

Geographic controls on nannoplankton extinction across the Cretaceous/Palaeogene boundary

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Calcareous nannoplankton, a large group of marine autotrophs that produce carbonate skeletons, were decimated to less than 10% of species during the Cretaceous/Palaeogene boundary mass extinction, 65 million years ago. Although the mass extinction followed an impact event, the exact cause of the nannoplankton mortality is not well understood. Here we assess the timing and spatial variability of nannoplankton extinction by analysing nannofossil counts in Cretaceous/Palaeogene boundary sections from all of the main ocean basins. We find that extinction rates were higher in the Northern Hemisphere oceans, and diversity remained low for 310,000 years. In contrast, Southern Hemisphere oceans showed lower extinction rates, and a nearly immediate recovery of normal nannoplankton populations. We propose that the oblique, northward impact concentrated ejected particulates into the Northern Hemisphere, blocking sunlight and suppressing photosynthesis. Increased rates of extinction and a prolonged recovery would then be associated with the greatest concentration of particulates. We speculate that metal poisoning from fallout of the particulates may have exacerbated and extended the nannoplankton crisis in the Northern Hemisphere, and thereby slowed the recovery of the Northern Hemisphere marine food web.

Mass extinction events have a key role in the history of life, abruptly changing extinction selectivity and setting the stage for intervals of profound species recovery^{1,2}. The mass extinction at the Cretaceous/Palaeogene (K/Pg) boundary (65.68 million years (Myr) before present) caused upheaval of habitats and eliminated ~75% of marine and ~50% of terrestrial species^{3,4}. The extinction was selective and particularly severe among plants and higher-order reptiles in terrestrial environments, and shallow-water grazers, nekton and plankton in the marine realm³⁻⁵. A considerable body of evidence supports the impact at Chicxulub as the ultimate trigger of the mass extinction⁶. The eruption of large volumes of lavas in the Deccan Traps overlapped the K/Pg boundary and has also been cited as a trigger of the extinctions⁷. However, the main eruptive phase of the Deccan Traps preceded the boundary⁸ (Supplementary Information).

Although impact winter, darkness, metal poisoning and ocean acidification have been proposed as kill mechanisms for the marine mass extinction⁹⁻¹⁴, the exact cause or causes have not been identified. The kill mechanisms probably operated over intervals far shorter than the resolution offered by the geologic record, making them impossible to determine directly from data. The extinctions are known to be selective within individual marine groups, and the ecologic attributes that allowed some species to survive as well as those that caused other species to go extinct offer valuable information on the kill mechanisms^{15,16}. Theoretically, higher levels of the food chain should have been afflicted by the wholesale decrease of primary production caused by the decimation of phytoplankton groups¹⁷. Thus, determining the causes of the extinction of organisms at the base of the food chain is critical. Calcareous nannoplankton, possibly the dominant group of phytoplankton at the K/Pg boundary, were decimated with approximately 85% of genera and 93% of species going extinct¹⁸.

The K/Pg mass extinction was followed by a lengthy interval of recovery of marine ecosystems¹⁹ under drastically changed physical environments, and an inefficient biological pump (the biological processes that transfer carbon, nutrients and many trace metals from surface to deep ocean)^{20,21}. Primary productivity

probably increased when light levels were fully restored but remained suppressed for a considerable interval of time as the main groups of plankton gradually recovered. The re-establishment of fully functional marine biogeochemical cycling with an efficient biological pump of carbon and nutrients from surface to deep waters took even longer, up to 3 Myr, presumably until new grazers evolved²². However, there remains considerable uncertainty on how restoration of light, nutrient cycling and ecosystem function affected the biotic recovery. Numerous detailed counts of nannoplankton in individual K/Pg boundary sections²³ provide a significant amount of assemblage data, but the lack of quantitative, global studies limits our understanding of the kill mechanisms and the selection of survivors.

