the plankton diversity remained low and the transfer of organic matter to the seafloor remained limited (D’Hondt et al.,

1998; D'Hondt, 2005; Coxall et al., 2006). During this partial recovery, lasting several hundred thousand years, lower gradients of benthic-planktic carbon isotope values persisted because of a severe decrease in food transfer to the seafloor due to ecosystem reorganization (e.g., loss of fecal pellet producers as a result of the mass extinction; shift to smaller-celled primary producers) (D'Hondt et al., 1998; Adams et al., 2004).

The lack of significant extinction of benthic foraminifera does not agree with the "Strangelove Ocean" model, and favors instead a model in which productivity as well as food transfer to the seafloor recovered more quickly, and more fully, than proposed even in the "living ocean" model (D'Hondt et al., 1998; Adams et al., 2004; D'Hondt, 2005; Coxall et al., 2006). Calcareous nannoplankton suffered very high rates of extinction, but other primary producers such as diatoms did not (Kitchell et al., 1986), cyanobacteria may not have been affected (D'Hondt et al., 1998), and the dinoflagellate calcareous cyst *Thoracosphaera* bloomed opportunistically worldwide (e.g., Thierstein, 1981; Perch-Nielsen et al., 1982; Gardin and Monechi, 1998). Surviving phytoplankton could be expected to bloom as soon as light conditions allowed, because the extinction of calcareous nannoplankton lessened competition for nutrients. The blooms of opportunistic phytoplankton may not have been global, but they occurred locally or regionally and led to local or regional anoxia, as observed, for instance, in the Caravaca and Agost sections of southern Spain (Coccioni et al., 1993; Coccioni and Galeotti, 1994; Kaiho et al., 1999; Alegret et al., 2003). There is not enough evidence to fully evaluate the severity, geographic and depth extent of hypoxia/anoxia after the Cretaceous-Paleogene boundary, but the lack of benthic foraminiferal extinction contradicts evidence in favor of global anoxia (e.g., Kajiwara and Kaiho, 1992).

Transport of organic matter to the seafloor may have recovered faster than envisaged by D'Hondt et al., (1998). Coagulation of organic particles by sticky diatoms and cyanobacteria may have assisted in forming large particles for rapid deposition (see above; Jackson, 2001; Armstrong et al., 2001), and various methods of ballasting particles with biogenic silica or terrigenous dust may have remained effective, even with less biogenic carbonate available. If atmospheric pCO₂ levels were very high after the impact (Beerling et al., 2002), calcification of the few surviving calcareous nannofossils may have decreased, but decreased calcification may have led to increased delivery of organic matter to the seafloor because of increased formation of sticky polysaccharides (Delille et al., 2005; Engel et al., 2004).

If both productivity and food transfer to the deep seafloor recovered faster than previously assumed, the recovery of marine ecosystems would be similar to the rapid recovery postulated for terrestrial ecosystems (Beerling et al., 2001; Lomax et al., 2001). The lack of extinction of benthic foraminifera could then be understood, but the persistent collapse of benthic-planktic carbon isotope gradients must be explained. I suggest that this collapse may not necessarily reflect a lack of operation of the biotic pump.

As a first possibility, the lighter values in bulk carbonate and planktic foraminiferal tests, reflecting the carbon isotope values

of total dissolved carbon in surface waters, may not reflect a drop in productivity. A negative carbon isotope anomaly has also been observed in terrestrial materials, indicating that a marine-productivity explanation is not sufficient (Arinobu et al., 1999; Arens and Jahren, 2000). The negative carbon isotope anomaly might have been caused by an input of light carbon in the surface ocean-atmosphere system (not penetrating into the deep sea), either as the result of biomass burning (Ivany and Salawitch, 1993) or methane liberation from dissociation of gas hydrates due to massive slumping on continental margins (Max et al., 1999; see also discussion in Alegret et al., 2003; Norris and Berger, 2003; Day and Maslin, 2005).

