

CONSEQUENCES OF THE CRETACEOUS/PALEOGENE MASS EXTINCTION FOR MARINE ECOSYSTEMS

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■ **Abstract** One of the greatest mass extinctions in Earth's history occurred at the end of the Cretaceous era, sixty-five million years (Myr) ago. Considerable evidence indicates that the impact of a large asteroid or comet was the ultimate cause of this extraordinary event. At the time of mass extinction, the organic flux to the deep sea collapsed, and production of calcium carbonate by marine plankton radically declined. These biogeochemical processes did not fully recover for a few million years. The drastic decline and long lag in final recovery of these processes are most simply explained as consequences of open-ocean ecosystem alteration by the mass extinction. If this explanation is correct, the extent and timing of marine biogeochemical recovery from the end-Cretaceous event was ultimately contingent on the extent and timing of open-ocean ecosystem recovery. The biogeochemical recovery may in turn have created new evolutionary opportunities for a diverse array of marine organisms.

INTRODUCTION

The end-Cretaceous mass extinction is one of the largest known extinction events in Earth's history (Sepkoski 1996). At the genus level, the total diversity of fossilized marine genera declined by nearly 50% from the end-Cretaceous Maastrichtian stage [~71 to 65 Mya] to the earliest Paleogene Danian stage (~65 to 61 Mya) (Sepkoski 1996; absolute age estimates from Berggren et al. 1995). Entire categories of organisms completely disappeared. In the marine realm, these categories included mosasaurs, sauropterygians (plesiosaurs and pliosaurs), ammonites, and heterohelcid planktic foraminifera. In the terrestrial realm, these categories included all forms of nonavian dinosaurs (Fastovsky & Sheehan 2005).

This event has historically been called the Cretaceous/Tertiary (K/T) mass extinction. However, the International Commission on Stratigraphy (ICS) does not recognize the Tertiary as a formal unit of Earth's history. In this review, I follow their lead and refer to the end-Cretaceous event as the Cretaceous/Paleogene (K/Pg) mass extinction.

Over the years, the end-Cretaceous extinction has been attributed to many ultimate causes including a supernova (Russell & Tucker 1971), flood-basalt eruption (Officer & Drake 1985), and the impact of a large asteroid or comet (Alvarez et al. 1980, Smit & Hertogen 1980). The vast majority of evidence favors the impact model.

The evidence for a large-body impact at the end of the Cretaceous is overwhelming (D'Hondt 1994, Smit 1999). Evidence of the impact is so widespread and clear that the ICS defines the K/Pg boundary as the base of the impact-debris layer, as exemplified by the iridium-bearing clay layer at El Kef, Tunisia (Cowie et al. 1989). The ICS has recently estimated the age of the K/Pg boundary to be 65.5 Mya. Herein I use an age estimate of 65 Mya for the K/Pg boundary because most paleontological and paleoceanographic studies of the last decade calibrated their data to a standard timescale that placed the boundary at 65 Mya.

Details of the K/Pg extinction remain a subject of occasional debate in the paleontological literature. However, the fossils observed in uppermost Cretaceous strata often demonstrate a striking pattern of occurrence; the more abundant, widely distributed, and often studied the fossil taxon, the more closely its final occurrence is associated with the impact-debris horizon. Rare but charismatic macrofossils, such as ammonite shells or articulated vertebrate bones, are rarely found close to the debris horizon (e.g., Marshall & Ward 1996). Abundant and widespread Maastrichtian fossils, such as the remains of calcareous nannoplankton (Pospichal 1994), planktic foraminifera (e.g., D'Hondt et al. 1996, Molina et al. 1998) and, in Denmark, cheilostome bryozoans (Håkansson and Thomsen 1999), generally occur very close below the debris horizon.

Local distributions of relatively rare fossils such as ammonites or dinosaur remains have occasionally been statistically analyzed to assess the possible rate and timing of end-Cretaceous extinction. The results of those analyses are consistent with the interpretation of mass extinction at the time of impact (e.g., Fastovsky & Sheehan 2005, Marshall & Ward 1996).

The coincidence of extinction and impact is particularly striking for planktic foraminifera, whose tests (skeletons) are abundant in upper Cretaceous marine limestones and carbonate oozes throughout the world. All latest Cretaceous morphospecies of planktic foraminifera occur just below the impact-debris horizon at one location or another (D'Hondt et al. 1996). Only two or three of these species consistently occur more than a few centimeters or tens of centimeters above the impact horizon in normally deposited marine sediments. The scattered tests of other Late Cretaceous species in lower Paleogene sediments exhibit carbon isotopic signatures, preservational states, and fossil distributions that indicate they were reworked from preimpact sediments (Huber 1996, Huber et al. 2002, Kaiho & Lamolda 1999, Zachos et al. 1992).

The proximate cause (or causes) of the end-Cretaceous extinction remains unknown. Advocates of the impact-extinction hypothesis (and their few but stalwart opponents) have proposed many potential causes (Kring 2000). These include

global darkness (Alvarez et al. 1980), global cooling (Toon et al. 1982), acid rain (Lewis et al. 1982), rapid thermal radiation (Emiliani 1980), and heavy metal poisoning (Erickson & Dickson 1987). The relative importance of these respective causes is model dependent and presumably varied from one environment to another. In marine environments, darkness and (perhaps) cooling may have been important causes of end-Cretaceous extinction. Brief thermal radiation is a highly unlikely cause of widespread marine extinction because the thermal inertia of the upper ocean is great. Acid rain is also an unlikely cause of the marine extinction because the acid-buffering capacity of the upper ocean exceeds most estimates of acid production by the end-Cretaceous impact (D'Hondt et al. 1994a).

Whatever the proximate cause of the end-Cretaceous extinction, it greatly affected the diversity of life on Earth. In one sense, diversity never recovered; the organisms that disappeared will never reappear. In another sense, diversity recovered, but took a very long time; analyses of stage-level (multi-million-year) data compilations suggest that evolutionary rates, measured as rates of genus origination, lagged rates of peak extinction by millions of years (Kirchner & Weil 2000, Sepkoski 1998).

SELECTIVITY OF THE END-CRETACEOUS MASS EXTINCTION

Studies of marine fossil assemblages in distant locations show that the diversity of Danian communities was consistently lower than that of Maastrichtian communities. For example, fossil deposits in Upper Maastrichtian sediments of New Jersey (United States) contain diverse remains of abundant bivalves, gastropods, ammonites, sharks, bony fish, turtles, mosasaurs, crocodiles, and an occasional brachiopod (Gallagher 2003). In contrast, fossil remains in the overlying Danian sediments make up a depauperate assemblage where the most abundant fossils are sponges, brachiopods, and solitary corals (each limited to a single species) (Gallagher 2003). The Danian molluscs are much smaller, less abundant, and far less diverse than their Maastrichtian counterparts. Occasional remains of crocodiles and lamnid sharks provide the only evidence of higher predators (Gallagher 2003). Studies of macroinvertebrate faunas in Denmark (Håkansson & Thomsen 1999) and of molluscan taxa in the Gulf Coast (United States) region [Alabama (Jones et al. 1987) and Texas (Hansen et al. 1993)] have similarly identified large decreases in diversity across the K/Pg boundary.