Here we report the results of a global investigation of the community structure of the calcareous nannoplankton at the K/Pg boundary using published counts in 823 samples from 17 sites (Fig. 1) using standard techniques including non-metric multidimensional scaling (NMS, a multivariate ordination technique designed for large ecological data sets, Supplementary Information). Two sites, one each in the Pacific and South Atlantic oceans, have orbital age control (see Supplementary Information for discussion of uncertainty), allowing high-resolution investigation of the recovery in these two basins. Our results shed light on the causes of nannoplankton extinction, how productivity was restored, the factors that controlled the origination of new species and, ultimately, how phytoplankton influenced restoration of the entire marine ecosystem.

Nannoplankton extinction patterns

The intensity of the nannoplankton extinction differs by latitude and ocean basin with between 92 and 98% of species going extinct in the North Atlantic, the North Pacific and Tethys oceans, between 88 and 91% in the South Atlantic Ocean and between 73 and 84% in the Indian and Southern oceans (Fig. 2).

Trends of Shannon–Wiener index, species richness and evenness are parallel in individual sections (Supplementary Fig. S2); we focus on the Shannon–Wiener index to compare diversity changes

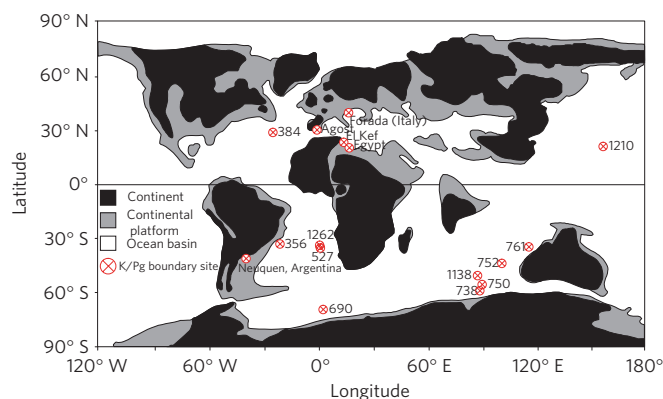


Figure 1 | Location and depositional environments of study sites at the K/Pg boundary (after ref. 51). See Supplementary Table S1 for more information on sites.

between the sites. Central Pacific Site 1210 shows a significant decrease in Shannon–Wiener index at the K/Pg boundary, low values for the first 100 kyr of the Danian then gradually increasing values in the following 300 kyr (Fig. 3). South Atlantic Site 1262 and Southern Ocean Site 690 show smaller decreases in Shannon–Wiener index at the boundary immediately followed by sharp increases in the next 50 kyr, then relatively stable values.

NMS ordination shows a clear separation of samples by time and latitude. Coding samples from Sites 1210 and 1262 by time (Fig. 4a) indicates that NMS axis 1 corresponds to time. Coding samples by ocean basin shows clearly that axis 2 corresponds to latitude (Fig. 4b). Samples from the Southern and Indian oceans have low axis 2 scores, whereas samples from the Tethys, North Pacific, North Atlantic and South Atlantic oceans have higher axis 2 values. Perhaps most interesting is that the Tethys, North Pacific and North Atlantic samples plot progressively higher on axis 2 in the middle of axis 1, before returning to the latest Cretaceous values. Common reworking of extinct Cretaceous species into Danian deposits has little or no impact on the overall structure of NMS ordinations (Supplementary Information and Supplementary Fig. S4).

NMS ordination of taxa suggests that axis 2 is also correlated with environmental conditions (Fig. 4c). Axis 2 seems to divide the survivor and new Danian taxa by ecology, with taxa known to be adapted to high-nutrient environments (eutrophic taxa; see Supplementary Table S2) characterized by lower values and known opportunistic, disaster and bloom taxa that tolerate high environmental stress (that is, *Braarudosphaera* and calcareous dinoflagellates or calcispheres (including the genera *Thoracosphaera* and *Orthopithonella*)) showing higher values. Taxa adapted to low-nutrient environments (oligotrophs) in the Danian are characterized by intermediate axis 2 values.