Alternatively, at least part of the surface isotope signal may reflect "vital effects" (e.g., Rohling and Cooke, 1999; Stoll and Ziveri, 2002; Maslin and Swann, 2005; Ziveri et al., 2003). The carbon isotope values reflecting isotope values of total dissolved carbon in surface waters must by necessity be measured on calcareous nannofossils (bulk records) and/or planktic foraminifera. Both groups underwent severe extinction, so that post- and pre-extinction records are derived from different species than the pre-extinction records. Post-extinction calcareous nannoplankton is dominated by bloom species such as *Thoracosphaera*, *Braarudosphaera* and *Biscutum* (Perch-Nielsen et al., 1982). Some of these taxa (*Thoracosphaera*) are calcareous dinoflagellates, and Cretaceous (Friedrich and Meijer, 2003) as well as Recent (Zonneveld, 2004) species of calcareous dinoflagellates have very light carbon isotope signatures.

Finally, the bulk record at some sites may be affected by diagenesis, which is common in low-carbonate sediments (e.g., Zachos et al., 2005). These three possibilities are not mutually exclusive, and the Cretaceous-Paleogene surface-bottom carbon isotope gradient collapse may reflect a more complex signal than one of collapsed productivity only.

PALEOCENE/EOCENE BENTHIC FORAMINIFERAL EXTINCTION

It has long been known that a major extinction of deep-sea benthic foraminifera occurred at the end of the Paleocene. Cushman (1946) placed the Cretaceous-Paleogene boundary at the end of the Paleocene, because the total foraminifera (planktic + benthic) show a much larger species turnover at that time, being dominated by the numerous benthic species (though low numbers of specimens). The extinction was documented in Trinidad by Beckmann (1960), in Austria by von Hillebrandt (1962), and in Italy by Di Napoli Alleata et al. (1970) and Braga et al. (1975) (review by Thomas, 1998). The extinction was first described in detail by Tjalsma and Lohmann (1983), using data from drill holes in the Atlantic Ocean and Gulf of Mexico. The scope and rapidity of the extinction, however, was not realized in these earlier studies, mainly because detailed, high-resolution age models were lacking. The event was first described as a major, rapid extinction (duration <10 k.y.) by Thomas (1989, 1990a). It was coeval with an episode of extreme global warming now called the Paleocene-

Eocene Thermal Maximum (PETM), with temperature increases of up to 9–10 °C in high-latitude sea surface temperatures, ~4–5 °C in the deep sea and in surface waters in equatorial regions (Zachos et al., 2003; Tripati and Elderfield, 2004, 2005), ~5 °C on land at midlatitudes in continental interiors (e.g., Wing et al., 2005), and in the Arctic Ocean (Sluijs et al., 2006). During this time, humidity and precipitation were high, especially at middle to high latitudes (e.g., Bowen et al., 2004, 2006; Pagani et al., 2006). Diversity and distribution of surface marine and terrestrial faunas and floras shifted, with rapid migration of thermophilic biota to high latitudes, as well as rapid evolutionary turnover (e.g., Crouch et al., 2001; Wing et al., 2005; papers in Wing et al., eds., 2003). Deep-sea benthic foraminifera, in contrast, suffered severe extinction (30%–50% of species), although these organisms survived such environmental crises as the asteroid impact at the end of the Cretaceous without significant extinction (e.g., Thomas, 1989, 1990a, 1990b, 1998; Thomas et al., 2006; Culver, 2003). Severe dissolution occurred in many parts of the oceans (Thomas, 1998), with the calcium carbonate compensation depth (CCD) shifting upward by at least 2 km in the southeastern Atlantic (D. Thomas et al., 1999; Zachos et al., 2005), although less in the Pacific Ocean (Colosimo et al., 2005).

Carbon isotope data on planktic and benthic foraminiferal tests and bulk marine carbonates (first documented by Kennett and Stott, 1991; Thomas and Shackleton, 1996), and on soil organic matter, soil carbonates, and herbivore teeth (Koch et al., 1992, 2003), show that there was a large perturbation to the global carbon cycle, affecting the whole ocean-atmosphere system, as seen by a negative excursion (carbon isotope excursion, CIE) of at least 2.5‰ in oceanic records (e.g., Zachos et al., 2001), and 5–6‰ in terrestrial records (e.g., Magioncalda et al., 2004; Koch et al., 2003; Bowen et al., 2004). The isotope anomalies indicate a rapid onset of these anomalies (<<20 k.y.; Roehl et al., 2000), followed by return to more normal values on time scales of 10⁵ years (Westerhold et al., 2007; Sluijs et al., 2007).

