

Resilience of Pacific pelagic fish across the Cretaceous/Palaeogene mass extinction

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Open-ocean ecosystems experienced profound disruptions to biodiversity and ecological structure during the Cretaceous/Palaeogene mass extinction about 66 million years ago¹⁻³. It has been suggested that during this mass extinction, a collapse of phytoplankton production rippled up the food chain, causing the wholesale loss of consumers and top predators³⁻⁵. Pelagic fish represent a key trophic link between primary producers and top predators, and changes in their abundance provide a means to examine trophic relationships during extinctions. Here we analyse accumulation rates of microscopic fish teeth and shark dermal scales (ichthyoliths) in sediments from the Pacific Ocean and Tethys Sea across the Cretaceous/Palaeogene extinction to reconstruct fish abundance. We find geographic differences in post-disaster ecosystems. In the Tethys Sea, fish abundance fell abruptly at the Cretaceous/Palaeogene boundary and remained depressed for at least 3 million years. In contrast, fish abundance in the Pacific Ocean remained at or above pre-boundary levels for at least four million years following the mass extinction, despite marked extinctions in primary producers and other zooplankton consumers in this region. We suggest that the mass extinction did not produce a uniformly dead ocean or microbially dominated system. Instead, primary production, at least regionally, supported ecosystems with mid-trophic-level abundances similar to or above those of the Late Cretaceous.

The Cretaceous/Palaeogene (K/Pg) event precipitated an 80–95% species-level extinction of calcareous nannoplankton (primary producers) and planktonic foraminifera (primary consumers), decimating part of the base of the open-ocean food web. This loss of productivity is thought to have driven extinction at higher trophic levels². For instance, ~34% extinction at the genus level has been inferred for sharks and rays, with the highest losses among coastal and surface ocean groups⁶. The K/Pg event also produced a major shift in coastal bony fish functional diversity with particularly large losses among predatory fishes with ecologies similar to modern tuna, billfish and jacks^{7,8}. Complete extinction of mosasaurs, plesiosaurs and ammonites further suggests that the extinction reverberated to the top of the food web^{3,9}. Whereas the response of well-fossilized plankton and megafauna to the K/Pg mass extinction has been well studied^{1,6,10,11}, the ecological and evolutionary response of the trophic link between the two groups, the mid-level consumers such as small-bodied fishes, is relatively unknown (as discussed in refs 7,8).

Ichthyoliths have an excellent, but underappreciated, fossil record that spans the K/Pg boundary in the deep ocean¹². Teeth are typically small (most abundant in the <150 µm sieve fraction)

and so are likely to represent small pelagic species or juveniles, whereas rarer denticles may come from sharks with a range of body sizes. Unlike most microfossils, ichthyoliths are composed of calcium phosphate, which is highly resistant to dissolution¹³. Ichthyoliths are thus found in nearly all sediment types, including pelagic red clays¹³. An analysis of stratigraphic ranges of teeth in Pacific red clay suggests that the K/Pg extinction of tooth morphotypes was slight in contrast to the marked extinction of top pelagic predators^{6,7}. A stage-level biostratigraphic compilation of ichthyolith morphological diversity throughout the Pacific Ocean shows extinction of only 5 of 42 morphotypes between the Late Cretaceous and the early Palaeocene (a ~12% loss; ref. 13). The low level of extinction of tooth morphotypes suggests that few basic trophic groups of fishes were lost among small pelagic taxa. However, these data indicate little about the magnitude of loss of fish taxa at the boundary, because the samples represent several million years of time-averaging. In addition, in modern fishes tooth shape can evolve rapidly among closely related species, and convergence is common in fishes exploiting similar prey¹⁴.