Some groups of organisms were far more resistant to the K/Pg mass extinction than others. Taxa that preferentially survived the mass extinction included benthic foraminifera (Alegret & Thomas 2004, Culver 2003) and fossilizable dinoflagellates (Brinkhuis et al. 1998, Wendler & Willems 2002). Microorganisms that preferentially survived the mass extinction generally exhibit life-history

characteristics that might have enabled them to wait out periods of extreme stress to open-ocean ecosystems. These characteristics include benthic lifestyles and the ability to form cysts (Brinkhuis et al. 1998, Kitchell et al. 1986, Wendler & Willems 2002). In contrast, the marine microorganisms most affected by the K/Pg mass extinction, planktic foraminifera and coccolithophorids, generally lack these life-history characteristics. Planktic foraminifera may be particularly susceptible to extinction when driven to very low population densities because, unlike dinoflagellates, diatoms, calcareous nannoplankton, and many radiolaria and benthic foraminifera, they can only reproduce sexually (D'Hondt et al. 1996).

Macrofossil groups that preferentially survived the mass extinction also exhibit consistent ecological characteristics. For example, several studies have inferred that detritus-feeding marine and terrestrial organisms were less susceptible than other organisms to end-Cretaceous extinction (Arthur et al. 1987, Sheehan & Hansen 1986). This trophic selectivity and the life-history selectivity described in the previous paragraph are consistent with the proximate cause of extinction being a drastic but short-lived decrease in photosynthesis brought about by a brief period of impact-induced global darkness (Arthur et al. 1987, Sheehan & Hansen 1986).

Taxonomic patterns of macrofossil extinction selectivity vary considerably from region to region (Hansen et al. 1993, McClure & Bohonak 1995). This variability is consistent with variation in selection factors from region to region and ecosystem to ecosystem (McClure & Bohonak 1995). It is also consistent with chance having played a significant role in taxonomic survival. Within some taxonomic groups, survival was so low that selective extinction is hard to distinguish from a null hypothesis of chance survival. On a local scale, these taxa include molluscs in the Brazos region of Texas (Hansen et al. 1993). On a global scale, they include planktic foraminifera.

Traits of species or higher taxa are sometimes considered to protect taxa against background extinction. Some of these properties—population size of species (Lockwood 2003), species-level geographic distributions, and species richness of clades (Jablonski 2001)—conferred no significant resistance to the K/Pg mass extinction. Geographic distribution may have played some role in genus-level survival of the K/Pg mass extinction, at least among bivalves (Jablonski 2003) and calcareous dinoflagellates (Wendler & Willems 2002). Nonetheless, it did not consistently protect organisms against the end-Cretaceous mass extinction. For example, almost all genera of Late Cretaceous planktic foraminifera were driven to extinction, despite being globally distributed. In at least some cases, mundane organismal properties visibly trumped geographic distribution in conferring resistance to the K/Pg mass extinction. A global study of echinoids showed that adult feeding strategies (omnivory and fine organodetritus deposit feeding) are strongly correlated to survival of the extinction event but geographic distribution is not (Smith & Jeffrey 1998).

BIOGEOCHEMICAL COLLAPSE AND RECOVERY AFTER THE MASS EXTINCTION

The mass disappearance of species and genera at the K/Pg boundary was an extraordinary event. Its potential consequences went well beyond biological diversity into the environmental realm. Per-area rates of deep-sea carbonate sedimentation drastically dropped at the time of mass extinction (e.g., Zachos & Arthur 1986). The flux of organic matter to the deep seafloor declined tremendously at the same time (e.g., Hsü et al. 1982, Zachos et al. 1989). These processes did not recover for millions of years (Arthur et al. 1987; D'Hondt et al. 1998a,b). Understanding of the extinction's ecological consequences requires a closer examination of these processes.

PRODUCTION OF CARBONATE MICROFOSSILS

Calcium carbonate (CaCO_3) microfossils produced by nannoplankton (principally coccolithophorids) and planktic foraminifera blanket approximately 70% of the deep seafloor in the modern ocean. These microfossils compose an unusually low percentage of sediments deposited during the Danian stage. Throughout the world ocean, the CaCO_3 fraction of deep-sea sediments crashed to nearly zero at the very end of the Cretaceous and did not completely return to pre-extinction values for three or four million years (Figure 1A).

Paleoceanographic studies have consistently shown that the Danian carbonate crash resulted from a radical and long-lasting decrease in the rate of CaCO_3 accumulation (D'Hondt et al. 1996, Zachos & Arthur 1986). This decrease in carbonate accumulation occurred in every ocean basin (Zachos & Arthur 1986) (Figure 1B). It began at the time of K/Pg impact and microfossil mass extinction (D'Hondt et al. 1996). Carbonate accumulation rates remained unusually low for more than a million years (Zachos & Arthur 1986). Present data suggest that carbonate accumulation may have remained unusually low for about four million years (D'Hondt et al. 1998b) (Figure 1B).

A large decrease in CaCO_3 accumulation can result from either (a) a large decrease in production of CaCO_3 microfossils or (b) a large increase in the dissolution of CaCO_3 microfossils by deep water. Records of microfossil preservation indicate that the unusually low carbonate accumulation rates of the Danian stage resulted from unusually low rates of microfossil production. For example, at moderate levels of carbonate dissolution, foraminiferal tests are visibly fragmented. Fragmentation of foraminiferal tests is much lower in sediments deposited during the postextinction interval of low CaCO_3 accumulation than in the sediments deposited before or after (Figure 1C). Fragmentation remained unusually low for about three million years (Figure 1C).

The unusually low rate of postextinction CaCO_3 accumulation principally resulted from the rate of calcareous nannofossil (fine carbonate) accumulation

