Cenozoic deep-sea benthic foraminifers: Tracers for changes in oceanic productivity?

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ABSTRACT

From late middle Eocene through earliest Oligocene, high-latitude regions cooled, and by the end of the period, continental ice sheets existed in Antarctica. Diversity of planktonic microorganisms declined, and modern groups of terrestrial vertebrates originated. Coeval faunal changes in deep-sea benthic foraminifers have been related to cooling of deep waters and increased oxygenation. Cooling, however, occurred globally, whereas species richness declined at high latitudes and not in the tropics. The late Eocene and younger lower-diversity, high-latitude faunas typically contain common *Epistominella exigua* and *Alabaminella weddellensis*, opportunistic phytodetritus-exploiting species that indicate a seasonally fluctuating input of organic matter to the sea floor. We speculate that the species-richness gradient and increase in abundance of phytodetritus-exploiting species resulted largely from the onset of a more unpredictable and seasonally fluctuating food supply, especially at high latitudes.

INTRODUCTION

During the latest middle Eocene through early Oligocene, high-latitude regions cooled, and by the end of the period, major ice sheets existed on Antarctica (e.g., Zachos et al., 1993). Macrofloral changes indicate continental cooling and increased aridity, terrestrial vertebrates underwent major overturn, and in the oceans the diversity of planktonic microorganisms decreased while provinciality increased; overall, global extinction rates were high (Corliss et al., 1984; Prothero and Berggren, 1992). Oceanic surface productivity probably increased, as inferred from biota (Hallock et al., 1991) and sediments (Diester-Haass, 1995; Hartl et al., 1995).

Major but gradual changes in deep-sea benthic foraminiferal faunas have been related to cooling of deep waters and ensuing increased oxygenation (Kaiho, 1994b) or $CaCO_3$ corrosivity (Thomas, 1992a). There is intensive discussion, however, regarding the influence on benthic foraminifers of physicochemical properties of bottom waters (temperature, oxygen content, salinity, total dissolved carbonate) as compared to changes in food supply from surface primary production (Loubere, 1994; Schnitker, 1994). Some insist that oxygenation is the major controlling variable (Kaiho, 1994a), but data on living faunas suggest that food supply is of prime importance and that oxygen concentration becomes a major factor only where high organic input leads to oxygen depletion (Sen Gupta and Machain-Castillo, 1993; Gooday, 1994; Schmiedl, 1995).

In most modern open-ocean settings, bottom waters are well oxygenated, but conditions may have been less uniform in the past. For instance, in the early Miocene an oxygen-depleted water mass with a characteristic benthic foraminiferal fauna may have existed in the Atlantic, Tethys, and Indian oceans (Smart and Ramsay, 1995). In the Paleogene, deep waters were warmer by more than 10 °C and possibly more variable in oxygen content (e.g., Zachos et al., 1993). Benthic faunas might thus reflect the long-term Cenozoic cooling of the deep oceans (e.g., Thomas, 1992b; Kaiho, 1994b). We look into deep-sea benthic foraminiferal faunal changes at the time that the world changed from "greenhouse" into "icehouse" and try to evaluate their most likely causes.

BENTHIC FORAMINIFERA AND ENVIRONMENTAL CHANGE

Correlations between benthic foraminiferal assemblages and bottom-water masses with their characteristic physicochemical properties have been recognized in the modern oceans (see Schnitker, 1994, for a review). In addition, stable isotope and trace element data for the Pleistocene glacial-interglacial alternations show that formation of North Atlantic Deep Water (NADW) was reduced during glacial maxima (e.g., Labeyrie et al., 1992); coeval benthic foraminiferal changes have thus been interpreted as indicative of the presence of less ventilated bottom-water masses during glacial periods (e.g., Schnitker, 1994).

Studies in all oceans spanning a wide depth range and time interval, however, have not established transfer functions linking benthic foraminiferal species abundances globally to physicochemical parameters (e.g., Gooday, 1993). Except around hydrothermal vent systems, deep-sea benthic foraminifers live in an environment where the nature and biomass of animal communities depend on organic matter input from surface primary production (Gage and Tyler, 1991). It therefore appears unlikely that the small differences in physicochemical parameters in the present deep sea could be the dominant determinant of the composition and abundance of deep-sea benthic foraminiferal assemblages (e.g., Gooday, 1994; Schnitker, 1994). Researchers thus considered food supply as a factor in determining the assemblage composition. *Uvigerina*, *Bolivina*, *Bulimina*, and *Melonis* species are largely controlled by the supply of organic material (e.g., Lutze and Coulboum, 1984; Caralp, 1989). Glacial-interglacial faunal change could then be explained as resulting from increased glacial productivity, instead of from reduced ventilation (e.g., Corliss et al., 1986).