We produced high-resolution time series of pelagic fish tooth abundance, in the North Pacific (Ocean Drilling Program (ODP) Site 886), Central Pacific (ODP Site 1209, Shatsky Rise), South Pacific (Deep-Sea Drilling Program (DSDP) Site 596) and the Tethys Sea (Bottaccione Gorge, Gubbio, Italy; Fig. 1). The absolute abundance of fish tooth remains is presented as an ichthyolith mass accumulation rate (MAR). Ichthyolith MAR accounts for changes in the sedimentation rate and density of deep-sea sediments, and provides an approximation for the relative abundance of pelagic fish in the overlying water column (Methods and Supplementary Information and Supplementary Figs 1–15). Our data sets use slightly different timescale and MAR metrics, based on the material and lithology of the site (Methods and Supplementary Information and Supplementary Figs 1–15). As a result, although absolute ichthyolith abundances are not equivalent across sites, the patterns and trends are comparable (Fig. 2).

Ichthyolith accumulation from the South Pacific Ocean (DSDP Site 596, Fig. 2c) increases across the boundary from an average of 41.8 ichthyoliths cm⁻² Myr⁻¹ in the last one million years of the Maastrichtian to 59.6 ichthyoliths cm⁻² Myr⁻¹ in the first million years of the Danian (two-sample *t*-test, *P* = 0.03; counts of ichthyoliths in the >106 µm fraction). The age model is based on cobalt accumulation rate and strontium isotope chronologies calibrated to the K/Pg boundary, which is placed at a prominent iridium anomaly and impact debris horizon^{15,16}. Teeth are preserved in red clay with a sedimentation rate of ~0.25 m Myr⁻¹, so it is possible that a brief decline in fish abundance could be masked

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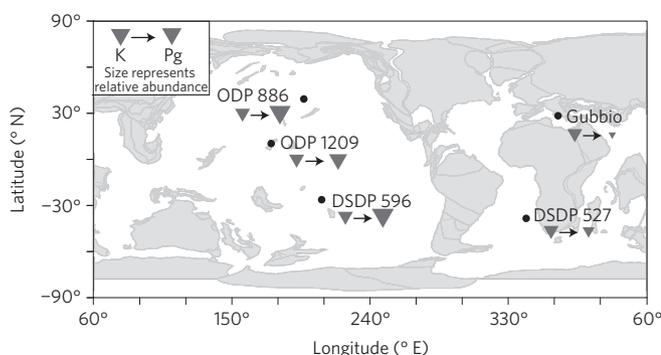


Figure 1 | Map of the sites included in this study and relative changes in ichthyolith accumulation across the boundary. The map shows the locations of the five sites from this study. The triangles underneath each site represent the relative change in ichthyolith accumulation from before (left) to after (right) the K/Pg boundary. The size of the triangles reflects average ichthyolith accumulation for the one million years before and after the boundary. See Methods for the source of the plate reconstruction.

by bioturbation. Still it is clear that there was no long-term decline in the export of fish remains to the deep sea following the mass extinction.

In the North Pacific Ocean (ODP Site 886C, Fig. 2a), ichthyolith accumulation is relatively constant in the Maastrichtian, at about 105 ichthyoliths $\text{cm}^{-2} \text{Myr}^{-1}$ (counts of ichthyoliths in the $>106 \mu\text{m}$ fraction). There is a substantial (5 \times) increase in ichthyolith accumulation in the half-million years following the boundary, after which ichthyolith accumulation stabilizes at nearly twice the Cretaceous level at 180 ichthyoliths $\text{cm}^{-2} \text{Myr}^{-1}$ (two-sample t -test, $P = 3 \times 10^{-9}$). Here the chronology is based on magnetostratigraphy, biostratigraphy and strontium isotope stratigraphy, tied to the K/Pg iridium anomaly; the record stops 64 million years ago (Ma) owing to a hiatus¹⁷. Together the North Pacific (ODP 886C) and South Pacific (DSDP 596) indicate that Pacific pelagic fish abundance was relatively unaffected, or even increased, following the K/Pg mass extinction.