Causes of nannoplankton mass extinction

Although nannoplankton experienced a global mass extinction at the K/Pg boundary, extinction intensity and the dynamics of the recovery varied between oceans and by latitude. The North Atlantic, North Pacific and Tethyan oceans (hereafter termed the Northern Hemisphere oceans) sustained the highest extinction levels (Fig. 2). Assemblages in these oceans changed markedly at the K/Pg boundary (Figs 3 and 4b) with the appearance of low-diversity, disaster and bloom taxa; these assemblages persisted for ~40 kyr until a ~270 kyr interval of recovery began (Fig. 4a,b). At the other extreme, the Southern and Indian oceans were marked by the lowest extinction intensities, a less pronounced change in diversity and near immediate return of a normal eutrophic²⁴ assemblage, whereas the South Atlantic Ocean was characterized by intermediate levels of extinction, a smaller change in diversity

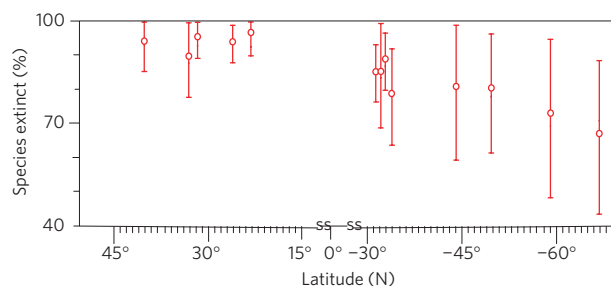


Figure 2 | The percentage of species that became extinct at the K/Pg boundary plotted against latitude. Percentage is calculated from the species present in samples from the uppermost 5 cm of the Maastrichtian that are not found in the lowermost 5 cm of the Danian at that location. The error bars represent the 95% confidence level (see Supplementary Information for more information).

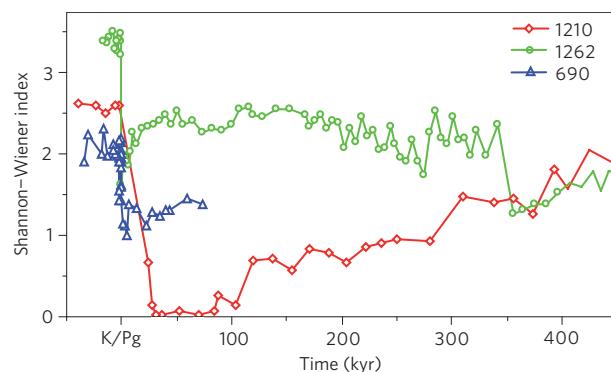


Figure 3 | The Shannon–Wiener diversity across the K/Pg boundary plotted versus age. The data shown are for three key study sites from the Pacific (Site 1210; 23° N), South Atlantic (Site 1262; 32° S) and Southern (Site 690; 67° S) oceans.

and assemblages with a mixture of eutrophic and disaster taxa (Figs 2, 3 and 4b). The strongly asymmetric geographic pattern has implications for the interpretation of potential extinction triggers.

Determining the trajectory of the bolide during the impact at Chicxulub is critical to constraining its environmental effects. The decimation of North American land plants, compared with the relatively minor changes on austral continents, provided the first indication of an oblique impact directed from the south and east towards the north and west²⁵. This interpretation was supported by asymmetrical gravity data from Chicxulub²⁶. The thickness of ejecta in proximal K/Pg deposits northwest of the crater has also been interpreted as evidence for a southeast to northwest impact, but this distribution may have been altered by Earth rotation²⁷. The structure of shocked quartz also suggests a low-angle, oblique impact²⁸. An oblique impact with ejection of material from the southeast to northwest, combined with Earth rotation and westerly winds, would initially concentrate particulates over the North Pacific, North Atlantic and Tethys oceans^{29,30}. However, the ultimate distribution and residence time of the ejecta and sulphate aerosols are uncertain, as are the extent of their atmospheric effects²⁹ (Supplementary Information).