Recently, not just the food supply to the sea floor but also its seasonality has been investigated (Pfannkuche, 1993; Rice et al., 1994). Phytodetritus material derived from the spring phytoplankton bloom is deposited to the sea floor during a highly seasonal pulse in the temperate northeast Atlantic, the Norwegian-Greenland Sea (Graf, 1989), and the central North and equatorial Pacific (Smith et al., 1994; Smith, 1994). In the northeastern Atlantic, opportunistic benthic foraminifers (e.g., *Epistominella exigua* and *Alabaminella weddellensis*) react to the phytodetritus deposition with increased population densities, presumably through rapid reproduction fueled by food derived from phytodetritus (Gooday, 1988, 1993). *Epistominella exigua* ingests fresh algal cells similar to those in phytodetritus (Gooday, 1993). The distribution patterns of these species may thus be linked to phytodetritus, although this possibility needs to be substantiated by more data (Gooday, 1993; Schmiedl, 1995).

Phytodetritus input cannot be equated in a simple way with high surface productivity (Rice et al., 1994), but reflects hydrographic conditions in the upper layers of the oceans

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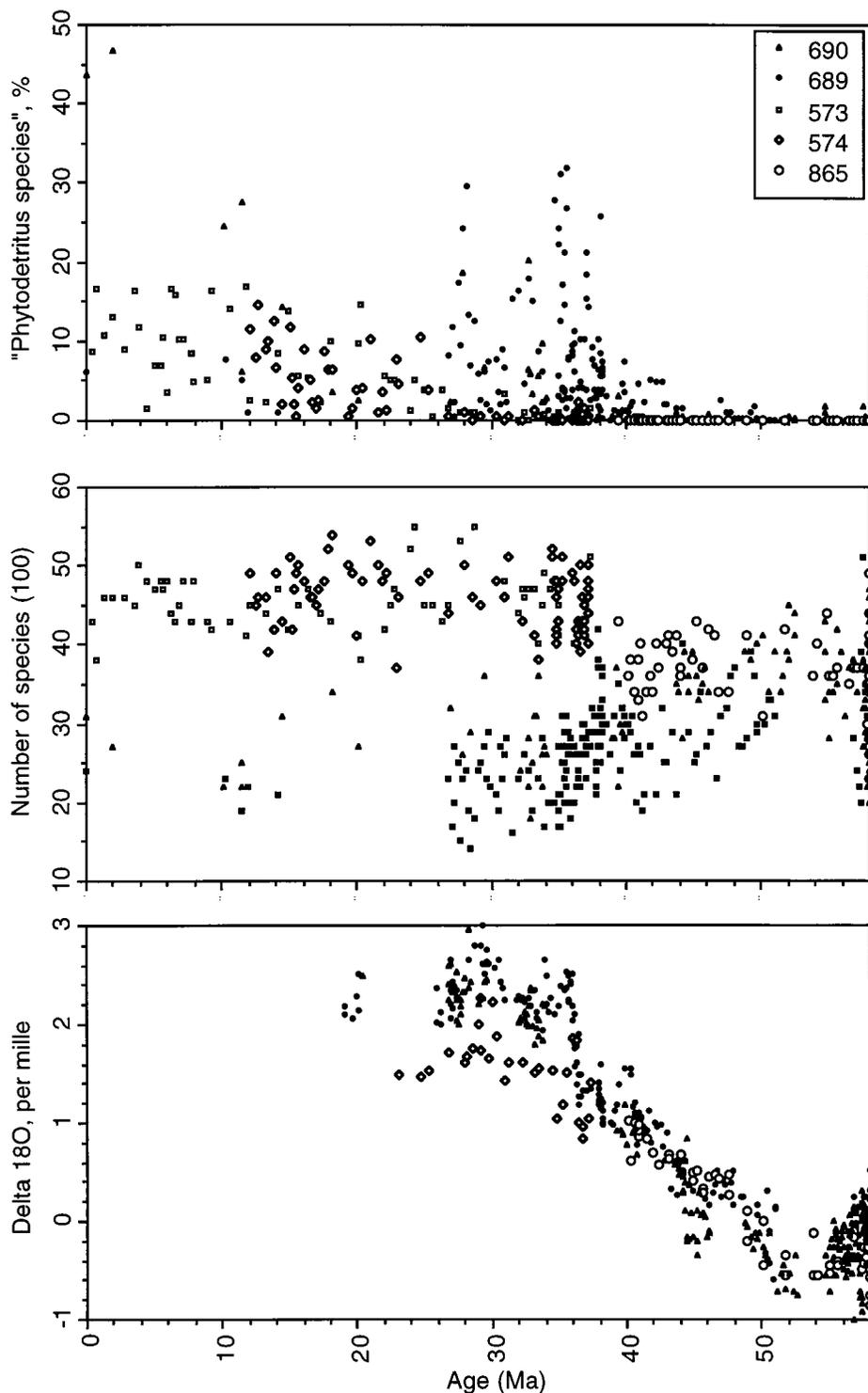**Data Repository item 9619 contains additional material related to this article.**