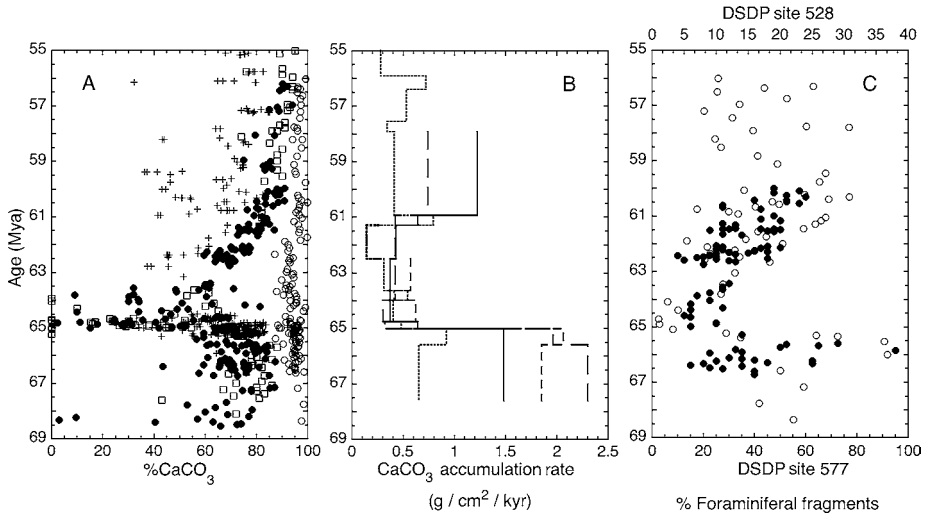


Figure 1 Patterns of K/Pg carbonate sedimentation at widely distant open-ocean sites: (A) Sedimentary carbonate concentrations (% CaCO₃) at Central Pacific DSDP Site 577 (white circles), South Atlantic DSDP Site 528 (black circles), South Atlantic DSDP Site 527 (white squares), and Caribbean ODP Site 1001A (crosses). (B) Mean CaCO₃ accumulation rates at Site 577 (dotted line), Site 528 (line with short dashes), Site 527 (line with long dashes), and Site 1001A (solid line). (C) Percent foraminiferal fragments [number of planktic foraminiferal fragments/(number of planktic foraminifera + fragments)*100]. Note the pronounced decreases in the properties exhibited by all three panels at 65 Ma (the K/Pg boundary) and their final recoveries at approximately 62–61 Ma. Age assignments are based on magnetic reversal data (Bleil 1985, Chave 1984, Sigurdsson et al. 1997), the K/Pg and Paleocene/Eocene (P/E) boundaries (Sigurdsson et al. 1997, D'Hondt et al. 1998a), the magnetic reversal timescale of Cande & Kent (1995), and age estimates for the K/Pg boundary and the P/E boundary from Berggren et al. (1995). Accumulation rates immediately above and below the K/Pg boundary (within paleomagnetic reversal interval 29R) are based on precessional cycle counts of D'Hondt et al. (1996). Except at the K/Pg boundary where precessional control precisely identifies the changes in mean accumulation rates, the step-like nature of the accumulation rate estimates in panel B results from the positions of the chronostratigraphic tie points used to calculate the rates. Actual changes in accumulation rates may be more gradual and may occur at any time between tie points.

decreasing by a factor of four or more (D'Hondt et al. 1996, Zachos & Arthur 1986). Foraminifera constitute a very small fraction of the total carbonate in upper Cretaceous sediments (Figure 2A). Furthermore, despite the extraordinary level of end-Cretaceous planktic foraminiferal extinction, the average rate of foraminiferal accumulation decreased by a factor of two or less across the mass extinction horizon

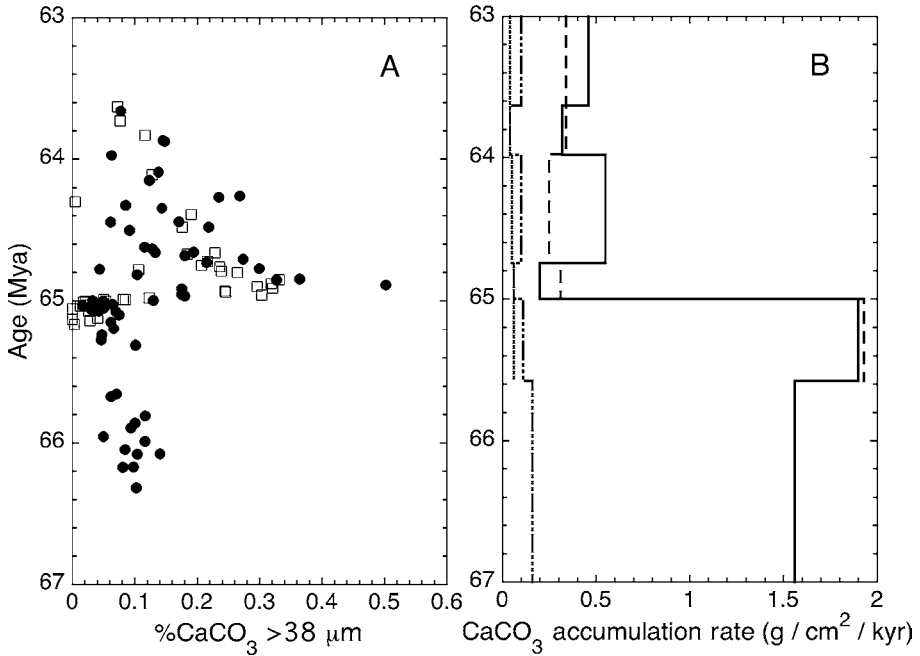


Figure 2 Carbonate constituents and their accumulation rates: (A) Percent $\text{CaCO}_3 >38 \mu\text{m}$ (foraminiferal tests and their fragments) at South Atlantic DSDP Sites 527 (white squares) and 528 (black circles). (B) Accumulation of CaCO_3 in the $>38 \mu\text{m}$ fraction at Sites 527 (dotted line) and 528 (line of alternating dots and dashes), and the $<38 \mu\text{m}$ fraction, principally composed of calcareous nannofossils, at Sites 527 (dashed line) and 528 (solid line). Age assignments and uncertainties in timing of changes in accumulation rates are as in Figure 1. Note the pronounced change at the K/Pg boundary (65 Mya) in both panels.

(Figure 2B). Consequently, the low carbonate accumulation rates in Danian deep sea sediments principally resulted from a radical and long-lasting decrease in CaCO_3 production by calcareous nannoplankton.

THE FLUX OF ORGANIC MATTER TO DEEP WATER

Four lines of evidence indicate that the organic flux to the global deep ocean radically decreased at the time of the K/Pg impact and microfossil mass extinction: The first line of evidence is the improved preservation of planktic foraminifera in Danian sediments (Figure 1C). The second line of evidence is a tremendous decrease in the carbon isotopic ($\delta^{13}\text{C}$) difference between planktic foraminifera and benthic foraminifera at sites throughout the world ocean (D'Hondt et al. 1998a; Stott & Kennett 1989; Zachos et al. 1989, 1992) (Figure 3A,B). The third line of evidence is convergence of the carbon isotopic signatures of benthic foraminiferal

