Pelagic evolution and environmental recovery after the Cretaceous-Paleogene mass extinction

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ABSTRACT

The evolutionary recovery of planktic foraminifera from the Cretaceous-Paleogene mass extinction was closely linked to recovery of the marine carbon system. Both the evolutionary recovery and the biogeochemical recovery occurred in two stages. The second stage of evolutionary radiation peaked nearly four million years after the extinction, immediately after the abrupt final recovery of the organic flux to deep waters. The timing of these events suggests that the final postextinction recovery of planktic foraminiferal diversity was directly contingent on the final recovery of the marine carbon cycle. This second radiation was defined by the diversification of tropical photosymbiotic forms that dominated low- and mid-latitude assemblages long into the Eocene. We hypothesize that this diversification was a result of the reappearance of oligotrophic oceans as the organic flux from the surface ocean to deep water fully recovered from the mass extinction.

Keywords: Cretaceous-Tertiary boundary, extinction recovery, carbon system, organic flux, pelagic ecosystem, planktic foraminifera, evolution.

INTRODUCTION

The marine ecosystem suffered tremendous taxonomic loss during the Cretaceous-Paleogene mass extinction, with pronounced extinction among vertebrates, invertebrates, phytoplankton, and zooplankton (Sheehan et al., 1996). Entire groups of organisms completely disappeared. Marine fossil records from the ensuing Paleocene period exhibit multimillion-year delays in evolutionary recovery (Sepkoski, 1998; Kirchner and Weil, 2000). For example, more than 90% of Maastrichtian planktic foraminifera species disappeared abruptly at the boundary (e.g., Smits, 1982; D’Hondt et al., 1996; Molina et al., 1998).

Postextinction planktic diversification involved evolution of entirely new taxa from a few Cretaceous survivors (Olsson et al., 1999). Full diversification was drawn out over a few million years (Corfield and Shackleton, 1988; Olsson, 1999).

The mass extinction was associated with a catastrophic decline in the flux of organic matter to the deep ocean (e.g., Hsu et al., 1982; Zachos et al., 1989). Evidence suggests that the recovery from this collapse took more than three million years (m.y.) (D’Hondt et al., 1998; Adams et al., 2004), but little is known about the timing of evolutionary diversification in relation to carbon cycling and the state of the recovering pelagic ecosystem. Here we explore links between the carbon system and the marine ecosystem by comparing Paleocene planktic foraminiferal evolutionary histories with geochemical records of Cretaceous-Paleogene environmental change from the Atlantic and Pacific Oceans.

MATERIALS AND METHODS

Our studies focused on two Cretaceous-Paleogene boundary sections: Deep Sea Drilling Project (DSDP) Site 528 (28°31.49′N; 02°19.44′E) and Site 577 (32°26.51′N; 157°43.40′E), with paleolatitudes and depths of ~38°S and 2500 m, and 8–10°N and 2400 m, respectively (D’Hondt et al., 1998). Stratigraphic control was achieved through biostratigraphy and magnetostratigraphy (Moore et al., 1984; Heath et al., 1985). The sequence at Site 528 is composed of Maastrichtian foram-nannofossil chalks overlain by Paleocene nanofossil marls. Foraminiferal preservation is moderate in the Upper Cretaceous and moderate to good in the Lower Paleocene. Site 577 sediments are nanofossil ooze throughout. Upper Cretaceous planktic foraminifera exhibit severe dissolution and fragmentation, but Paleocene specimens are well preserved. Carbonate (CaCO₃) accumulation decreased across the Cretaceous-Paleogene boundary by ~85% at Site 528 and ~60% at Site 577 (D’Hondt, 2006). The smaller decrease at Site 577 is the result of lower CaCO₃ accumulation in the Cretaceous, probably because of deposition at lysoclinal depths (Zachos et al., 1989). The accumulation of CaCO₃ in the foraminiferal size fraction (>38 μm) at Site 528 did not change appreciably at the boundary. In combination with the greatly improved preservation of Paleocene foraminiferan tests relative to Maastrichtian tests, the relative stability of mean foraminiferal accumulation indicates that decreased accumulation resulted from decreased nanofossil accumulation rather than from increased dissolution (D’Hondt, 2006).