In the Central Pacific (ODP Site 1209, Shatsky Rise, Fig. 2b) ichthyolith MAR (based on both ichthyolith weights and counts) is also relatively unchanged across the K/Pg boundary (Fig. 2a), with the possible exception of a 62 kyr interval coincident with the deposition of impact debris. Contamination by impact tektites prevents us from estimating ichthyolith weights at the K/Pg boundary, but counts of teeth and denticles (measured as ichthyoliths per square centimetre per million years) show no significant drop associated with the extinction horizon (Fig. 3a). Counts of fish ichthyoliths ($>600 \mu\text{m}$ and $>63 \mu\text{m}$) and total ichthyolith mass (tooth weight $>38 \mu\text{m}$) are significantly correlated (Supplementary Fig. 16), supporting our interpretation of little or no change in ichthyolith accumulation rates immediately across the K/Pg boundary at Shatsky Rise (Fig. 2). This Central Pacific record adds key support for the similar patterns observed in the North and South Pacific, as it has the best constrained age model for calculating accumulation rates.

There are two primary astronomical timescales for Site 1209, and both suggest that ichthyolith MAR was relatively stable immediately across the boundary (Supplementary Information and Supplementary Fig. 13). Between 65.65 Ma and 65.71 Ma (Fig. 2a), the Westerhold Option 1 (refs 18,19) age model suggests that there is a sharp increase in ichthyolith MAR (measured as ichthyolith weight) to an average of $0.31 \text{ g cm}^{-2} \text{ Myr}^{-1}$. This is well above average pre-extinction fluxes of $0.11 \text{ g cm}^{-2} \text{ Myr}^{-1}$ and confirmed by repeated sampling. From 65.6 to 62.1 Ma fish flux oscillates between $0.06 \text{ g cm}^{-2} \text{ Myr}^{-1}$ and $0.42 \text{ g cm}^{-2} \text{ Myr}^{-1}$ (average = $0.21 \text{ mg cm}^{-2} \text{ kyr}^{-1}$). The alternative Hilgen *et al.* age model²⁰ also shows no drop in ichthyolith weight across the boundary, but the sustained spike in ichthyolith abundance in the earliest Danian suggested by the Westerhold Option 1 age model¹⁸ disappears (Supplementary Figs 12 and 13). We note that a post-boundary increase in fish debris accumulation, similar to that implied by the Westerhold Option 1 age model¹⁸, is observed in the South Pacific (Site 596) and North Pacific (Site 886C) as well (Fig. 2), suggesting that this pattern may be robust and record a Pacific-wide boom in ichthyolith accumulation during the first million years of the Danian.

One notable difference among the Pacific records is the degree of variability in ichthyolith accumulation rates, particularly in