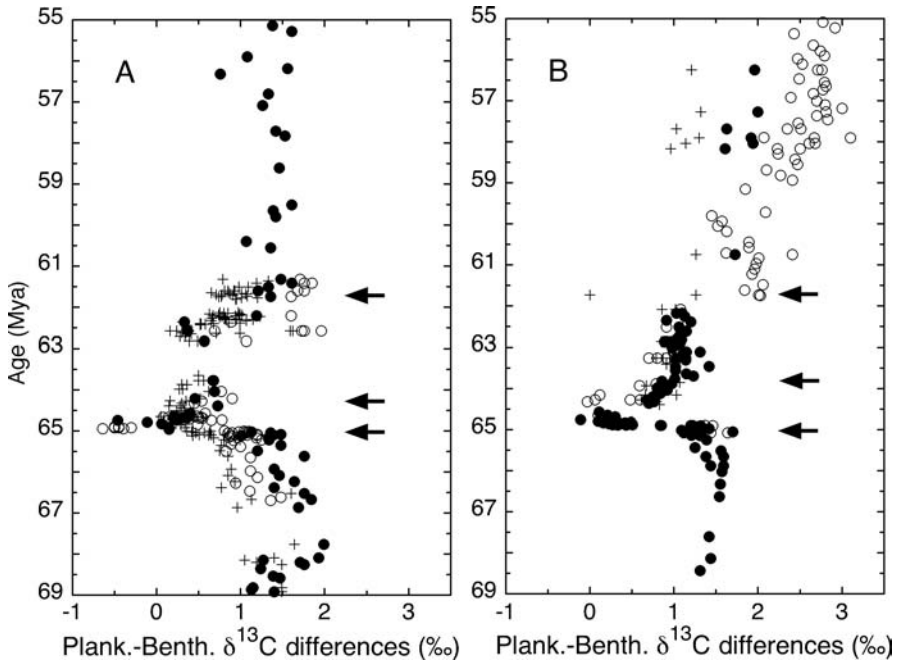


Figure 3 Carbon isotopic proxies for organic flux to the deep sea: (A) $\delta^{13}\text{C}$ differences between planktic foraminifera and benthic foraminifera at South Atlantic DSDP Site 528; (B) $\delta^{13}\text{C}$ differences between planktic foraminifera and benthic foraminifera at central Pacific DSDP Site 577. Age assignments are as in Figure 1. The black circles represent $\delta^{13}\text{C}$ differences between fine carbonate (principally calcareous nannofossils) and benthic foraminifera, the white circles represent differences between planktic foraminifera that dwelt near the sea surface and benthic foraminifera, and the crosses represent differences between deeper water (thermocline) planktic foraminifera and benthic foraminifera. Isotopic data are from D'Hondt et al. (1998b) and S. D'Hondt and J.C. Zachos (unpublished data). Note the sharp negative shift in both records at 65 Mya (the K/Pg boundary) (*bottom arrow* in each panel), the partial recovery of the $\delta^{13}\text{C}$ differences within the following Myr (*middle arrow* in each panel), and the eventual recovery of both records at approximately 62 Mya (*top arrow* in each panel).

tests from the Atlantic and Pacific oceans (Stott & Kennett 1989, Zachos et al. 1992). The fourth line of evidence is collapse of the $\delta^{13}\text{C}$ gradient between infaunal and epifaunal benthic foraminifera (Zachos et al. 1989).

A fuller understanding of these lines of evidence requires a brief discussion of the oceanic carbon system. The concentration of dissolved inorganic carbon ($\text{DIC} = \text{HCO}_3^- + \text{CO}_3^{2-} + \text{CO}_2$) in surface seawater is approximately in equilibrium with the atmosphere and is inversely proportional to temperature. Consequently, DIC concentrations in the surface ocean are lowest in the warm subtropical waters ($1900 \mu\text{mol/kg}$) and highest in the cold high-latitude ocean ($2200 \mu\text{mol/kg}$)

(Broecker & Peng 1982). Deep water DIC concentrations depend on (a) the atmospheric equilibration in the surface-ocean region(s) of deep water formation and (b) the oxidation of sinking organic matter from the surface ocean.

In seawater, CO₂ released by oxidation of organic matter increases the solubility of CaCO₃ by decreasing pH and carbonate ion (CO₃²⁻) concentration (Pilson 1998). Consequently, the sinking and decay of organic carbon renders deep water corrosive to CaCO₃ microfossils. The decreased fragmentation of planktic foraminifera in lowermost Paleogene sediments indicates that the postextinction ocean was less corrosive to carbonate microfossils than the pre-extinction ocean for about three million years (Figure 1C). This in turn suggests that the decay of organic carbon in deep waters and, by implication, the flux of organic carbon to deep water were unusually low for the same interval of time.

Carbon 12 constitutes 98.89% of the stable carbon in the world (Faure 1986). The remaining 1.11% is ¹³C. The ratio of stable carbon isotopes in environmental samples is typically expressed in parts per thousand (‰) relative to a standard value, using δ notation:

$$\delta^{13}\text{C} = [({}^{13}\text{C}/{}^{12}\text{C})_{\text{sample}} - ({}^{13}\text{C}/{}^{12}\text{C})_{\text{standard}}] / ({}^{13}\text{C}/{}^{12}\text{C})_{\text{standard}} * 1000.$$

The conventional standard value is the ¹³C/¹²C ratio of the PDB standard, a sample of fossil belemnites from the Cretaceous PeeDee Formation of South Carolina (United States) (Faure 1986).

The δ¹³C of dissolved carbon in the modern deep ocean is 1‰ to 2‰ more negative than the δ¹³C of dissolved carbon in the surface ocean (Kroopnick 1980, Kroopnick et al. 1970) (Figure 4). This difference ultimately results from the flux of organic carbon from the surface ocean to the deep sea. The δ¹³C of marine plankton is about 20‰ more negative than the δ¹³C of the surface ocean (Anderson & Arthur 1983). Consequently, deep water oxidation of sinking organic matter from the surface ocean renders deep-ocean δ¹³C more negative than surface-ocean δ¹³C by adding DIC with the δ¹³C of marine plankton to the deep ocean. The δ¹³C of DIC in the modern deep ocean is least negative in the North Atlantic basin, which contains relatively young deep water, and most negative in the North Pacific basin, which contains deep water that has accumulated DIC from organic oxidation for many hundreds of years (Figure 4).

Because foraminifera derive most of the carbonate in their tests from DIC in their environment, δ¹³C differences between surface water DIC and deep water DIC are approximated by δ¹³C differences between the tests of planktic foraminifera that live in the surface ocean and the tests of benthic foraminifera that live on the seafloor (epibenthic foraminifera). Similarly, δ¹³C differences between seawater DIC in the thermocline (tens to hundreds of meters beneath the sea surface) and deep water DIC are approximated by δ¹³C differences between thermocline-dwelling planktic foraminifera and the tests of epibenthic foraminifera.

Carbon isotopic differences between planktic and benthic foraminiferal tests of the latest Cretaceous (Figure 3A,B) are roughly equivalent to δ¹³C differences between surface water DIC and deep water DIC in the modern ocean (Figure 4). This equivalence indicates that the distribution of oceanic DIC in the pre-extinction

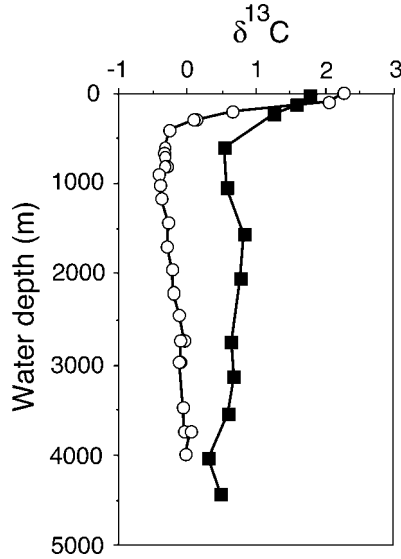


Figure 4 $\delta^{13}\text{C}$ of dissolved inorganic carbon in the modern North Pacific [Geosecs Site, SIO data (*white circles*)] and South Atlantic [Site 103 data (*black squares*)]. Data from Kroopnick et al. (1970) and Kroopnick (1980).

Cretaceous was much as it is today. For this to be so, patterns of organic-matter oxidation in the deep ocean and, by inference, the flux of organic matter to the deep ocean, must have been similar to what it is today.