Paleocene planktic foraminifera stratigraphic distributions were recorded using 140 core samples from Site 528 and 126 samples from Site 577. Species identifications were cross-checked by R.K. Olsson and I. Premoli-Silva. Evolutionary patterns were derived from range charts by counting: (1) the number of first occurrences, (2) the number of last occurrences, and (3) the total number of species present through 5 m intervals for Site 528 and 2.5 m intervals for Site 577. We used the surface- to deep-water δ¹³C differential as a proxy for the strength of the carbon pump that delivers organic matter to the seafloor (D’Hondt et al., 1998). The isotopic data presented in Figures 1 and 2 are from D’Hondt et al. (1998), supplemented with new analyses that were performed at the University of Santa Cruz, California.

PLANKTIC FORAMINIFERA EVOLUTIONARY RECOVERY

Site 528 records reveal an initial burst of diversification within 300 k.y. of the extinction that contributed 18 new species in 8 new genera, representing >60% of total Paleocene diversity (Fig. 1). This occurred at the beginning of the two of abrupt increases in planktic-benthic and fine CaCO₃-benthic calcite δ¹³C, identified as “initial δ¹³C recovery” (~404 m below seafloor [bsf], base of magnetostratigraphic C29n) (Fig. 1A). A second phase of diversification and turnover began almost 3 m.y. after the extinction between 375 m and 395 m depth, adding a further 3 genera and 16 species. This phase lasted 2–3 m.y. and spanned a second, final stage of δ¹³C recovery when planktic-benthic and fine-fraction CaCO₃-benthic δ¹³C gradients returned to pre-extinction values (Fig. 1A–C). Thereafter, extinctions and originations stabilized until the Paleocene–Eocene boundary, when evolutionary turnover was renewed (Corfield and Shackleton, 1988; Kelly et al., 2001).

Pacific Ocean Site 577 records show a similar relationship between the timing of the second phase of diversification and δ¹³C change (Fig. 2A–C). The lower stratigraphic occurrence of Praemurica uncinita and its descendents, the morozovellids, at this site compared to Site 528 suggests that either Morozovella began to diversify before final δ¹³C recovery in the tropics or a section of younger sediment was displaced down-core. Despite the minor biostratigraphic differences,
Figure 1. Planktic foraminiferal evolutionary records from Deep Sea Drilling Project (DSDP) Site 528 compared to Cretaceous-Paleogene (K/Pg) boundary carbon isotopes ($\delta^{13}$C). Isotopic analysis was performed on an Optima gas-source mass spectrometer equipped with an Autocarb common acid bath. A: Differences between surface (planktic foraminifer and fine-fraction CaCO$_3$) and deep-sea (benthic foraminifer $Gavelinella$ sp. + $N$. truempyi) calcite $\delta^{13}$C (from D’Hondt et al., 1998, supplemented with 87 new data points). $\delta^{13}$C is measured in $\%$ relative to the PeeDee belemnite (PDB) standard; mbsf is m below seafloor. Major decrease in surface- to deep-water $\delta^{13}$C gradients occurs at the K/Pg boundary. Dashed gray lines mark (1) initial and (2) final $\delta^{13}$C recovery from K/Pg excursion values. B: Foraminiferal stratigraphic ranges, minimum 1 cm sample spacing across the K/Pg. Majority of Cretaceous species went extinct at the boundary. C: Evolutionary turnover. Species first and last occurrences (FOs and LOs) were counted from B. Cretaceous diversity data are from D’Hondt et al. (1996). Genus abbreviations: Ps.—$Pseudotextularia$, R.—$Rugoglobigerina$, Gu.—$Guembelitria$, Pv.—$Parvularugoglobigerina$, G.—$Globoconusa$, Z.—$Zeauvigerina$, W.—$Woodringina$, C.—$Chiloguembelina$, H.—$Hedbergella$, Gl.—$Globanomalina$, E.—$Eoglobigerina$, P.—$Parasubbotina$, S.—$Subbotina$, Pr.—$Praemurica$, I.—$Igorina$, M.—$Morozovella$, A.—$Acarinina$.

the pattern and timing of $\delta^{13}$C recovery relative to the magnetic reversal sequence, and the timing of the main morozovellid diversification are consistent at the two sites.