Significantly reduced photosynthesis caused by fine-grained dust, soot and sulphate aerosol loading has the potential to cause extinction of nannoplankton³. Darkness would cause failure in a number of light-regulated metabolic activities, in particular suppressing photosynthesis. Lower light levels also reduce reproduction rates in phytoplankton³¹ and promote sexual rather than vegetative reproduction³². Holococcoliths produced during the haploid stage of certain coccolithophores³³ are among the high-latitude

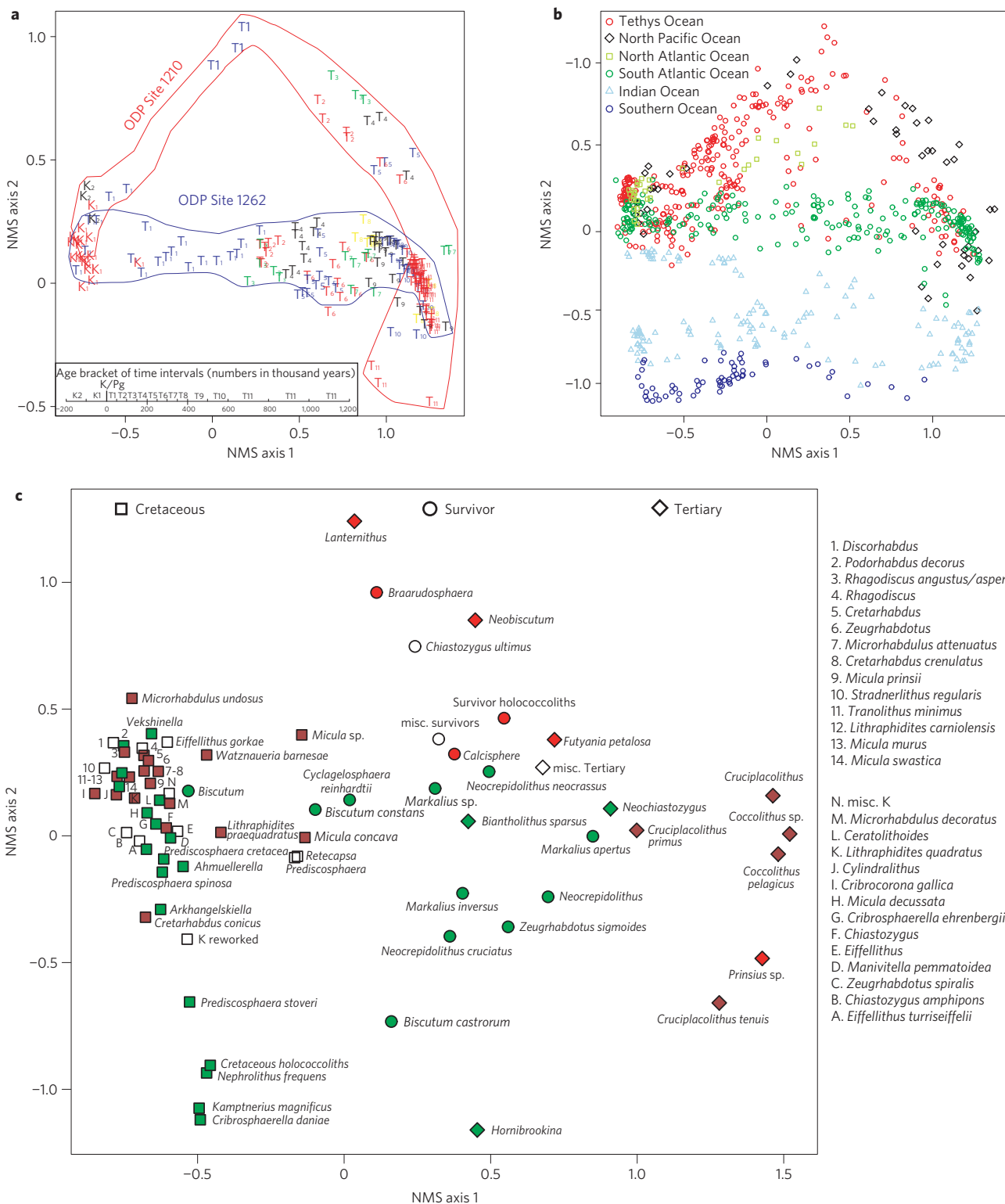


Figure 4 | NMS ordination of K/Pg samples and species for all sites studied. **a**, Sample scores on NMS axes 1 and 2 for Sites 1210 and 1262 coded by time interval (as shown at base). **b**, Sample scores for all sites grouped by ocean basin. **c**, Taxon scores on NMS axes 1 and 2: oligotrophic taxa in brown, eutrophic taxa in green, bloom/stress/disaster taxa in red symbols, respectively. Open symbols are taxa for which the ecology is unknown.

survivors (Fig. 4c). Stressful environmental conditions also promote production of diploid naked cells³⁴ that are morphologically identical to haploid gametes and can disrupt normal reproduction.

The amount of submicrometre-size dust ejected from Chicxulub was not sufficient to completely shut down photosynthesis²⁹

but probably had an optical effect for up to six months¹³. Nannoplankton extinction patterns are consistent with an oblique, northward impact, concentration of particulates in the Northern Hemisphere, thus lower light levels and more pronounced cooling than in the Southern Hemisphere. The few surviving taxa at Northern Hemisphere sites included resting cysts (for example,

calcspheres) and species adapted to high-latitude and neritic environments that were tolerant to lower light levels²³. Likewise, most of the Southern Hemisphere survivors were eutrophic (Supplementary Table S2) with similar tolerances. Conversely, exclusively tropical and temperate nannoplankton species were virtually eradicated³⁵. Most of the species that went extinct were oligotrophs (Supplementary Table S2) probably adapted to higher light levels; they included many of the dominant Cretaceous taxa. An intriguing question is how ecologic strategy was critical to survivorship, and why species with widespread or cosmopolitan distributions, and probably large standing crops, did not survive.