This carbon isotopic system changed radically at the time of end-Cretaceous extinction, when the $\delta^{13}\text{C}$ values of planktic and benthic foraminiferal tests converged (Figure 3A,B) (D'Hondt et al. 1998a; Stott & Kennett 1989; Zachos et al. 1989, 1992). The $\delta^{13}\text{C}$ difference between planktic tests and benthic tests did not fully recover to pre-extinction values until approximately three million years after the extinction event (Figures 3A,B) (Adams et al. 2004, D'Hondt et al. 1998a). The K/Pg convergence of planktic and benthic $\delta^{13}\text{C}$ signals provides strong evidence that the impact and mass extinction coincided with a radical decrease in the flux of organic matter to the deep sea. Coeval convergence of benthic foraminiferal $\delta^{13}\text{C}$ signals from distant ocean basins similarly indicates a radical decrease in the flux of organic matter to the deep ocean (Stott & Kennett 1989, Zachos et al. 1992). The long delay in recovery of planktic to benthic $\delta^{13}\text{C}$ differences indicates that the flux of organic matter to deep water did not recover for about three million years. The Danian difference between planktic and benthic $\delta^{13}\text{C}$ signals recovered in two stages (Adams et al. 2004, D'Hondt et al. 1998a). The first recovery stage is marked by continuous relaxation toward an interval of low but relatively stable $\delta^{13}\text{C}$ differences between planktic and benthic foraminifera. The second stage is defined by a discontinuous adjustment to approximately pre-extinction $\delta^{13}\text{C}$ differences about three million years after the end-Cretaceous impact and mass extinction. Like the

postextinction changes in CaCO_3 preservation and the end-Cretaceous collapse of planktic to benthic $\delta^{13}\text{C}$ differences, the two-stage recovery of planktic to benthic $\delta^{13}\text{C}$ differences occurred in both the Atlantic and Pacific Oceans (Figure 3).

ECOLOGICAL MODELS OF THE POSTEXTINCTION OCEAN

Two models have been proposed to explain the interval of low organic flux and low nannofossil production that followed the end-Cretaceous impact. It was first interpreted as the result of unusually low marine biological productivity throughout the postextinction ocean (e.g., Hsü et al. 1982). This interpretation is usually described as the Strangelove Ocean model, following Broecker & Peng (1982), who called an ocean with no life a “Strangelove ocean.” The alternative model, proposed by D’Hondt et al. (1998b), holds that marine productivity was relatively high but the fraction of total productivity that sank to the deep sea was relatively low during the multi-million year interval of low organic flux. This interpretation has been called the Living Ocean model (e.g., Adams et al. 2004).

Interpretations of the Danian postextinction ocean as a Strangelove ocean (e.g., Hsü & McKenzie 1985) implicitly redefine a Strangelove ocean as one where life is present but biological productivity is low. On very short timescales, such an ocean would naturally have resulted from at least one hypothetical consequence of the K/Pg impact—a large reduction in sunlight at Earth’s surface owing to high concentrations of impact dust (Alvarez et al. 1980) and sulfuric aerosol released by vaporization of anhydrite at the impact site (Brett 1992). Such a reduction in sunlight may have greatly reduced photosynthesis for a short period of time after the impact. However, quantitative models of large impact events and their consequences suggest that dust and aerosols would have been swept from the atmosphere in less than a year (Kring 2000).

Maintenance of low phytoplankton production on significantly longer timescales is difficult to envision (Arthur et al. 1987). Marine phytoplankton have typical doubling times of hours to days. Given such doubling times, a multi-million-year decrease in phytoplankton production would require some key environmental property, such as availability of a biologically limiting nutrient, to instantly decrease at the K/Pg boundary and remain anomalously low for a few million years. However, no physical consequences of large impacts are predicted to last as long as a million years by quantitative models. In fact, very few environmental consequences of large impacts have been inferred to last beyond a decade. Furthermore, the physical consequences of large impacts are not obviously linked to the long-term state of biologically limiting properties, such as marine nutrient availability.

D’Hondt et al. (1998b) addressed these issues by hypothesizing that marine phytoplankton production quickly returned after the impact and mass extinction. In this Living Ocean model, low organic flux to the deep ocean was principally a consequence of ecosystem structure in the postextinction ocean. The proportion

of organic production that sinks from the surface ocean is controlled by several ecosystem properties, including the ratio of phytoplanktonic respiration to photosynthesis; phytoplankton size (only the largest plankton sink rapidly enough to settle to deep waters); the ability of phytoplankton to aggregate into larger particles; and the size, trophic efficiency, and gut structure of animals (which may repackage biomass into large particles that sink rapidly).

Given these factors, many rearrangements of the open-ocean ecosystem could decrease the flux of organic matter to the deep sea. These possible rearrangements include a decrease in the mean size of marine phytoplankton (increased dominance of marine production by picoplankton), a decrease in the abundance of colonial or aggregating phytoplankton, a decrease in the mean photosynthesis/respiration ratio of phytoplankton, a decrease in the mean size of pelagic grazers, or a shift in dominance from grazers that create fecal pellets (fish) to grazers that do not (e.g., jellyfish). Any or all of these changes could result from mass extinction. In such altered ecosystems, an increased fraction of total production would be shunted through the microbial food web. By allowing essential nutrients to remain in easily remineralized forms (such as tiny microbially grazed plankton) in the euphotic zone, such changes may also increase rates of nutrient recycling and biomass production in the near-surface ocean.

Application of this model to the Danian postextinction ocean suggests that dissolved nutrient availability and biological productivity may have been relatively high in the near-surface ocean throughout the three-million-year interval of reduced organic flux to the deep sea. If so, final recovery of the organic flux to the deep sea at the end of this interval would have increased the rate at which nutrients were lost from the near-surface ocean in sinking organic matter. It would have also reduced the rate of nutrient recycling in the near-surface ocean. Both of these effects would have shifted large portions of the ocean to an oligotrophic state that more closely resembled the pre-extinction ocean (and the modern ocean).

FOSSIL EVIDENCE OF POSTEXTINCTION ECOSYSTEM STRUCTURES AND RECOVERY

Microfossil Evidence of Open-Ocean Ecosystem Structure and Recovery

Records of fossil occurrences have rarely been placed in the context of the biogeochemical and sedimentological data that define the long lag in postextinction recovery of organic flux and nannofossil production. Because the carbon isotopic records are principally derived from foraminiferal calcite, planktic foraminiferal records allow the most straightforward comparison of the biological and biogeochemical responses to the K/Pg event.

Planktic foraminiferal occurrence data show that faunal turnover was nearly 100% throughout the world at the time of mass extinction (e.g., D'Hondt et al.

1996, Molina et al. 1998, Smit 1977, Troelsen 1957). They also provide intriguing evidence of faunal succession during the early and final stages of biogeochemical recovery. The survivor *Guembelitra cretacea* and its immediate descendants (Olsson et al. 1999) dominated assemblages during the earliest postextinction interval (D'Hondt et al. 1996, Gerstel et al. 1987), when planktic to benthic $\delta^{13}\text{C}$ differences were lowest. As the first stage of $\delta^{13}\text{C}$ recovery proceeded, descendants of a different survivor [*Hedbergella monmouthensis* (Olsson et al. 1999)] came to dominate planktic foraminiferal assemblages. This group dominated planktic foraminiferal communities until the time of final $\delta^{13}\text{C}$ recovery at the end of the Danian, when a third group became dominant. The *Morozovella* and *Acarinina* species that dominated this last assemblage have been interpreted as descendants of the third survivor taxon, *Hedbergella holmdelensis* (Olsson et al. 1999). This group went on to dominate tropical and temperate planktic foraminiferal assemblages for millions of years. Its close coincidence with the final $\delta^{13}\text{C}$ recovery indicates that the ascendance of this group to dominance closely coincided with the final recovery of the organic flux to the deep sea.