Researchers agree that the episode of rapid global warming was caused by the massive input of isotopically light carbon into the ocean-atmosphere system. Although there has been intensive research and vigorous discussion, there is no agreement on the source of the added carbon (e.g., Sluijs et al., 2007). The usual mechanisms called upon for carbon isotope excursions do not work at the PETM time scale: the isotopic composition of volcanic emissions is not light enough and their rate of emission too slow, the weathering of organic carbon-rich rocks is too slow, and the CIE is too large to have been caused by destruction of land biomass (e.g., Thomas and Shackleton 1996). Since 1995 (Dickens et al., Matsumoto) the most widely accepted hypothesis for the cause of the isotope anomalies has been the release of ~2000–2500 Gt of isotopically very light (~-60‰) carbon from methane clathrates in oceanic reservoirs, with subsequent severe greenhouse-gas induced warming. Oxidation of the methane in the oceans could have led to low oxygen conditions in the oceans, and oxidation in ocean or atmosphere would have led to widespread dissolution of carbonates, thus shallowing of the CCD.

The trigger for clathrate dissociation is not known; possible explanations include rapid warming of the intermediate ocean waters as a result of changing oceanic circulation patterns (e.g., Thomas, 1989, 1998; Kennett and Stott, 1991; Kaiho et al., 1996; Thomas et al., 2000; Dickens, 2001; Bice and Marotzke, 2002; Tripati and Elderfield, 2005; Nunes and Norris, 2006), continental slope failure as the result of increased current strength in the North Atlantic Ocean (Katz et al., 1999, 2001), sea-level lowering (Speijer and Wagner, 2002; Schmitz et al., 2004), the impact of a comet (Kent et al., 2003; Cramer and Kent, 2005) or other extraterrestrial body (Dolenec et al., 2000), explosive Caribbean volcanism (Bralower et al., 1997), North Atlantic basaltic volcanism (Eldholm and Thomas, 1993; Schmitz et al., 2004), or some combination of various of these possibilities.

Arguments against the gas hydrate dissociation hypothesis as the only explanation for the CIE include low estimates (500–3000 Gt C) for the size of the global oceanic gas hydrate reservoir in the recent oceans and thus even lower ones in the warm Paleocene oceans (e.g., Milkov, 2004; Cramer and Kent, 2005; Archer, 2007), and the magnitude and timing of the warming event (Cramer and Kent, 2005; Bowen et al., 2004). Moreover, the rise of the CCD by >2 km is much greater than estimated by assuming that 2000–2500 Gt carbon in methane was the sole source of carbon (Dickens et al., 1997). Finally, the full extent of the CIE and thus the exact amount of isotopically light carbon and its isotopic signature are still somewhat uncertain (discussion in Zachos et al., 2005). The many alternative hypotheses for the source of the isotopically light carbon include the body of a comet (Kent et al., 2003; Cramer and Kent, 2005), thermal liberation of methane from organic matter by igneous intrusions in the North Atlantic (Svensen et al., 2004) or from sediments in the Alaskan accretionary prism (Hudson and Magoon, 2002), burning of extensive peat deposits (Kurtz et al., 2003), oxidation of organic matter following desiccation of inland seas (Higgins and Schrag, 2004), and mantle-plume-induced lithospheric gas explosions (Phipps Morgan et al., 2004), possibly associated with the late Paleocene–early Eocene Canadian kimberlite province (Creaser et al., 2004).

Several years ago it was suggested that the PETM might not have been a singular event, but only the most severe out of a series of global warming events coupled with carbon isotope anomalies and carbonate dissolution (called hyperthermals; Thomas and Zachos, 2000; Thomas et al. 2000). Hyperthermals have now been documented in upper Paleocene–lower Eocene sediment sequences in the southeastern Atlantic Ocean (ODP Leg 208, Shipboard Scientific Party, 2004) and the Pacific Ocean (ODP Leg 198, Shipboard Scientific Party, 2002), and in land sections in Italy (Galeotti et al., 2005; Agnini et al., 2005) and the United States (Lourens et al., 2005).