DISCUSSION

The general pattern of planktic evolutionary recovery shown by our data is one of initial colonization by a few Cretaceous-Paleogene survivors, followed by two stages of diversification: (1) a rapid initial phase, which established basic test shapes and generic diversity but had relatively low species diversity, and (2) a delayed second phase, which peaked $\sim$4 m.y. after the extinction and contributed further important Paleogene lineages and returned Paleocene diversity to close to pre-extinction levels. The timing of these evolutionary waves bears a striking resemblance to the $\delta^{13}$C recovery.

The $\delta^{13}$C recovery has been shown to represent a multimillion-year staged recovery of surface to deep organic flux following a catastrophic decline at the Cretaceous-Paleogene boundary (D’Hondt et al., 1998; Adams et al., 2004). This indicates that recovery of planktic foraminifera from the mass extinction was closely linked to recovery of marine carbon cycling. Reduced primary production is often invoked to explain low surface to deep $\delta^{13}$C gradients. Although productivity may have declined in the immediate aftermath of the extinction (e.g., Hsu et al., 1982; Zachos et al., 1989), it is unlikely to have persisted for millions of years. An alternative hypothesis to explain the $\delta^{13}$C records is a living ocean model (D’Hondt et al., 1998). This assumes that biological productivity returned rapidly (within years of the extinction), but that organic flux was drastically reduced for millions of years because of a greatly altered ecosystem (such as a general absence of larger grazers, e.g., macrozooplankton and fish), which normally acts to export biomass to the deep sea, and/or a relatively low mean size of phytoplankton (D’Hondt et al., 1998).

The model explains the two stages of $\delta^{13}$C recovery as an initial gradual recovery in the proportion of biological production that sank to the deep sea followed by an abrupt final recovery a few million years later as larger grazers evolved and/or average phytoplankton size increased. This is consistent with ecological models of biodiversity recovery after mass extinctions that predict multimillion-year lags in diversification as consecutive tiers of trophic webs are reconstructed (e.g., Kirchner and Weil, 2000). Paleontological evidence for this may be lacking, because pelagic macrofossils are extremely rare (D’Hondt, 2006). The apparent contradiction of this interpretation with benthic foraminifera records, which show no major extinction at the
CRETAalic-Paleogene boundary (Culver, 2003), has been attributed to the fact that deep-sea benthic foraminifera by their nature are tolerant of low food supply and are well suited to survive periods of low productivity (e.g., Thomas, 1990). In any case, we do not argue that organic flux ceased completely but that it was greatly reduced for an extended period. Transfer of particulate organic carbon to the deep sea is a complex process, and other factors, such as biomineral ballasting (e.g., Armstrong et al., 2002), may also have been important to carbon flux recovery as the mean size of planktic foraminiferal shells (and calcareous nanoplankton; P. Bown, 2005, personal commun.) increased.

**Planktic Foraminifera Ecological Radiation**

The second major wave of diversification shortly followed full carbon cycle recovery. Evolution was most pronounced in the genus *Morozovella*, the dominant group of Paleocene-Eocene surface mixed-layer dwellers, and produced a series of large (200–400 μm) species with peripheral keels and a pustulose (muricate) wall. The morozovellid radiation was shortly followed by diversification of two additional muricate genera, *Igorina* and *Acarinina*. Muricate species exhibit strong positive correlations between δ¹³C and test size, which is thought to result from δ¹³C fractionation by algal symbionts (Spero and DeNiro, 1987; Pearson, et al., 1993; Norris, 1996). This symbiosis-related δ¹³C enrichment in *Morozovella* spp. exaggerates the δ¹³C gradient (Figs. 1A and 1B). However, δ¹³C increase during the final recovery is not limited to these taxa, and fine-fraction CaCO₃ and asymbiotic planktics (*Subbotina* spp.) to benthic δ¹³C differentials increase at the same time (Figs. 1A and 2A). Moreover, it seems unlikely that final δ¹³C recovery in fine-fraction CaCO₃ is the result of simultaneous changes in vital effects in all the fossil groups, including nanoplankton (Bralower, 2002). Instead, we interpret the results as representing an ocean-wide shift in the surface- to deep-water δ¹³C gradient and recovery of the carbon pump to pre-extinction strength. The symbiotic ecology of the muricate taxa has interesting implications for understanding the post—Cretaceous-Paleogene boundary environment.