The genera that dominated the first two postextinction assemblages were generally distributed throughout the open ocean. However, their isotopic signatures and the geographic distribution of their relative abundances suggest that each genus in these assemblages inhabited a slightly different niche, in terms of seasonality, water depth and, possibly, a weak degree of photosymbiont reliance (D'Hondt & Zachos 1993). The genera that came to dominate planktic foraminiferal assemblages at the time of final $\delta^{13}\text{C}$ recovery differed in two critical ways from the principal members of the earlier assemblages. First, their tests were generally much larger. Second, their carbon and oxygen isotopic signatures indicate that they relied very strongly on photosymbionts for nutrition (D'Hondt et al. 1994b, Norris 1996). In both regards, these postrecovery taxa resembled members of modern oligotrophic communities (D'Hondt et al. 1994b, Norris 1996) and many members of the pre-extinction communities (D'Hondt & Zachos 1998, Houston & Huber 1998).

Records of planktic foraminiferal test size provide additional evidence of ecosystem structure during the long interval of biogeochemical recovery (Schmidt et al. 2004). For example, at South Atlantic Site 528 and Equatorial Pacific Site 577, tiny tests made up an unusually high fraction of the mass of planktic foraminiferal calcite during the long postextinction interval of low organic flux to the deep sea (Figure 5A). In contrast, large foraminiferal tests were common before the extinction event, were rare throughout the long interval of low organic fluxes, and returned to pre-extinction abundance at the approximate time of final biogeochemical recovery (Figure 5B). The relative abundance of tiny tests in the earliest Paleogene sediments becomes even more striking if the individual masses of large and small tests are considered. For example, a 212- μm diameter test weighs nearly an order of magnitude more than a 106- μm diameter test (D'Hondt et al. 1994b) and approximately two orders of magnitude more than a 38- μm diameter test. Consequently, an earliest Paleogene sample with 70% of its mass composed of 38- μm to 106- μm tests and 7% of its mass composed of >212 μm tests contains roughly

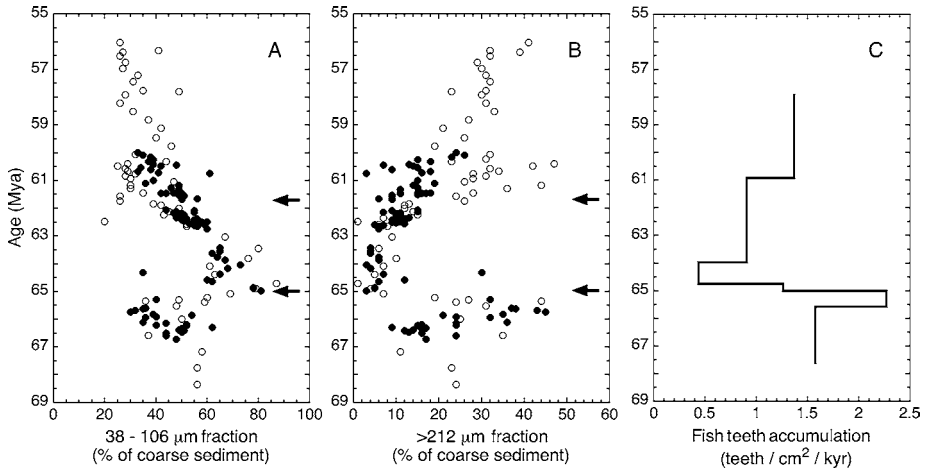


Figure 5 Records of planktic foraminiferal test diameter and fish teeth accumulation. Planktic foraminiferal tests comprise most of the coarse (>38 μm) sediment at Site 528 (black circles) and Site 577 (white circles): (A) Percent of coarse sediment in the 38- to 106- μm diameter fraction. (B) Percent of coarse sediment in the >212- μm diameter fraction. (C) Mean rates of fish teeth accumulation at South Atlantic DSDP Site 527. In panels A and B, the lower arrow marks the K/P event horizon and the upper arrow marks the approximate time of final recovery of the carbon isotope system (see Figure 3). Accumulation rates are based on fish teeth counts from Shackleton et al. (1984) and the chronostratigraphic data described in the Figure 1 caption. Age assignments and uncertainties in timing of changes in accumulation rates are as in Figure 1.

1000 times as many tiny tests as large tests. Given these mass differences and the relative constancy of foraminiferal calcite accumulation across the mass extinction horizon (Figure 2B), the flux of individual foraminiferal tests to the seafloor was very high over at least the first two million years of the postextinction interval.

Numerous studies have documented tremendous mass extinction of calcareous nannofossils at the K/Pg boundary (e.g., Pospichal 1994). However, few studies have closely examined the postextinction recovery of calcareous nannofossil assemblages. Study of Antarctic ODP Site 738 showed that successive changes in assemblage composition occurred in the first few million years after the extinction (Wei & Pospichal 1991). No studies have closely examined the relationship, if any, between calcareous nannofossil assemblages, CaCO_3 accumulation, and organic fluxes to the deep sea throughout the entire postextinction interval of biogeochemical recovery.

Fossil occurrences of silica-secreting plankton, such as diatoms and radiolaria, are generally scarcer and more rarely examined than the fossil occurrences of carbonate-secreting planktic foraminifera and calcareous nannofossils. Fortunately, diatom frustules and radiolarian tests are relatively abundant in upper

Cretaceous and lower Paleogene marine sediments of eastern New Zealand (Hollis et al. 1995). In these sediments, the broad composition of radiolarian assemblages radically changed at the K/Pg boundary (Hollis et al. 1995). At several sites in this region, concentrations of silica normalized to titanium or aluminum (and inferred to be composed of radiolarian tests and diatom frustules) increased at the K/Pg boundary and remained high for at least one or two million years (Hollis et al. 2003). These patterns of silica concentration have been interpreted as evidence of an increase in biosiliceous productivity across the K/Pg boundary, followed by high biosiliceous productivity for at least the first 1.5 million years after the mass extinction (Hollis et al. 2003). Whether the final recovery of organic flux to the deep sea coincided with significant changes in diatom and/or radiolarian assemblages remains to be determined.

Macrofossil evidence of open-ocean ecosystem structure is rare because macrofossils are rare in deep-sea sediments and are almost never recovered in deep-sea cores. However, some macroorganisms (particularly fish) leave a microfossil record that can be used to infer some characteristics of open-ocean ecosystems. At least one such record spans the entire multi-million-year interval of carbon-system collapse and recovery. This record, from South Atlantic DSDP Site 527, shows that the average fish teeth accumulation rate declined at the time of mass extinction, increased within about a million years, and increased again at the approximate time of final organic flux recovery (Figure 5C).

Macrofossil Evidence of Ecosystem Structure and Recovery in Shallow Marine Communities

Lower Paleogene records of marine macrofossils are very patchily distributed. Consequently, the precise timing and geographic extent of postextinction changes in marine macroinvertebrate and vertebrate communities are poorly constrained. The Brazos region of Texas (United States) may be the only location where marine macroinvertebrate faunal succession has been directly compared with the earliest stages of postextinction planktic foraminiferal succession (Hansen et al. 1993). At that location, the postextinction succession of macroinvertebrate assemblages closely coincides with the postextinction succession of planktic foraminiferal assemblages. A pronounced bloom of a microherbivorous gastropod occurred during the earliest Paleogene reign of the guembeltriid-dominated foraminiferal assemblage. Deposit-feeding molluscs grew to dominate the macroinvertebrate assemblages as the descendants of *H. monmouthensis* grew to dominate the planktic foraminiferal community (Hansen et al. 1993). Comparison of these foraminiferal records with records at open-ocean sites suggests that this ecologic ascendance of deposit-feeding molluscs approximately coincided with the initiation of the first stage of open-ocean carbon system recovery.