Lourens et al. (2005) argued that the PETM occurred at a time of orbital modulation similar to that of an event ~2 m.y. later (Elmo) as well as at an event 1.2 m.y. after the Elmo event, called the X-event (Roehl et al., 2005). If the PETM was one of a series of events of varying magnitude, occurring at orbital periodicities

(Lourens et al., 2005), its cause probably was not singular (e.g., a comet impact or a volcanic eruption), but intrinsic to Earth's climate system. There is as yet no agreement on the linkage of the PETM to a specific orbital configuration (Cramer et al., 2003; Westerhold et al., 2007).

It is outside the range of this paper to discuss climatic and biotic events during the PETM in detail (see e.g., papers in Aubry et al., 1998; Wing et al., 2003). Regardless of the exact cause(s) of the addition of isotopically light carbon to the environment, the question remains, What caused the extinction of deep-sea benthic foraminifera (see Thomas, 1998, for a review)? Shelf foraminifera were also affected by the end-Paleocene events (e.g., Speijer et al., 1997; Speijer and Schmitz, 1998; Alegret et al., 2005; Ernst et al., 2006), although neither shelf nor deep-ocean foraminifera were affected by the asteroid impact at the end of the Cretaceous (Culver, 2003). In contrast, calcareous planktic organisms did not suffer severe extinction at the end of the Paleocene, although planktic foraminifera (e.g., Kelly et al., 1996, 1998; Kelly, 2002) and calcareous nannoplankton show rapid evolutionary turnover and evolution of short-lived taxa (e.g., Bralower, 2002; Tremolada and Bralower, 2004). Major extinctions of planktic and benthic organisms in the oceans thus appear to have been decoupled (e.g., Thomas 1990b; Kaiho 1994a), in agreement with the above arguments that benthic-pelagic coupling was less close during the Late Cretaceous-Paleogene than it is today.

What could have caused a global extinction in the deep sea? Possible causes include (1) low oxygenation, as mentioned by many authors (see review in Thomas, 1998), either as a result of increased deep-sea temperatures or as a result of oxidation of methane in the water column; (2) increased corrosivity of the waters for CaCO_3 as a result of methane oxidation (Thomas, 1998; D. Thomas et al., 1999; Zachos et al., 2005) or invasion by CO_2 from the atmosphere (Feely et al., 2004; Sabine et al., 2004; Orr et al., 2005); (3) increased or decreased productivity or expansion of the trophic resource continuum (e.g., Hallock, 1987; Hallock et al., 1991; Boersma et al., 1998; Thomas, 1998; Bak, 2005); or (4) a combination of several of these. In considering possible causes, it should be kept in mind that the extinction was global, affecting 30%–50% of species globally, and post-extinction faunas worldwide are low-diversity, dominated by small, thin-walled calcareous species or agglutinants (Thomas, 1998). Unfortunately, such assemblages might result from such differing environmental factors as high temperature, undersaturation with calcite, low dissolved oxygen levels, and either high or low food levels (Boltovskoy et al., 1991). In addition, such small individuals could be opportunistic taxa indicating a disturbed environment, as expected after a major extinction (e.g., Schröder et al., 1987).

Low oxygen conditions have been well documented in marginal ocean basins such as the Tethys and northeastern peri-Tethys, as shown by the occurrence of the extinction at the base of laminated, dark-brown to black sediments with high concentrations of organic matter (Gavrilov et al., 1997, 2003; Stupin and Muzylöv, 2001; Speijer and Schmitz, 1998; Speijer and Wagner, 2002; Alegret et al., 2005), as well as in New Zealand (Kaiho et al.,