Figure 1. Benthic foraminiferal oxygen isotope values (left), species richness (center), and relative abundance of phytodetritus-exploiting species *Epistominella exigua* and *Alabaminella weddellensis* (right) for equatorial Pacific (open symbols) and Weddell Sea sites (closed symbols). Present locations and water depths in equatorial Pacific: Site 573—00°29.91′N, 133°18.57′W, 4301 m; Site 574—04°12.52′N, 133°19.81′W, 4561 m; Site 865—18°26′N, 179°33′W, 1530 m. Present locations and water depths in Weddell Sea: Site 689—64°31.01′S, 03°06.00′E, 2080 m; Site 690—65°9.64′S, 1°12.30′E, 2914 m. Numerical ages according to Berggren et al. (1985); age models for Sites 573 and 574 after Barron et al. (1985), for Sites 689 and 690 after Thomas et al. (1990), and for Site 865 after Bralower et al. (1995a). Isotope data after Miller and Thomas (1995b) for Site 574, after Kennett and Stott (1990) for Sites 689 and 690, after Bralower et al. (1995b) for Site 865. Species richness and relative abundance data after Thomas (1985) for Sites 573 and 574, after Thomas (1990) for Sites 689 and 690, table in GSA Data Repository (see footnote 1) for Site 865. Note the strong decline in species richness at 58 Ma (the late Paleocene benthic foraminiferal extinction, Thomas, 1990), partial recovery in early Eocene, and declining species richness from latest middle Eocene on only at high latitude sites.

(particularly, a deep layer of winter mixing) that lead to a strong phytoplankton bloom (Campbell and Aarup, 1992). Such conditions do not necessarily lead to high organic carbon accumulation rates because labile organic matter is quickly degraded on the sea floor by bacteria and protists, given adequate oxygen (Gooday and Turley, 1990; Turley and Lochte, 1990; Poremba, 1994).

We can distinguish benthic foraminiferal faunas with abundant phytodetritus-exploiting species—indicative of well-oxygenated, generally oligotrophic open-ocean regions with a seasonal phytodetritus pulse—from faunas with abundant *Uvigerina*, *Bolivina*, *Bulimina*, or *Melonis* species—which indicate a high, continuous flux of organic matter to the sea floor, possibly associated with reduced bottom-water oxygenation (Gooday, 1994; Schmiedl, 1995). The paleontological record thus may be used to identify periods when seasonal phytodetritus deposition influenced benthic communities (Smart et al., 1994; Thomas et al., 1995).

EOCENE-OLIGOCENE DEEP-SEA BENTHIC FORAMINIFERA

Many studies of benthic foraminifers have been based on size fractions larger than 125 μm, but many *E. exigua* and *A. weddellensis* specimens fall in the 63–125 μm size fraction (Gooday, 1988). Studies based on coarser residues suggested that *E. exigua* originated in the earliest Oligocene (e.g., Van Morkhoven et al., 1986), but investigators examining the >63 μm size fraction reported it from the lowermost Eocene, suggesting that the discrepancy results from the fact that the species became larger and more common in the earliest Oligocene (Boltovskoy et al., 1991; Thomas, 1990). We used data gathered by Thomas from >63 μm fractions of material from the equatorial Pacific and the Weddell Sea (Fig. 1).[1] To prevent dissolution from affecting the data, we used only samples that contained dissolution-prone taxa such as spiny *Stilostomella* species. All species-richness numbers were recalculated to the number of species per one hundred specimens by using rarefaction as outlined for deep-sea benthos by Sanders (1968).

Species richness fluctuated considerably, but decreased among high-latitude faunas during the late Eocene, resulting in a species-richness gradient between high and low latitudes. Because of dissolution at the Antarctic sites, few data are available from 24

Ma on but suggest that the gradient persists to today. This pattern parallels the latitudinal gradient in species richness seen in pelagic, shallow-water, and terrestrial ecosystems (e.g., Pianka, 1966; Gage and Tyler, 1991) and recently recognized in the Northern Hemisphere, in deep-sea metazoans (Rex et al., 1993). Our foraminiferal data suggest that this gradient originated during the transition from a "greenhouse" to an "icehouse" world, although no such gradient has been recognized for modern deep-sea Antarctic macrofauna (Brey et al., 1994).

Thomas (1992a) explained the decline in foraminiferal species richness at high latitudes in terms of declining temperatures, increased corrosivity of the bottom waters to $CaCO_3$, and, possibly, increased oxygenation. Oxygen isotope records, however, show similar deep-ocean cooling worldwide (e.g., Zachos et al., 1993), whereas in the tropics, species richness did not decline with increasing $\delta^{18}O$ values (Fig. 1). Therefore, cooling and its consequences (increased corrosivity, oxygenation) cannot be the only cause of faunal change.