Similarly detailed records of macroorganismal assemblage succession are known from few other localities. Succession aside, available data suggest that broad patterns of ecologic dominance in postextinction communities were somewhat

different at other localities. In particular, remains of suspension-feeding organisms are relatively more abundant in Danian sediments of Alabama (United States) (Bryan & Jones 1989), New Jersey (United States) (Gallagher 2003), and Denmark (Håkansson & Thomsen 1999) than in the Brazos, Texas, sediments. The categories of organisms that dominate these fossil assemblages differ considerably from region to region. To some extent, these compositional differences may result from sub-million-year differences in the ages of the assemblages being compared (Hansen et al. 1993). However, they are also contingent on the different environments and pre-extinction assemblages of the different localities.

These contingencies can be illustrated by brief examination of the K/Pg record in Denmark. The K/Pg communities of the Gulf Coast and New Jersey inhabited shallow-water siliclastic sedimentary environments. In contrast, the Danish communities inhabited—and, in the Maastrichtian, created—a shallow water carbonate environment. In Denmark, bryozoan fossils dominate Maastrichtian assemblages, but are almost entirely absent from sediments deposited during the first several tens of kyrs (tens of thousands of years) after the end-Cretaceous extinction (Håkansson & Thomsen 1999). The lowermost Danian sediments of this region are nearly devoid of macrofossils. The fossils present in this zone are dominated by skeletal elements from two genera of crinoids; they also contain fragments from a few echinoid taxa and very rare cheilostome bryozoa. Bryozoans returned to faunal dominance within a few hundred kyrs after the mass extinction (Håkansson & Thomsen 1999), during the first stage of open-ocean carbon system recovery. This bryozoan-dominated recovery fauna was much less diverse taxonomically and ecologically than the bryozoan-dominated pre-extinction fauna (Håkansson & Thomsen 1999).

Paleogene records of marine macrofossils are not known in enough detail to determine whether marine macroinvertebrate ecosystems significantly changed at the time of final carbon-system recovery. The few available records are consistent with close linkage of benthic recovery to carbon system recovery. The bryozoan-dominated ecosystem and its shallow-water carbonate habitat disappeared from Denmark by the end of the Danian (61.7 Mya) to be replaced by clastic sediments (Håkansson & Thomsen 1999). In New Jersey, macrofossil diversity returned to pre-extinction levels by the Thanetian stage (58.7 to 55.8 Mya) (Gallagher 2003). However, the exact timing of these events (the disappearance of the Danish carbonate communities, the recovery of macrofossil diversity on the New Jersey shelf) and the exact timing of final ecosystem recovery in other shallow marine environments remain largely unconstrained. Consequently, their relationship to final recovery of the marine carbon system also remains to be determined.

Fossil Evidence and Ecological Models of the Postextinction Ocean

Many studies have interpreted the composition of Danian macrofossil assemblages to be consistent with a Strangelove (low-productivity) model of the post-extinction ocean (e.g., Arthur et al. 1987, Gallagher 2003, Hansen et al. 1993).

The composition of these assemblages is also generally consistent with a Living Ocean model. For example, Gallagher (2003) interpreted the postextinction abundance of sponges and brachiopods in the Atlantic Coastal Plain (United States) to be consistent with a low-productivity (Strangelove) ocean where plankton are small and scarce. In making this argument, Gallagher (2003) states that sponges and brachiopods are “minimalist” organisms that specialize in filtering fine organic matter from large volumes of water. These properties are also consistent with a Living Ocean model of the postextinction ocean, where productivity is normal (or even high) and plankton are abundant but tiny. The nearly four-million-year interval of low fish-tooth accumulation at Site 527 (Figure 5) is similarly consistent with either (a) reduced food availability in a very long-lasting postextinction Strangelove ocean or (b) reduced transfer of biomass to relatively large grazers and higher predators in a normal-productivity ocean where a relatively higher fraction of biomass is shunted through the microbial community.

Other results are inconsistent with a low-productivity (Strangelove) model of the Danian ocean but very consistent with a Living Ocean model. Most notably, the New Zealand records of siliceous microfossil abundance have consistently been interpreted as evidence of regionally high primary production (e.g., Hollis et al. 2003). Planktic foraminiferal data are also more readily consistent with a Living Ocean model than a Strangelove Ocean model (D’Hondt et al. 1998a). The abundance of planktic foraminifera with tiny tests and low photosymbiont reliance required an abundance of suitably tiny prey throughout the long interval of low organic flux to the deep sea (Figure 5). Furthermore, the large, highly photosymbiotic individuals that characterized planktic foraminiferal assemblages after the final recovery of organic fluxes are fossil analogues to modern taxa that are highly adapted for oligotrophic conditions (with scarce nutrients and relatively scarce but large prey) (D’Hondt et al. 1994b, Norris 1996).

BIOGEOCHEMICAL AND BIOLOGICAL RECOVERY FROM MASS EXTINCTION

If the Living Ocean model of the Danian ocean is correct, the rapid and long-lasting K/Pg changes in planktic carbonate production and the organic flux to the deep sea were direct consequences of the mass extinction. Furthermore, if this model is correct, the marine biogeochemical recovery from the K/Pg event was a direct consequence of the biological recovery from the mass extinction. For example, the two stages of recovery of the organic flux to the deep sea should be closely linked to stages of ecosystem recovery.

In evaluating this possibility, three scenarios must be considered. In the first scenario, recovery of the marine carbon system was contingent on ecological recovery. For example, the evolution of one or more key components of the ecosystem (such as large phytoplankton or large grazing zooplankton) may have returned the marine carbon system to its pre-extinction state. In the second scenario, ecological

recovery was contingent on biogeochemical recovery. Here, final recovery of the marine carbon system sparked biological diversification by creating a broad range of new opportunities for other organisms. It is conceivable that both the first and second scenarios apply, with positive feedback between the ecological recovery and the biogeochemical recovery. In the third scenario, the composition of marine ecosystems and the state of the marine biogeochemical system are largely independent of each other. This scenario corresponds to a Strangelove Ocean scenario where the long delays in environmental recovery are consequences of unknown multi-million-year physical or chemical consequences of the K/Pg impact. In this scenario, no direct link is necessarily expected between the timing of biological recovery and the timing of environmental recovery.

The relative timing of biological events and the biogeochemical events suggests that the two categories of events were closely linked. The mass extinction directly coincided with the collapse of the organic flux to deep water (e.g., Hsü et al. 1982) and the drastic decline in nannofossil production (e.g., Zachos et al. 1986). Furthermore, as described in the preceding subsections, the first stages of recovery in diverse marine communities roughly coincided with the first stage of carbon-flux recovery. This stage of recovery occurred during the first million years after the extinction, as marine ecosystems were reassembled by a patchwork of migration and evolution. Also as described in preceding subsections, the final stage of organic-flux recovery globally coincided with pronounced turnover of planktic foraminiferal assemblages a few million years after the mass extinction. More strikingly, this final stage of recovery of the organic flux to the deep sea was closely followed by rapid diversification of the previously monospecific morozovellid and acarinid lineages (H.K. Coxall, S. D'Hondt, J.C. Zachos, manuscript submitted). For many subsequent millions of years, these clades constituted the most species-rich components of planktic foraminiferal assemblages (Olsson et al. 1999). A recent study suggests that clades of calcareous nannofossils underwent similar rapid diversification shortly after the final recovery of the organic flux to the deep sea (Fuqua & Bralower 2004). These relationships between final carbon-system recovery and planktic diversification support the second scenario outlined above.