1996). The record for open-ocean settings, however, is not so clear. At some pelagic locations, post-extinction benthic foraminiferal assemblages may be interpreted as indicative of a high food supply or low oxygenation because of the abundant occurrence of buliminid foraminifera (see Thomas, 1998 for a review; Thomas, 2003; Nomura and Takata, 2005). There is, however, no sedimentological or geochemical evidence for hypoxia or anoxia (e.g., high organic carbon content, laminated sediments). Organic carbon in the PETM clay layers may well have been oxidized post-depositionally (van Santvoort et al., 1996). Trace element information, including low levels of Mn in the PETM clay layer at ODP Site 926, suggests that low oxygen conditions might have been more widespread than is now accepted (Thomas and Röhl, 2002) but anoxia or even hypoxia was not a global phenomenon. The sedimentology at Maud Rise Sites 689 and 690 and Pacific Sites 1209 and 1210 clearly indicates persisting oxygenation (Thomas and Shackleton, 1996; Thomas, 1998; Kaiho et al., 2006), and Walvis Ridge sites show bioturbation through the Paleocene-Eocene clay layer (Shipboard Scientific Party, 2004). There thus should have been refugia available for deep-sea benthic foraminifera: many species are cosmopolitan and have early life stages that are easily dispersed by ocean currents (Alve and Goldstein, 2003). Even if locally the oceans were hypoxic or even anoxic, some regions should have remained suitable for benthic foraminifera, which have considerable tolerance for low oxygen levels (down to ~ 1 mg/L; e.g., Gooday, 2003). Return to more favorable conditions should have been followed by rapid re-establishment of foraminiferal populations (e.g., Hess and Kuhnt, 1996; Hess et al., 2001).

Similarly, refugia should have existed for carbonate corrosivity, because at Maud Rise Sites 689 and 690 the carbonate percentage decreased, but not below $\sim 65\%$ (D. Thomas et al., 1999), and there is no clear clay layer (e.g., D. Thomas et al., 1999; Cramer et al., 2003). Dissolution along depth transects in the Pacific Ocean was not as severe as at Walvis Ridge (Colosimo et al., 2005; Nomura and Takata, 2005; Kaiho et al., 2006). Extinction levels at these sites are similar to those at sites where dissolution is intense (Zachos et al., 2005). If carbonate corrosivity and the rise of the CCD had been the main cause of the benthic foraminiferal extinction, organic-agglutinated foraminifera below the CCD would not have been affected, but these also suffered extinction (e.g., Kaminski et al., 1996; Bak, 2005; Galeotti et al., 2005; Kaminski and Gradstein, 2005).

It seems improbable that decreasing productivity in the surface waters could have caused a major benthic extinction, given that such extinction did not occur at the end of the Cretaceous. Decreased productivity remains a possible cause (e.g., Kaminski and Gradstein, 2005), however, because productivity decrease at the end of the Cretaceous might have been short-lived, as argued above, but could have been more long-term during the PETM, with a duration of ~ 100 k.y. (e.g., Zachos et al., 2005). The effect of the PETM on oceanic productivity, however, was not consistent globally. Evidence from sections close to continental margins and in epicontinental basins indicates high productivity, leading to hypoxia or anoxia (Gavrilov et al., 2003; Speijer et al.,

1997; Speijer and Schmitz, 1998; Speijer and Wagner, 2002). Overall, however, it appears that productivity decreased in much of the open ocean (e.g., Kaminski and Gradstein, 2005), although proxy data on productivity are sometimes in conflict. For example, Bralower (2002) argued for oligotrophic conditions during the PETM at one location (Site 690 in the Weddell Sea), whereas Thomas and Shackleton (1996), Bains et al. (1999), Stoll and Bains (2003) argued for eutrophic conditions at that same location (but see also Thomas, 2003). At tropical Pacific Sites 865 and 1209 planktic foraminifera and calcareous nannofossils suggest oligotrophy, benthic foraminiferal accumulation rates, and faunal composition eutrophy (Kelly et al., 1996; Kelly et al., 2005; Thomas et al., 2000; Kaiho et al., 2006). At other locations (e.g., Walvis Ridge Sites 525, 527, 1262, 1263; Ceara Rise Site 929), benthic foraminiferal evidence indicates a decrease in productivity (Thomas, 1998), but this apparent decrease might have resulted from rising temperatures thus higher metabolic rates at a stable food supply (Thomas and Shackleton, 1996; Boersma et al., 1998; Thomas and Röhl, 2002). These different observations may suggest that the trophic resource continuum expanded, i.e., gyral regions became more oligotrophic, continental margins more eutrophic (e.g., Boersma et al., 1998). The overall evidence indicates neither global increase nor decrease in productivity (Fig. 3), but the benthic extinction was global, suggesting that productivity changes by themselves probably were not the main cause of the benthic foraminiferal extinction.