What could be the cause of the foraminiferal species-richness gradient between high and low latitudes? A major difference between pre– and post–late Eocene faunas is the decrease in abundance of *Bulimina* species at lower bathyal and abyssal depths (e.g., Thomas, 1992b; Kaiho, 1994b), which could be interpreted as resulting from decreased oceanic productivity. Such a decrease appears unlikely, however, because the cooler oceans of the Oligocene and later generally are thought to have been characterized by increased productivity (Hallock et al., 1991; Prothero and Berggren, 1992), resulting from either increased oceanic overturn rates due to steeper latitudinal and vertical temperature gradients or high nutrient input due to increased erosion of continental regions as indicated by the strontium isotope record (Raymo et al., 1988).

The late Eocene decrease in abundance of bathyal-abyssal buliminid species thus probably was not caused by decreasing primary productivity. It could have been caused by a decrease of organic matter deposition to the sea floor (even at higher surface productivity) as a result of increased oxygenation of bottom waters (Kaiho, 1994b). Another factor, however, may have been the increased seasonality at high latitudes. With the intense cooling at high latitudes, sea ice started to form, leading to concentration of productivity in a few months of the year. By analogy with the modern Southern Ocean, this process would have led to increased but highly fluctuating

deposition of organic matter to the sea floor (Berger and Wefer, 1990).

The strong sample-to-sample fluctuation in relative abundance of "phytodetritus species" may reflect spatial patchiness in phytodetritus accumulation, as observed on the modern ocean floor (Rice et al., 1994). Only if phytodetritus accumulated persistently in a particular area will the abundance of such taxa be expressed in the fossil record. Overall, abundance peaks of >10% of *Epistominella exigua* and *Alabaminella weddellensis* occur at the Southern Ocean sites from the time of initiation of decreasing species richness on (about 38 Ma). This suggests that the late Eocene high-latitude decrease in diversity coincided with an increase in seasonal phytodetrital flux to the sea floor.

The concomitant size increase of *E. exigua* is difficult to explain. In foraminifera, large size has been related to optimum food supply, but also to the reverse, since lack of food keeps individuals from reproducing successfully and leads to continued growth (Boltovskoy et al., 1991). Oligocene specimens of *E. exigua* have been reported to be smaller but have more chambers than more recent specimens, suggesting slower growth (Boltovskoy, 1984). The species might thus have become adapted more and more to an opportunistic lifestyle, obtaining larger size at fewer chambers, with the energy required supplied by increasing deposition of food to the sea floor.

Species diversity in the deep sea depends upon complex factors, making the impact of widespread increase in phytodetritus deposition difficult to assess. At scales of metres to kilometres the overall effect is probably to increase environmental heterogeneity and hence increase diversity (Grassle and Morse-Porteous, 1987; Grassle and Maciolek, 1992). At regional to global scales (100–1000 km), however, the impact may be different. If a seasonal flux of phytodetritus would be sustained over geologic time scales, it could lead to an overall decrease in foraminiferal diversity and increased dominance by the few species that exploit phytodetritus (Gooday, 1993; Rex et al., 1993). Decreased diversity and increased dominance are the typical response of communities to organic enrichment (Pearson and Rosenberg, 1978; Hallock et al., 1991), and lower species richness was coupled with increased abundance of phytodetritus species in the northeastern Atlantic (Thomas et al., 1995).

In our data (Fig. 1), decreasing species richness during the late Eocene at high latitudes was coeval with increased relative abundances of *E. exigua* and *A. weddellensis*, suggesting that the two trends are linked.

We believe therefore, that the deep-sea species-richness gradient resulted from an increasing but highly seasonal food influx into the deep oceans, coincident with global cooling just before and during the establishment of the Antarctic ice sheets. We suggest that this latitudinal gradient reflects the onset of a more seasonally varying environment (especially as to food availability) at high latitudes. The fact that this variability seems to have influenced bathyal and abyssal faunas implies that coupling between ocean surface and deep-sea benthic processes was established at this time.

CONCLUSIONS

In the late Eocene–early Oligocene when the Earth moved from a "greenhouse" to an "icehouse" state, deep-sea benthic foraminifers developed a latitudinal species-richness gradient, the highest species richness being at low latitudes, as in modern land, planktonic, and shallow-ocean biota. We speculate that the development of this gradient was largely due to an increasing but strongly pulsed food input into the deep oceans at high latitudes, as suggested by the increasing abundance of the opportunistic, phytodetritus-exploiting benthic foraminiferal species *Epistominella exigua* and *Alabaminella weddellensis*.

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