End-Cretaceous marine mass extinction not caused by productivity collapse

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Edited by Karl K. Turekian, Yale University, New Haven, CT, and approved November 22, 2011 (received for review June 30, 2011)

An asteroid impact at the end of the Cretaceous caused mass extinction, but extinction mechanisms are not well-understood. The collapse of the sea surface to sea floor carbon isotope gradients has been interpreted as reflecting a global collapse of primary productivity (Strangelove Ocean) or export productivity (Living Ocean), which caused mass extinction higher in the marine food chain. Phytoplankton-dependent benthic foraminifera on the deep-sea floor, however, did not suffer significant extinction, suggesting that export productivity persisted at a level sufficient to support their populations. We compare benthic foraminiferal records with benthic and bulk stable carbon isotope records from the Pacific, Southeast Atlantic, and Southern Oceans. We conclude that end-Cretaceous decrease in export productivity was moderate, regional, and insufficient to explain marine mass extinction. A transient episode of surface ocean acidification may have been the main cause of extinction of calcifying plankton and ammonites, and recovery of productivity may have been as fast as in the oceans as on land.

Results and Discussion

At the Cretaceous/Paleogene (K/Pg) boundary (~65.5 Ma) a large asteroid impacted the Yucatan Peninsula (Mexico), triggering severe but selective extinctions (1). Proposed causes of mass extinction resulting from the impact include global timescales include global darkness due to emission of dust and aerosols, ozone destruction, global cooling or warming, and ocean acidification (1–3). Light levels sufficiently low to prevent photosynthesis for longer than the life cycle of oceanic phytoplankton (weeks to months), have commonly been seen as the prime cause of collapse of oceanic primary productivity and the subsequent mass extinction at higher levels of the marine food chain (e.g., ammonites, large predatory fish, mosasaurs) (2). A collapse in oceanic surface-bottom gradient in carbon isotope values (i.e., the difference in carbon isotope values in shells of benthic and planktic organisms) persisted for hundreds of thousands to a million years (13). All sites show a sharp decrease in bulk carbonate δ13C values at the boundary as reported earlier (1, 3–5).

There is considerable evidence that there was no long-term, global collapse of primary productivity (5). Extinction in calcareous nanoplanктon was severe, although geographically variable (14) and followed by low-diversity blooms. Extinction in other photosynthesizers, such as the related noncalcifying haptophytes (15), which may have been dominant photosynthesizers (16), the siliceous diatoms (17, 18), and the organic-walled and calcareous dinoflagellates (19, 20) was much less severe (21). Algal biomarkers indicate a rapid recovery of primary productivity (22). At least regionally, dinoflagellates (19, 20) and heterotrophic and mixotrophic plankton such as planktic foraminifera (23) and radiolarians (17) flourished after the K/Pg extinction, and benthic foraminifera indicated a high food flux (9) (Fig. 1). Postextinction planktic foraminiferal and nanoplanктon assemblages indicate eutrophic conditions, with oligotrophic assemblages evolving later (24).

According to ecological theory, one would expect productivity in terms of biomass (though not biodiversity) to recover as soon as environmentally possible after the asteroid impact, probably with large opportunistic blooms reflecting nutrient availability and environmental instability (5). The collapse in vertical δ13C gradient has been argued to represent only a slight increase (from 90 to 95%) in the fraction of total organic production remineralized in the upper 200 m of the oceans (5), but others invoked catastrophic decline of the organic flux to the sea floor (6). A regionally variable, moderate decrease in export productivity agrees with deep-sea benthic foraminiferal evidence (9, 25) (Fig. 1) and geochemical export productivity proxies (26), but a global collapse of export productivity for several millions of years (4) is in strong disagreement with foraminiferal and geochemical evidence.

We attempt to reconcile records of benthic foraminiferal assemblage change with bulk carbon isotope records (reflecting calcification by calcareous nanoplanктon in the upper few hundred meters of the ocean, e.g., ref. 27) and bottom (benthic foraminiferal) records obtained on the same samples from four sites (Fig. 1).