A global feature of the PETM is warming, for which there were no refugia as far as we know: at all investigated sites, at all latitudes, in all oceans, there is evidence for rapid warming of benthic environments. This suggests that warming may have been the main cause of the global benthic foraminiferal extinction. Understanding whether this was indeed the case is important for predicting behavior of benthic global biota during possible future anthropogenic global warming, especially because there is evidence that the oceans are warming (e.g., Levitus et al., 2000). It is questionable whether benthic foraminiferal assemblages that today live in deep waters at fairly high temperatures, e.g., those of

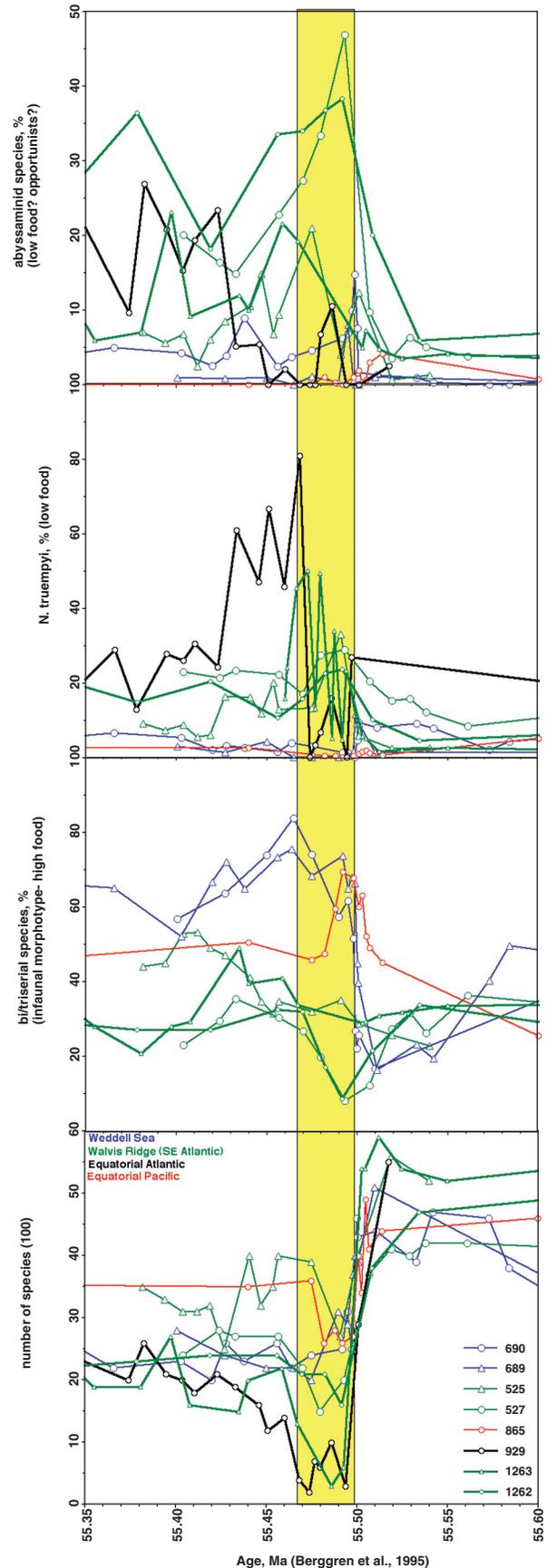


Figure 3. Faunal patterns during the benthic foraminiferal extinction (modified after Thomas, 1998). Numbers in the legend identify DSDP and ODP sites. Blue—Sites 689 and 690, Weddell Sea. Red—ODP Site 865, equatorial Pacific. Black—ODP Site 926, western equatorial Atlantic Ocean. Green—Walvis Ridge, southeastern Atlantic Ocean including DSDP Sites 525 and 527 and ODP Sites 1262 and 1263. The net loss of diversity is similar at different sites outside the interval of dissolution, but the patterns of dominance differ by site. Species indicative of low-oxygen and/or low oxygenation (bi/triseserial species) increased in relative abundance at Sites 865, 689, and 690 but not at the Walvis Ridge sites; these species were absent from Site 929. *Nuttallides truempyi*, a possible low-food indicator (Thomas, 1998) increased in abundance at Site 929 (after the interval of dissolution) and at Walvis Ridge sites. Abyssaminid taxa, which are small, thin-walled species that might indicate oligotrophy or might be opportunistic species, increased in abundance at the Walvis Ridge sites, especially the deepest sites, and at Site 929, and decreased at Site 865.

the Red Sea, could assist in interpretation of Paleocene-Eocene events. These assemblages live at high but constant temperatures (Thiel et al., 1987; Edelman-Furstenberg et al., 2001), and in a special setting (small ocean basin surrounded by desert).