Present data are insufficient to determine whether other groups of marine organisms underwent significant radiation at the time of final organic-flux recovery. However, analyses of stage-level (multi-million-year) data compilations suggest that evolutionary rates, measured as rates of genus origination, lagged the K/Pg extinction by millions of years (Kirchner & Weil 2000, Sepkoski 1998). This long lag in taxonomic recovery is not unique to the early Paleogene. Similarly long lags followed the other major mass extinctions (Sepkoski 1998). A long lag in recovery of the marine carbon cycle is also not unique to the early Paleogene. Carbon isotopic records from marine sediments throughout the world demonstrate that the largest known mass extinction (at the end of the Permian, 250 million years ago) altered the marine carbon cycle for approximately one million years after the extinction event (D'Hondt et al. 2000, Holser et al. 1989).

The delays in evolutionary recovery from mass extinctions have been attributed to the internal dynamics of diversification (Erwin 2001, Kirchner & Weil 2000, Sepkoski 1998). Some of those dynamics may well have played out in the biogeochemical arena. For example, if the Living Ocean model of the Danian postextinction ocean is correct, the final recovery of the organic flux to the deep sea would have stripped nutrients from the surface ocean and driven it toward more broadly oligotrophic conditions. In doing so, this final recovery of the marine carbon system may have created new evolutionary opportunities for a diverse array of marine organisms.

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CONTENTS

THE GENETICS AND EVOLUTION OF FLUCTUATING ASYMMETRY, <i>Larry J. Leamy and Christian Peter Klingenberg</i>	1
LIFE-HISTORY EVOLUTION IN REPTILES, <i>Richard Shine</i>	23
THE EVOLUTIONARY ENIGMA OF MIXED MATING SYSTEMS IN PLANTS: OCCURRENCE, THEORETICAL EXPLANATIONS, AND EMPIRICAL EVIDENCE, <i>Carol Goodwillie, Susan Kalisz, and Christopher G. Eckert</i>	47
INDIRECT INTERACTION WEBS: HERBIVORE-INDUCED EFFECTS THROUGH TRAIT CHANGE IN PLANTS, <i>Takayuki Ohgushi</i>	81
EVOLUTIONARY HISTORY OF POALES, <i>H. Peter Linder and Paula J. Rudall</i>	107
THE EVOLUTION OF POLYANDRY: SPERM COMPETITION, SPERM SELECTION, AND OFFSPRING VIABILITY, <i>Leigh W. Simmons</i>	125
INDIVIDUAL-BASED MODELING OF ECOLOGICAL AND EVOLUTIONARY PROCESSES, <i>Donald L. DeAngelis and Wolf M. Mooij</i>	147
THE INFLUENCE OF PLANT SECONDARY METABOLITES ON THE NUTRITIONAL ECOLOGY OF HERBIVOROUS TERRESTRIAL VERTEBRATES, <i>M. Denise Dearing, William J. Foley, and Stuart McLean</i>	169
BIODIVERSITY AND LITTER DECOMPOSITION IN TERRESTRIAL ECOSYSTEMS, <i>Stephan Hättenschwiler, Alexei V. Tiunov, and Stefan Scheu</i>	191
THE FUNCTIONAL SIGNIFICANCE OF RIBOSOMAL (R)DNA VARIATION: IMPACTS ON THE EVOLUTIONARY ECOLOGY OF ORGANISMS, <i>Lawrence J. Weider, James J. Elser, Teresa J. Crease, Mariana Mateos, James B. Cotner, and Therese A. Markow</i>	219
EVOLUTIONARY ECOLOGY OF PLANT ADAPTATION TO SERPENTINE SOILS, <i>Kristy U. Brady, Arthur R. Kruckeberg, and H.D. Bradshaw Jr.</i>	243
BIODIVERSITY-ECOSYSTEM FUNCTION RESEARCH: IS IT RELEVANT TO CONSERVATION? <i>Diane S. Srivastava and Mark Vellend</i>	267
CONSEQUENCES OF THE CRETACEOUS/PALEOGENE MASS EXTINCTION FOR MARINE ECOSYSTEMS, <i>Steven D'Hondt</i>	295
LANDSCAPE ECOLOGY: WHAT IS THE STATE OF THE SCIENCE? <i>Monica G. Turner</i>	319
ECOLOGY AND EVOLUTION OF APHID-ANT INTERACTIONS, <i>Bernhard Stadler and Anthony F.G. Dixon</i>	345

EVOLUTIONARY CAUSES AND CONSEQUENCES OF IMMUNOPATHOLOGY, <i>Andrea L. Graham, Judith E. Allen, and Andrew F. Read</i>	373
THE EVOLUTIONARY ECOLOGY OF GYNOGENESIS, <i>Ingo Schlupp</i>	399
MEASUREMENT OF INTERACTION STRENGTH IN NATURE, <i>J. Timothy Wootton and Mark Emmerson</i>	419
MODEL SELECTION IN PHYLOGENETICS, <i>Jack Sullivan and Paul Joyce</i>	445
POLLEN LIMITATION OF PLANT REPRODUCTION: PATTERN AND PROCESS, <i>Tiffany M. Knight, Janette A. Steets, Jana C. Vamosi, Susan J. Mazer, Martin Burd, Diane R. Campbell, Michele R. Dudash, Mark O. Johnston, Randall J. Mitchell, and Tia-Lynn Ashman</i>	467
EVOLVING THE PSYCHOLOGICAL MECHANISMS FOR COOPERATION, <i>Jeffrey R. Stevens, Fiery A. Cushman, and Marc D. Hauser</i>	499
NICHE CONSERVATISM: INTEGRATING EVOLUTION, ECOLOGY, AND CONSERVATION BIOLOGY, <i>John J. Wiens and Catherine H. Graham</i>	519
PHYLOGENOMICS, <i>Hervé Philippe, Frédéric Delsuc, Henner Brinkmann, and Nicolas Lartillot</i>	541
THE EVOLUTION OF AGRICULTURE IN INSECTS, <i>Ulrich G. Mueller, Nicole M. Gerardo, Duur K. Aanen, Diana L. Six, and Ted R. Schultz</i>	563
INSECTS ON PLANTS: DIVERSITY OF HERBIVORE ASSEMBLAGES REVISITED, <i>Thomas M. Lewinsohn, Vojtech Novotny, and Yves Basset</i>	597
THE POPULATION BIOLOGY OF MITOCHONDRIAL DNA AND ITS PHYLOGENETIC IMPLICATIONS, <i>J. William O. Ballard and David M. Rand</i>	621
INTRODUCTION OF NON-NATIVE OYSTERS: ECOSYSTEM EFFECTS AND RESTORATION IMPLICATIONS, <i>Jennifer L. Ruesink, Hunter S. Lenihan, Alan C. Trimble, Kimberly W. Heiman, Fiorenza Micheli, James E. Byers, and Matthew C. Kay</i>	643
INDEXES	
Subject Index	691
Cumulative Index of Contributing Authors, Volumes 32–36	707
Cumulative Index of Chapter Titles, Volumes 32–36	710

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