Author contributions: L.A. and E.T. designed research; L.A., E.T., and K.C.L. performed research; L.A. and E.T. analyzed data; and L.A. and E.T. wrote the paper.

The authors declare no conflict of interest.

*This Direct Submission article had a prearranged editor.

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This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1110601109/-/DCSupplemental.
difference in BFAR, with overall declining values of infaunal taxa. Southeast Atlantic site 1262 shows declining values in both proxies, with a further decline about 400 kyr after the boundary (Fig. 3, Fig. 4). In general, the benthic foraminiferal patterns agree with biogenic Ba records (26). There is thus disagreement between benthic foraminiferal and geochemical proxies and stable isotope records from the same samples: Where the vertical carbon isotope gradient collapsed (suggesting decreased export productivity), benthic foraminifera and biogenic Ba records either show little change (Southeast Atlantic, Southern Ocean), or an increase (Pacific).

It has been argued that benthic foraminifera survived because they are adapted to food-starved environments (4). We argue that it is precisely because the deep-sea is food starved that food supply is the most important ecologically limiting variable (12), and a long-term global collapse of the food supply would have caused massive extinction. We argue that the collapsed carbon isotope gradient (~500 kyr, Fig. 2) does not reflect a severe global collapse in export productivity. Extinction of fecal pellet producing zooplankton does not have to lead to a collapse in export productivity: Flocs of organic matter (marine snow) are transported to the sea floor more efficiently in the absence of zooplankton (28), because zooplankton’s activity disaggregates these particles.

The bulk carbon isotope records probably represent complex, multiple signals (29). The rapid and sharp decrease coincident with the K/Pg boundary may well represent a moderate decline in export productivity (5). Another part of the decrease reflects the extinction of the carriers of the isotopic record, calcareous nannoplankton, rather than a change in δ¹³C of dissolved inorganic carbon (DIC) in the oceans (29). Benthic δ¹³C records are based on the same species throughout, but the bulk records before and after extinction are measured on different components because of the mass extinction of pelagic calcifiers (Fig. 2) (1, 5, 6, 14). Postextinction values in part show the isotopically light signature of calcareous dinocysts (Table S3), similar to the isotopic signature of the living Thoracosphaera heimi (30). Small biserial and triserial planktic foraminifera are abundant after the boundary and their fragments contribute to the bulk signal, and generally have a light isotopic signature, as does the living triserial planktic Galtellia vivans (31). Planktic foraminiferal δ¹³C values declined because smaller forms are generally isotopically lighter because of metabolic effects, and postextinction, nonsymbiont bearing species were isotopically lighter than preextinction symbiont bearers (32). In addition, the effect of the solubility pump on δ¹³C of DIC, working in the opposite way as the biological pump, became more pronounced during decreased export productivity (33). Finally, the long-term (several 10⁸ years) bulk carbon isotope record is influenced by orbital scale variability (34), in part linked to hyperthermal events with associated carbon isotope excursions, one of which might have occurred about 250 kyr after the K/Pg boundary (35), coeval with the minimum bulk value at site 1262 (Fig. 2). A discussion of hyperthermal events and variability in long-term δ¹³C records is outside the range of this paper, but we conclude that the bulk carbon isotopic record cannot be explained by the effect of the K/Pg extinction on vertical gradients in DIC only.

What caused the marine mass extinction if we are correct in our argument that severe collapse in productivity (in terms of biomass) did not occur? Noncalciﬁng phytoplankton (dinoflagellates, diatoms, haptophytes) did not suffer severe faunal
ternover, suggesting that darkness may have contributed, but may not have been the most important cause of extinction, in agreement with arguments that not sufficient fine dust was generated by the impact to cause prolonged, severe darkness (36). Patterns of nannoplankton extinction as well as changes in the benthic foraminiferal assemblages confirm that phytoplankton extinction may have been less severe at high southern latitudes (14, 24) (Figs. 1, 3, and 4), possibly because the impact occurred during southern hemisphere winter when photosynthesizers would have been hibernating because of seasonal darkness. Changes in overall composition of oceanic phytoplankton, due in part to the extinction of calcareous nannoplankton and replacement by other photosynthesizers, could have severely affected higher levels of the food chain, even if primary productivity was high (37).