Symbiotic associations with algae are widespread among modern planktic foraminifera and allow hosts to attain high-population densities in low-nutrient, central-ocean regions (Hemleben et al., 1989; Caron et al., 1995). Strong size-related δ¹³C trends characteristic of symbiosis occur in *M. praeangulata* (Kelly et al., 1996) and all subsequent species of *Morozovella* (Pearson et al., 1993; D’Hondt et al., 1994; Norris, 1996). In contrast, species of *Praemurica*, with the possible exception of *P. uncinata* (Norris, 1996), show no such trend and are
considered asymbiotic. This suggests that the evolutionary transition from *Praemurica* to *Morozovella* involved evolution of a symbiotic ecology (Norris, 1996). Our results show that *M. praenagulata* and its muricate symbiosis evolved before final $^{3}$H$^{12}$C recovery at Sites 528 and 577, but the main evolutionary diversification of *Morozovella* came directly after. A concomitant increase in average test size (D'Hondt, 2006) supports this hypothesis, because symbiotic species tend to build larger tests to maximize symbiont benefit (Spero and DeNiRo, 1987). A possible interpretation of this is that the pattern and timing of radiation in *Morozovella* and other muricate genera represent diversification of eutrophic specialists as organic flux to the deep ocean fully recovered, stripping of nutrients from the surface ocean resumed, and specialization to low food availability became a selective advantage. Although symbiosis appears to have been central to this in the final stage of diversification (Koutskous, 1996; Norris, 1996), it could not have been the key innovation that triggered the evolutionary event, because the signature for this ecology was present in ancestral morozovellid species before the diversification occurred. Rather, the radiation appears to have principally resulted from diversification of symbiotic forms exploiting an expanding eutrophic opportunity that in turn resulted from final recovery of the marine carbon cycle.

**CONCLUSIONS**

This study provides an ecological dimension to the understanding of the Cretaceous-Paleogene boundary biotic crisis and recovery and a broader window into the extent and impact of the perturbation in the pelagic realm. The photic zone ecosystem is the principal driver of the marine carbon pump, shunting organic carbon through increasingly complex food chains into aggregates large enough to survive export to the seafloor. Recovery of the carbon pump, therefore, is contingent on recovery of integrated ecosystems. Our results suggest that this ecosystem-driven cycling has the potential to provide a positive feedback once the system attains full complexity (i.e., when a broad spectrum of herbivores and predators involved in the trophic web have evolved) by triggering diversification of low-food tolerant oligotrophic specialists. The three million year delay in organic flux and planktic foraminifer evolutionary recovery attests to the far-reaching effects of the extinction in the marine realm and implies that the time required to repair food chains and reestablish an integrated ecosystem is extremely long (millions of years) compared to the immediate physical effects of the disaster.

**ACKNOWLEDGMENTS**

This work was supported by a U.S. National Science Foundation grant to S. D'Hondt. We thank R.K. Olsson and I. Premoli-Silva for discussions and assistance with Paleocene foraminiferan taxonomy, William Chaisson for assistance with planktic foraminiferan isolate samples, and Miranda Smith for assistance with data handling and drafting. Thanks also are due to Harriet Leong, Julia Frazier, Steven Bohaty, and Robert Becker for assistance with isotope analysis.

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Manuscript received 9 March 2005

Revised manuscript received 14 December 2005

Manuscript accepted 16 December 2005

Printed in USA