Significantly reduced photosynthesis is unlikely to be solely responsible for the magnitude of the extinctions observed at the K/Pg boundary. Experiments on living phytoplankton (not exclusively coccolithophorids) showed that only 68% of species went extinct after three months of darkness³⁶. Darkness and suppression of primary productivity presumably resulted in widespread eutrophication that would have favoured eutrophic taxa. However, these conditions ended once light levels were restored²¹. Eutrophication is unlikely to have been a killing mechanism for cosmopolitan, oligotrophic species as refuges almost certainly existed. For these reasons, we explore other kill mechanisms with asymmetric effects.

An oblique, northward impact with a larger atmospheric effect in the Northern Hemisphere would cause significant cooling on the northern continents. However, such an 'impact winter' scenario would be muted in the oceans, as their heat capacity is sufficient to prevent significant cooling³⁷; thus, we can rule out this mechanism for the extinction of nannoplankton. Acidification of surface waters from emission of SO₂ would be intensified in regions near the impact site as well as in stratified parts of the ocean¹². However, the buffering potential of the oceans would make the effect of SO₂ acidification extremely short-lived. Experimental studies of extant taxa yield conflicting evidence concerning whether delicate or more heavily calcified taxa are better adapted to acidification^{38,39}. Regardless, there is strong evidence from the K/Pg boundary that delicate taxa (low-latitude holococcoliths and certain high-latitude survivors, such as *Biscutum castrorum*) as well as moderately calcified taxa (for example, *Cyclagelosphaera*), occur continuously across the K/Pg boundary, suggesting that acidification was not a major factor.

Trace-metal poisoning is another impact-related stressor that could have been particularly severe in the Northern Hemisphere oceans. Toxic metals such as Cu, Cr, Al, Hg and Pb would have been released into solution during the dissolution of highly soluble high-temperature condensed impact ejecta in surface seawater, and probably reached levels lethal to plankton¹¹. Even metals such as Fe, Zn and Mn that are typically considered micronutrients could have reached deleterious concentrations in the immediate aftermath of the impact. Metals may have also been derived from soils leached by acid rain or from wildfires⁴⁰. Moreover, it is possible that metal loading produced toxins that were distributed by ocean and atmosphere circulation⁴¹.