We speculate that rapid ocean acidification could have been a major causal factor (2, 3). Acidification probably was not caused by high atmospheric CO$_2$ levels (38), but nitric acid may have been generated by N$_2$-oxidation due to heating of the atmosphere by the impactor (with N-deposition contributing to nutrients for blooms), and sulfuric acid by an impact on gypsum-containing sediment (1, 3). Fragile, thin-walled foraminifera in the clay interval deposited during about 10,000 y following the extinction are preserved in pristine condition, but this observation does not preclude a transient (months to years) event of severe acidification of surface waters. A severe but short, rapidly buffered period of acidification of surface waters may well explain the extreme severity of extinction of short-lived, open-ocean unicellular calcifiers (1–6, 14), and possibly Caribbean rudists (39). There is insufficient evidence that the extinction of planktic foraminifera and calcareous nannoplankton was caused by their lack of resting cysts: non-cyst-forming groups such as radiolarians (17) and non-calcifying haptophytes (15) survived as well. Calcifying dinoflagellates survived and bloomed after the extinction (19, 20), but their modern relatives have noncalcifying life stages. Hermatypic corals did not suffer extreme extinction (40), but these organisms could have survived short-term, ocean acidification (41), which was rapidly buffered in shallow waters.

Transient severe acidification could have been a factor in the differential extinction of ammonites and nautiloids. Both groups form aragonitic shells, but the planktivorous ammonites lived within the uppermost few hundred meters of the oceans, whereas nautiloids live deeper and form large, lecithotrophic eggs in protective egg capsules (42), in contrast to the small floating egg masses of ammonites. Nautiloids would therefore have been less affected by acidification. Extinction of such an important group of large invertebrates may have reverberated through the food chain, specifically affecting top-level predators such as large, active fish (43) and mosasaurs. Removal of the top-predators in its turn may have had cascading effects on the lower levels of the food chain (44). Calcifying organisms in coastal waters, from which living planktic foraminifera and nannoplankton evolved after the extinction, may have been protected from the short-term surface water acidification if the coastal regions became eutrophic (45), because of destruction of flora and resulting increase in nutrient-rich runoff.

Finally, rapid acidification could have been a cause of decreased export productivity in some regions because of its effects on the pelagic calcifiers, leading to increased remineralization (5), and thus to low oxygen conditions in eutrophic regions (46), as, e.g., observed in the Danish K/Pg sections (3, 19, 22).

The rapid onset of the acidification event due to an impact (more rapid than even anthropogenic acidification) may have led to a transient, severe acidification of the surface ocean followed by rapid buffering, but leading to the massive extinction of the short-lived pelagic calcifiers while providing for the survival of deep-sea benthos including ostracodes (10). This pattern of extinction contrasts with the much slower acidification at the
end of the Paleocene, when deep-sea benthos suffered severe extinction but calcifying plankton survived (47).

We conclude that it was not a collapse of primary or export productivity that caused the marine mass extinction after the asteroid impact at the K/T boundary. The oceans may have been relatively eutrophic, supporting plankton blooms while oceanic productivity in terms of biomass, but not in terms of diversity, recovered rapidly, as proposed for terrestrial productivity (7, 48). Mass extinction in the oceans may have been caused mainly by a transient period of extreme acidification of the surface oceans. Study of the effects of the end-Cretaceous extinction thus may assist in evaluation of the effects of extreme and rapid acidification, having more severe effects on calcifying plankton in the surface waters and less on deep-sea benthos than slower acidification.

Materials and Methods

Samples were provided by the integrated Ocean Drilling Program. Sediments were dried, then soaked in warm water with detergent, and wet-sieved over a 63-μm sieve. Benthic foraminifera were picked from the >63-μm size fraction, with taxonomy and assignment to infaunal and epifaunal groups and calculation of BFAR according to refs. 9, 12, and 25 (SI Materials and Methods, Table S1, Table S2). We use the percentage of infaunal taxa and the BFAR as independent proxies for food flux to the sea floor (12, 25) (Table S1, Table S2). We are grateful to three anonymous reviewers for valuable comments. Funding from the Spanish Ministry of Science and Innovation Grant CGL2007-63724/BTE and CGL2009-07101-E (to L.A.), National Science Foundation Grant OCE-720049 (to E.T.). Samples were provided by the Integrated Ocean Drilling Program.