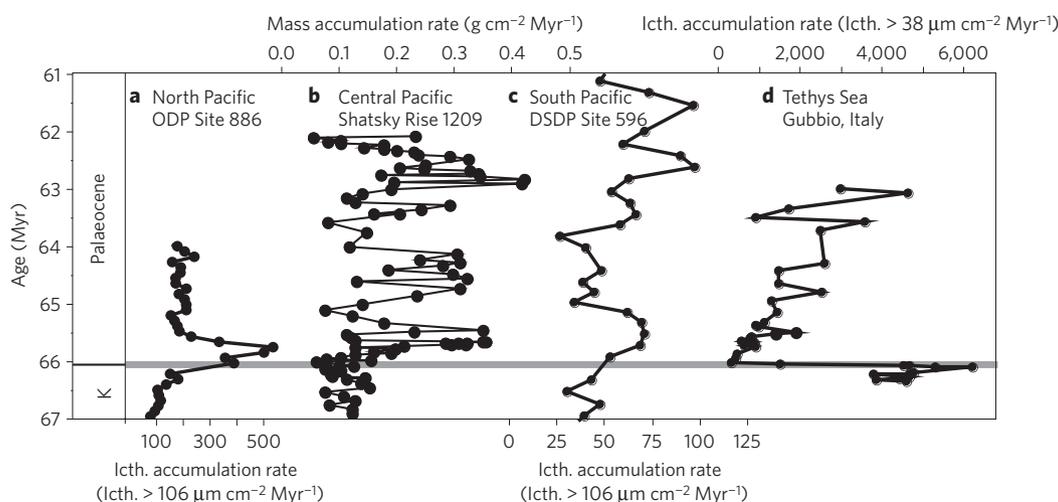


Figure 2 | Global pattern of ichthyolith accumulation rates through the K/Pg mass extinction. a–d, Ichthyolith accumulation in the North Pacific (ODP Site 886; ichthyoliths $>106 \mu\text{m cm}^{-2} \text{ Myr}^{-1}$), age model based on compilation of biostratigraphy, magnetostratigraphy, strontium isotopes and iridium anomaly¹⁷ (a), the Central Pacific (Shatsky Rise, ODP Site 1209; $\text{g cm}^{-2} \text{ Myr}^{-1}$ of $>38 \mu\text{m}$ fish debris), age model after Westerhold solution 1 (ref. 18) and shipboard biostratigraphy²⁹ (b), the South Pacific (DSDP Site 596; ichthyoliths $>106 \mu\text{m cm}^{-2} \text{ Myr}^{-1}$), age model based on cobalt accumulation¹⁵ (c), and the Tethys Sea (Gubbio, Italy; ichthyoliths $>38 \mu\text{m cm}^{-2} \text{ Myr}^{-1}$), age model based on bio- and magnetostratigraphy^{21,22} (d). All age models use GTS 2012 ages for the K/Pg boundary and biostratigraphic and magnetostratigraphic datums³⁰.

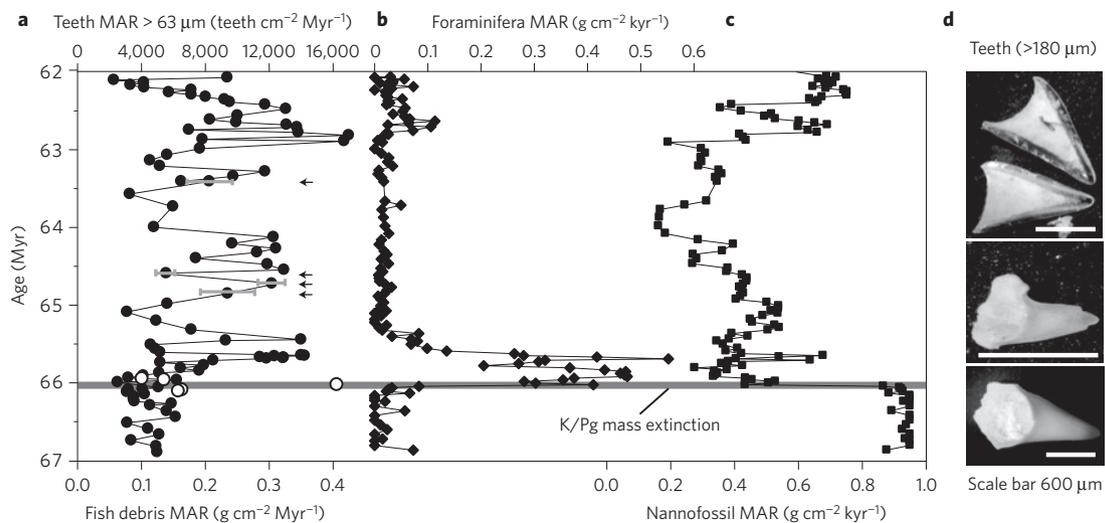


Figure 3 | Central Pacific (ODP Site 1209) comparison of mass accumulation rates for different trophic groups through the K/Pg mass extinction.