The susceptibility of modern coccolithophorid species to metal toxicity is not fully understood. At modern oceanic levels, biogenic ligands significantly reduce the free concentration of most trace metals to non-toxic (nutrient) levels, despite total concentrations that for many organisms would be toxic⁴². Trace metals such as Cd, Cu, Fe and Zn serve as important micronutrients for plankton and concentrations generally follow nutrient profiles in the photic zone⁴³. At elevated concentrations, however, metals can become toxic and inhibit reproduction, as in the case of Cu, or calcification as in the case of Cd (ref. 44).

The calculated loadings of most metals derived from the impactor exceeded modern surface concentrations by at least an order of magnitude, whether we assume a worst-case scenario

of complete (Supplementary Table S5a) or relatively minor (1%; Supplementary Table S5b) mobilization of the ejecta material; Erickson and Dickson¹¹ estimated a range of solubilities from 1–10% for Fe, 50% for Ni, to 90% for Cu and Pb. Metal loadings, therefore, were probably closer to the worst-case scenario. The sudden increase in metal loading also may have exceeded the ability of the biota to produce detoxifying organic ligands, leading to widespread metal poisoning. The resulting loss of an efficient biological pump, as reflected in the collapse of the surface–deep gradient in $\delta^{13}\text{C}$ especially in the Northern Hemisphere (Supplementary Table S6) would have extended the lifetime of toxic metals in the photic zone. Such poisoning has the potential to amplify the effect of darkness on nannoplankton and would be most lethal in the Northern Hemisphere oceans where the ejecta were deposited (although multi-year stratospheric residence times of the vaporized meteorite would have tended to distribute the materials across the hemispheres¹³). Metal poisoning thus helps explain the extinction of cosmopolitan oligotrophs, probably with large standing crops, that were not adapted to elevated free-metal concentrations and already decimated by darkness and eutrophication. Rarer species endemic to high-latitude and neritic environments may have been better adapted to darkness and the high nutrient and trace-metal concentrations that occur in nearshore or in upwelling environments.

Dynamics of the nannoplankton recovery

The first 350 kyr after the K/Pg mass extinction involved the appearance of species with a range of ecologies (Supplementary Tables S2). Orbital time control (see Supplementary Information) allows us to compare the timing of the origination of nine species in the tropical Pacific (Site 1210) and the subtropical South Atlantic (Site 1262; Supplementary Table S4). Eight of these species occurred first in the South Atlantic and appeared in the Pacific on average 82 kyr later. The first taxon to originate in both locations was *Neobiscutum parvulum* (0 kyr in the South Atlantic, 23 kyr in the Pacific). That most new taxa appeared first in the South Atlantic substantiates the asymmetry of the nannoplankton recovery and points to harsh conditions persisting in the Pacific for millennia after the K/Pg impact.

Among the nannoplankton, the long-ranging 'disaster' taxa, calcspheres and *Braarudosphaera* dominate the crisis interval. Nannoplankton assemblages in the recovery interval are generally high dominance and low diversity (Fig. 3). They include a number of short-lived, opportunistic 'bloom' taxa (the genera *Futuyania*, *Lanternithus*, *Neobiscutum*, *Prinsius* and *Hornibrookina*; Fig. 4c) that are eutrophic, and long-ranging oligotrophs including *Coccolithus* and *Cruciplacolithus*. Ultimately, however, oligotrophic genera became the dominant, successful nannoplankton in the Palaeocene ocean. How did their recovery take place? With a general warming trend in the Palaeocene, and a gradual, global increase in thermal stratification⁴⁵, conditions in the Palaeocene increasingly favoured the oligotrophs, and the shallow-dwelling, eutrophic taxa became increasingly uncompetitive. Thus, the ecologies that were characterized by some of the highest extinction rates at the K/Pg boundary ultimately included the most successful taxa of the Palaeocene.