ACKNOWLEDGMENTS. We are grateful to three anonymous reviewers for valuable comments. Funding from the Spanish Ministry of Science and Innovation Grant CGL2007-63724/BTE and CGL2009-07101-E (to L.A.), National Science Foundation Grant OCE-720049 (to E.T.). Samples were provided by the Integrated Ocean Drilling Program.


Supporting Information

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SI Materials and Methods

Age Models and Map. For age models for Ocean Drilling Program (ODP) sites 1210 and 1262 we used orbitally tuned age models (1) to determine sedimentation rates, and placed the Cretaceous/Paleogene (K/Pg) boundary at 65.5 Ma. For site 1210, we used the revised composite depth (2). Ages were estimated for samples from Deep Sea Drilling Project (DSDP) site 465 using the correlation of the carbon isotope record of benthic foraminifera, which shows the same pattern at all sites (3), to the orbitally tuned age model for site 1210. We used these benthic isotopes also to modify the age model in ref. 4, and correlate the record for site 690 more precisely to that at the other sites (Fig. 2). The map (Fig. 1) was made using ref. 5.

Benthic Foraminiferal Data. The consistency of our dataset is unprecedented (6): The same authors used the same procedures, studied the same size fraction (≥63 μm) and used the same taxonomic concepts (7) for all sites. To construct Fig. 1 in the text, we used our published data from North-West Atlantic Blake Nose ODP site 1049 (8, 9); Gulf of Mexico sections La Lajilla, El Mulato, Coxquihui, and La Ceiba (8, 10–13); Caribbean section Loma Capiro (Cuba) (14); North-East Atlantic sections Bidart and Loya Bay (France) (15, 16); Tethyan sections Agost (Spain) (17); and Aïn Settara and El Kef (Tunisia) (8, 18).

As a proxy for diversity of the benthic foraminiferal assemblages, we calculated the Fisher-α diversity index (19) (Table S1, Table S2). As proxies for trophic conditions at the sea floor (20), we calculated the benthic foraminiferal accumulation rates (BFARs), and changes in relative abundance of habitat-related benthic foraminiferal morphgroups (infaunal vs. epifaunal) across the boundary (Table S1, Table S2). There is a relationship between test morphology and microhabitat (20, 21), and despite significant exceptions, this relation appears to be accurate about 75% of the time (22). Based on this assumption, variations in the proportion of habitat-related benthic foraminiferal morphgroups (infaunal vs. epifaunal) can be considered as proxies for the oxygenation and trophic conditions at the sea floor (20), with epifaunal morphgroups supposedly flourishing in more oligotrophic environments. We allocated all specimens to morphgroups (23–25), with extinct taxa assigned following ref. 3. Variations in the percentage of infaunal taxa across the K/Pg boundary are shown in Fig. 4, Fig. S1, and in Table S1 and Table S2.

The benthic foraminiferal data for sites 1262, 1210, and 465 have been published (3, 10, 26), but we checked all assignments to infaunal or epifaunal taxa to ensure consistency between sites, and recalculated all BFAR to ensure the use of the same age model for all sites. To calculate BFAR, we weighed the sample split from which benthic foraminifera were picked and obtained the number of benthic foraminifera per gram of sample in the size fraction larger than 63 μm. We then calculated the number of benthic foraminifera per gram bulk sediment, using the weight percent of dry sample material larger than 63 μm, as obtained during sample processing. We used sedimentation rates as determined from the orbitally tuned age models, number of foraminifera per gram dry bulk sediment, and density of sediment to calculate benthic foraminiferal accumulation rates (number of foraminifera per square cm per 1,000 y). Bulk density of the sediment is after ref. 27 for site 1262, ref. 28 for site 465, ref. 29 for site 1210, and ref. 30 for site 690.