a–c, Ichthyolith MAR (filled circles indicate $\text{g cm}^{-2} \text{ Myr}^{-1}$ for the $>38 \mu\text{m}$ fraction; open circles indicate $\text{teeth cm}^{-2} \text{ Myr}^{-1}$ for the $>63 \mu\text{m}$ fraction; **a**), foraminiferal MAR ($\text{g cm}^{-2} \text{ kyr}^{-1}$; ref. 10; **b**) and calcareous nannofossil MAR ($\text{g cm}^{-2} \text{ kyr}^{-1}$; ref. 10; **c**). The horizontal grey line is the K/Pg boundary. **d**, Examples of large fish teeth from the Palaeocene (scale bar = $600 \mu\text{m}$). The arrows in **a** indicate replicated samples (Supplementary Discussion); error bars are 95% confidence intervals. Timescale after Westerhold *et al.* solution 1 (ref. 18) and shipboard age model²⁹ updated to GTS 2012 (ref. 30).

North Pacific ODP Site 1209. The observed variability is not a simple function of sedimentation rates, because both ODP Site 1209 (with the highest sedimentation rates) and DSDP Site 596 (with the lowest) show distinct cycles in ichthyolith MAR. In addition, these differences in variability among sites are clear only in the Palaeocene portion of the record. We suggest that differences in Palaeocene variability in fish MAR may reflect a real, and in some cases prolonged, change in fish production initiated by the K/Pg extinction, but this conclusion remains to be verified in comparably long records of Cretaceous ichthyolith accumulation.

In contrast to the Pacific Ocean, there is an abrupt collapse in ichthyolith accumulation in the Tethys Sea (Gubbio, Italy, Fig. 2d), followed by a slow ‘recovery’ period of 3 million years (Fig. 2d). The standard age model based on biostratigraphy and magnetostratigraphy^{21,22} shows that ichthyolith abundance drops from approximately $4,672 \text{ ichthyoliths cm}^{-2} \text{ Myr}^{-1}$ in the latest Cretaceous to just $589 \text{ ichthyoliths cm}^{-2} \text{ Myr}^{-1}$ in the earliest Palaeocene, a nearly 88% decrease in ichthyolith abundance. An alternative helium-age model for this site²³ reveals at least a 50% decline in ichthyolith accumulation at the boundary (Supplementary Fig. 13b), and compresses the recovery into a 700,000 year period. Thus, regardless of age model, there is a large, abrupt and sustained reduction in ichthyolith abundance at Gubbio in the Tethys Sea. The collapse and slow recovery of ichthyolith accumulation that we observe in the Tethys was also reported, in a low-resolution ichthyolith record from the South Atlantic at DSDP Site 527 (Supplementary Fig. 16; ref. 24). Considered jointly, both the Atlantic and Tethys basins show a marked decline in fish production consistent with traditional expectations for a collapse of mid to upper trophic levels in pelagic food webs that contrasts directly with our findings in the Pacific.

Our results suggest that the mass extinction did not cause a uniformly dead ocean or one lacking a robust zooplankton community, but instead generated diverse responses of fish in different ocean environments and geographic regions. Fish production in the Tethys and perhaps the South Atlantic was suppressed much longer than in the open Pacific Ocean. Although there is a well-known global extinction and drop in export production of calcareous plankton, this evidently is not a reflection

of the entire community of primary producers^{25,26}, because Pacific pelagic fish were able to find sufficient food to maintain populations at levels comparable to or higher than pre-extinction communities. Previous work has found similar geographic heterogeneity in other aspects of pelagic ecosystems^{10,25}. Export production indicated by both biogenic barium and benthic foraminifer communities suggests that Pacific primary production did not fall after the mass extinction²⁶. Our results show that pelagic fish, at least, seem to have either been able to switch to the new resources or to have been replaced by Danian fish groups that were equally productive as those of the Late Cretaceous in the Pacific Ocean, even in the face of major changes in lower trophic levels.