The K/Pg extinction in the Southern Hemisphere oceans was followed by near immediate return of an open-ocean nannoplankton assemblage. Presumably this recovery was facilitated by the higher survivorship in these regions (Fig. 2). In contrast, the 40-kyr-long assemblage crisis and the 100 kyr reduction in diversity in the Northern Hemisphere oceans (Figs 3 and 4a) was much longer lasting than impact-related darkness alone can explain and requires an alternative explanation.

Trace metals normally have residence times in the oceans ranging from 10¹ to 10⁴ yr being scavenged onto both inorganic and,

importantly, biogenic particles. Decimation of the surface plankton would pose a predicament for the biota in terms of recovery: with the loss of the principal mechanism for metal detoxification (biogenic ligand production) and removal from surface waters (biotic uptake and scavenging onto biogenic particles), residence times would be significantly lengthened and toxicity enhanced. Under such conditions the probably toxic effects of Ni and Cr could persist for up to at least 10^4 yr (Supplementary Table S5a), although this speculation depends strongly on the extent to which the original ejecta-born metals were dissolved¹¹ (Supplementary Table S5b). As ocean thermohaline circulation in the early Palaeogene probably involved Southern Ocean deep-water sources and Northern Hemisphere upwelling⁴⁶, the recovery interval in the Northern Hemisphere oceans could also have been extended by accumulation of trace metals in the older waters of the Northern Hemisphere, just as today the highest concentrations of nutrients and nutrient trace metals occur in the Pacific⁴⁷. Upwelling of trace metals (along with major nutrients) at toxic concentrations into Northern Hemisphere ocean surface waters could have sustained inimical conditions for timescales much longer than the ocean mixing time⁴⁸, even in gyres where less-efficient biological pumping^{21,22} would result in increased metal concentrations.

The asymmetric nannoplankton response to the K/Pg boundary impact seems to have ramifications for immediately higher parts of the marine food chain. The severity of the planktonic foraminiferal extinction and subsequent crisis in open-ocean sites is directly related to the fate of nannoplankton⁴⁹. Benthic foraminifera in many locations, however, seem to have been buffered from demise of plankton groups. Assemblages in the North Pacific seemed to thrive during the nannoplankton crisis interval, suggesting that they subsisted on calcispheres, other dinoflagellates or prokaryotes⁵⁰.

Nannoplankton extinction intensity at the K/Pg boundary was greater in the Northern Hemisphere oceans, compared with the Southern Hemisphere oceans. This pattern is consistent with darkness and suppression of photosynthesis and metal poisoning resulting from oblique impact with material ejected to the north and west. Survivors in the high latitudes were largely eutrophic taxa adapted to low light and elevated metal and nutrient levels. Cosmopolitan species, probably with large standing crops, were generally oligotrophic taxa unable to cope with the light and metal stresses. Metal poisoning probably delayed the onset of the recovery for 40 kyr in the Northern Hemisphere oceans where the biological pump had stalled and the most metal-enriched waters upwelled.

Received 10 September 2009; accepted 15 January 2010;
published online 28 February 2010

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Acknowledgements

We thank J. Pospichal, P. Bown and H. Thierstein for sharing their unpublished nannofossil counts. This research was sponsored by the NASA Exobiology grant NNX07AK62G. Samples acquired from the Integrated Ocean Drilling Program funded by NSF.

Author contributions

T.J.B., S.J. and M.E.P. designed the experiment, S.J., L.R.K. and J.D.S. conducted the analysis, T.J.B., L.R.K., M.E.P., S.J. and J.D.S. wrote the manuscript.

Additional information

The authors declare no competing financial interests. Supplementary information accompanies this paper on www.nature.com/naturegeoscience. Reprints and permissions information is available online at <http://npg.nature.com/reprintsandpermissions>. Correspondence and requests for materials should be addressed to T.J.B.