Low-resolution benthic foraminiferal data but not BFAR across the K/Pg transition of Southern Ocean Maud Rise ODP site 690 were published (31), but we provide higher resolution data. Calcareous chalks and oozes were deposited at upper abyssal to lower bathyal depths (~1,900 m paleodepth). Benthic foraminiferal assemblages were quantitatively analyzed in 31 samples from sections 690C–24H–7 to 24H–1, comprising the upper 4.6 m of the Maastrichtian (planktic foraminiferal Abathomphalus mayorensis zone and calcareous nanofossil Cribroshphaera daniiae zone) and the lower 9.8 m of the Danian (up to planktic foraminiferal zone AP1b and calcareous nanofossil zone CP2) (4). Samples were spaced at few centimeters directly below and above the K/Pg boundary, with decreasing resolution (50 cm to ~1 m) further away from the boundary. Sediments were dried, then soaked in warm water with detergent, and wet-sieved over a 63-μm sieve. Approximately 300 specimens of benthic foraminifera larger than 63 μm were picked and identified per sample (Table S2).

BFAR and percentage infaunal taxa are shown for each site compared to the carbon isotope record in Figs. 3 and 4, and for all sites combined in Figs. S1 and S2.

Isotope Analyses. Isotope analyses were performed at the University of Santa Cruz, Yale University, and the University of Michigan. All results are reported in per million (‰) relative to the Vienna PeeDee belemnite (VPDB) standard (Table S3). Stable isotopes for bulk samples of site 1262 were published in ref. 32. Stable isotope analyses on benthic foraminifera (Nuttalilides truempyi) were performed at the University of Michigan on a Thermo MAT 253 coupled to a Kiel IV carbonate device. Samples were reacted at 70 °C and measured enrichments were converted to VPDB utilizing a normalization based on the analysis of National Bureau of Standards (NBS)-18, NBS-19, and Atlantis II, an isotopic standard whose composition closely approaches the benthic values. Analytical precision is maintained better than 0.1‰ for both δ13C and δ18O, based upon routine replication of standard materials.

Stable isotope data for site 690 include data published in ref. 33, and additional data on bulk samples, benthic foraminifera (N. truempyi, Stensioeina beccariiformis) and calcareous dinocysts collected at the Earth Systems Center for Stable Isotopic Studies at Yale University, using a Thermo Gasbench II interfaced to a DeltaXP Stable Isotope Ratio mass spectrometer with a CTC Analytics GC-PAL autosampler, with analytical precision averages 0.07% for δ18O and 0.04% for δ13C. Precision was monitored by analysis of NBS-19 and NBS-18 every 10 samples. Benthic foraminifera (N. truempyi) and bulk isotope data for site 1210 were also collected at the Yale facility.

Stable isotopes on benthic foraminifera (S. beccariiformis) and bulk samples for site 465 were generated at an Autocarb coupled to a PRISM mass spectrometer at the University of California at Santa Cruz Stable Isotope Laboratory facilities. All values are reported relative to the VPDB standard. Analytical precision based on replicate analyses of in-house standard Carrara marble and NBS-19 averages 0.06% for δ18O and 0.03% for δ13C (1σ).

We used bulk fraction stable isotopes as recorder of the palaeoenvironmental signal in waters relatively close to the ocean surface, i.e., within the mixed layer down to the lower thermocline, with dominant production of living coccolithophores occurring in the middle photic zone (~50–100 m depth) (34), see refs. 32 and 35. The persistent offset between carbon isotope...
values for bulk and benthic foraminifera during the Cretaceous and after the disturbance due to the extinction indicates that the two signals indeed reflect bottom waters and waters closer to the surface, with bulk values more positive.


Fig. S1. Relative abundance of infaunal species across the K/Pg boundary at sites in the Pacific, Southeast Atlantic, and Southern Ocean. See Fig. 1 for location.
Fig. S2. BFAR across the K/Pg boundary at sites in the Pacific, Southeast Atlantic, and Southern Ocean. See Fig. 1 for location.

Other Supporting Information Files
Table S1 (DOC)
Table S2 (DOC)
Table S3 (DOC)