There are also large inter-ocean differences in the pace and dynamics of the ecological recovery from the mass extinction. All three Pacific records show an early Danian increase in ichthyolith accumulation (Fig. 2), which coincides with evidence for increased export productivity^{25–27}. Our Central Pacific and South Pacific records also show two other periods of increased ichthyolith accumulation in the early Palaeocene, one from approximately 65 to 64 Ma, and one that begins at approximately 63 Ma. These increases in fish debris accumulation coincide with a major diversification of planktonic foraminifera and the recovery of nannofossil mass accumulation rates in Central Pacific Site 1209 (Fig. 3; refs 10,28). It seems that marked extinction and loss of productivity in calcareous algae was not devastating to the entire food web, at least in the Pacific Ocean. This is possibly because other groups of non- (or poorly) fossilized primary producers were able to sustain comparable levels of new production in the immediate aftermath of the extinction in the Pacific²⁷. In contrast, the decline in fish remains, biogenic barium and benthic foraminifer assemblages lasts for hundreds of thousands to millions of years in the Atlantic and Tethys. The duration of this inter-basinal contrast suggests that differences between the ocean basins are not purely the direct results of the extinction but are reinforced by geographic differences in productivity of ecosystems following the extinction. Our findings support an emerging view of the end-Cretaceous mass extinction^{10,11,25–27} where there is considerable variation in the effects of the extinction both among trophic groups and between ocean regions as well as in the timing of the recovery of ecosystem structure and function.

Methods

Ichthyolith isolation methods varied between sites owing to lithological differences. At all sites, samples were dissolved in 5% acetic acid and washed over a 38 µm sieve to isolate the ichthyoliths. Sample size varied by site and lithology: 10 g in pelagic carbonate oozes at ODP 1209, 5–10 g red clay at DSDP 596 and ODP 886, 100 g limestone at Gubbio. For Gubbio, the limestone was broken up into ~1 cm³ chunks and dissolved in 5–10% acetic acid (bath changed every 24 h) until no carbonate remained in the >150 µm fraction. At Shatsky Rise, after dissolution, samples were visually checked to confirm that the remaining material was entirely fish debris. Then the pure fish debris residue was weighed to calculate MAR using two astronomically tuned timescales for ODP Site 1209 in the Palaeocene^{18,20}, shipboard sedimentation rates in the Late Cretaceous²⁹, and variable dry bulk density (Supplementary Information and Supplementary Figs 1–5). Measurement reproducibility of ichthyolith weights is good based on replicate measurements of splits of samples (Supplementary Information). Additional debris (non-ichthyolith) in the non-carbonate fraction at DSDP Site 596, ODP 886 and Gubbio precluded a weight-based assessment of fish MAR. Instead, ichthyoliths were manually picked from the >106 µm (DSDP 596 and ODP 886) and >38 µm (Gubbio, owing to low abundance of large ichthyoliths) size fractions, and counted. The DSDP 596 timescale is based on a cobalt accumulation model¹⁵ and tied to the K/Pg Boundary. The ODP Site 886 timescale is based on a compilation of radiolarian biostratigraphy and strontium isotopes, and is also tied to the K/Pg boundary¹⁷. The age model for Gubbio was constructed using bio- and magnetostratigraphy^{21,22} and tied to the boundary. We also computed the Gubbio fish MAR using a published helium isotope stratigraphy (Supplementary Fig. 13; ref. 23). All sites were calibrated using the Geologic Time Scale 2012 (GTS 2012; ref. 30). See the Supplementary Information for a discussion of other factors considered in our interpretation including preservation, sediment mixing, the MAR of the non-biogenic fraction, and age model accuracy.

Data. The 66.0 Ma palaeo-continent reconstruction was generated using the ODSN plate reconstruction service (www.odsn.de/odsn/services/paleomap/paleomap.html). Supplementary data are available online through <http://www.nature.com/ngeo/index.html> or at <http://dx.doi.org/10.1594/PANGAEA.834235>.

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Author contributions

R.D.N. and P.M.H. conceived the study; E.C.S. developed the methods, collected field samples, and generated and analysed the data; all authors contributed to the writing of the manuscript.

Additional information

Supplementary information is available in the online version of the paper. Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to E.C.S.

Competing financial interests

The authors declare no competing financial interests.