Unfortunately, the mechanism by which global warming would have caused the benthic extinction is not clear: the effects of present global warming on oceanic ecosystems and biogeochemistry are predicted to be significant, but they are not understood (e.g., Petchey et al., 1999; Laws et al., 2000; Archer et al., 2004; Sarmiento et al., 2004). Because temperature is such an important regulator of metabolic rates and affects food supplies of all components in the marine benthic ecosystem, a major and rapid temperature change would be expected to affect energy cycling within ecosystems, possibly affecting productivity by calcareous nannoplankton (Feely et al., 2004), predation by such foraminifer-specializing predators as gastropods and scaphopods (Hickman and Lipps, 1983; Culver and Lipps, 2003), and even the rate of evolutionary processes (Gillooly et al., 2004). Many deep-sea benthic foraminifera feed on organic matter and Bacteria and Archaea within the sediments, and temperature changes affect not only metabolic rates of prokaryotes, but also which species are most active, and which labile compounds are generated (Weston and Joye, 2005). Changing temperatures thus may have changed the compounds and the amount of labile organic matter available for foraminiferal feeding.

How might we determine whether warming indeed caused the extinction? Highly detailed stable isotope and trace element records on benthic foraminifera, preferably along a depth transect, are not yet available because of the problems with analysis of biota across a major extinction, and the small size of post-extinction individuals. Such analyses, however, might establish whether warming occurred just before or at the beginning of the extinction. Investigation of the apertural configuration of benthic foraminiferal species groups could reveal changes in feeding strategy. Carbon isotope analyses of different benthic foraminiferal species may help elucidate the environmental preferences of now-extinct taxa (shallow-deep infaunal, epifaunal). Unfortunately, such high-resolution studies are not possible across the PETM at many locations, because of the severe carbonate dissolution and thus incompleteness of records (Zachos et al., 2005). High-resolution investigations of faunal and isotope patterns across PETM-like events in the early Eocene (Shipboard Scientific Party, 2004; Lourens et al., 2005; Roehl et al., 2005) may provide more detailed information on the possible linkage between global warming events and the extinction of deep-sea biota; because dissolution was less severe than during the PETM, high-resolution records may be obtainable.

CONCLUSIONS

In the present-day oceans, deep-sea benthic foraminiferal faunas are strongly influenced by primary producers at the sea surface, which constitute their food supply. During the early part of the Cenozoic, however, including the Cretaceous-Paleogene boundary and the Paleocene-Eocene boundary, extinctions in surface

and deep-ocean biota were decoupled. Benthic foraminifera may not have suffered severe extinction at the Cretaceous-Paleogene boundary because oceanic productivity as well as food transfer to the bottom recovered more quickly than previously thought, and/or because a larger fraction of food was produced by lithoautotrophic prokaryotes in the warm oceans of the Cretaceous and Paleogene. The major benthic extinction at the Paleocene-Eocene boundary is not easy to explain; possible causes include changing oceanic productivity, lowered oxygenation, and carbonate corrosivity, but none of these factors occurred globally, and survival in refugia followed by repopulation would have prevented extinction of cosmopolitan species. Global warming might have been the most important cause of extinction, but mechanisms are not understood. Benthic-pelagic coupling as we see it in today's oceans may have originated by the Eocene-Oligocene transition, during an episode of growth of the Antarctic ice sheet. The gradual benthic foraminiferal turnovers during the Eocene-Oligocene, middle Miocene, and middle Pleistocene all occurred during episodes of cooling, and all included the loss of similar species that might have indicated a high or continuous food supply. Primary productivity, however, probably increased during these times, suggesting that transfer of food to the ocean floor was different during the warm Paleogene. Benthic faunal turnover during Cenozoic episodes of global cooling may reflect the increased seasonality of primary productivity and increased delivery of labile organic matter to the seafloor.

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