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New Age of Fishes initiated by the Cretaceous–Paleogene mass extinction

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Ray-finned fishes (Actinopterygii) comprise nearly half of all modern vertebrate diversity, and are an ecologically and numerically dominant megafauna in most aquatic environments. Crown teleost fishes diversified relatively recently, during the Late Cretaceous and early Paleogene, although the exact timing and cause of their radiation and rise to ecological dominance is poorly constrained. Here we use microfossil teeth and shark dermal scales (ichthyoliths) preserved in deep-sea sediments to study the changes in the pelagic fish community in the latest Cretaceous and early Paleogene. We find that the Cretaceous–Paleogene (K/Pg) extinction event marked a profound change in the structure of ichthyolith communities around the globe: Whereas shark denticles outnumber ray-finned fish teeth in Cretaceous deep-sea sediments around the world, there is a dramatic increase in the proportion of ray-finned fish teeth to shark denticles in the Paleocene. There is also an increase in size and numerical abundance of ray-finned fish teeth at the boundary. These changes are sustained through at least the first 24 million years of the Cenozoic. This new fish community structure began at the K/Pg mass extinction, suggesting the extinction event played an important role in initiating the modern “age of fishes.”

Cretaceous–Paleogene boundary | ichthyoliths | fossil fish | age of fishes | mass extinction

Ray-finned fishes are a dominant and exceptionally diverse member of modern pelagic ecosystems; however, both the fossil record and molecular clocks suggest that the vast majority of living ray-finned fishes developed only recently, during the last 100 million years (1–3). It has been proposed that the explosion in actinopterygian diversity in the Late Mesozoic and Early Cenozoic represents a new “age of fishes” in contrast to the initial diversification of fish clades in the Devonian (2, 3). However, the mechanisms and timing of this Mesozoic–Cenozoic radiation and rise to dominance by ray-finned fishes are not well constrained in current molecular phylogenies or from the relatively sparse fossil record. While the Cretaceous–Paleogene (K/Pg) mass extinction occurred ~66 million years ago (Ma), in the middle of this radiation, there is little clear phylogenetic evidence linking any changes in fish diversity directly to this event (1), although a recent phylogenetic study on pelagic fish families suggested that open ocean fishes radiated during the early Paleogene following the extinction (4).

The K/Pg extinction had a dramatic effect on open ocean marine ecosystems (5–7), although the severity of the extinction varied around the globe (7–9). Major groups at both the base and top of the food web were decimated (5, 6, 10). While the traditional model of mass extinction due to primary productivity collapse (11) has been generally discredited due to the continued productivity of select consumer groups (12, 13), it is likely that upheaval among primary producers reverberated up the food web to cause extinctions at higher trophic levels. In the open ocean, calcifying plankton such as foraminifera and calcareous nanofossils suffered >90% species-level extinctions (9, 14). These changes in the structure of the base of the food web likely helped to cause the extinctions of pelagic consumers such as ammonites and marine reptiles (10). The trophic link between the plankton and large consumers in pelagic ecosystems is small pelagic fish, which would be expected to be similarly decimated by changes in food web

structure. However, recent work has shown that while there was a collapse of small pelagic fish production in the Tethys Sea, in the Pacific Ocean, these midlevel consumers maintained Cretaceous-like or higher levels of production in the earliest Danian (15).

Changes in abundance do not tell the whole story of how pelagic fishes responded to the extinction event. Indeed, despite dramatic levels of extinction, a few species of planktonic foraminifera thrived in the postextinction oceans, reaching abundances in the ~500,000 y following the event that far exceed those of typical high-diversity Cretaceous assemblages (7). This foraminifer response shows that taxonomic diversity and biological production can be decoupled in postdisaster ecosystems like those of the earliest Danian. Fishes are highly diverse and occupy a range of ecological niches, from the smallest plankton feeders through predatory sharks. This means that different groups could exhibit differential responses to the extinction (16). Work on well-preserved body fossils has found that there was a selective extinction of shallow marine predatory fishes at the K/Pg extinction, and a radiation during the early Cenozoic (17, 18). Additionally, a low level of extinction (<33%) of sharks and rays has been inferred across the event (19, 20). However, the magnitude of pelagic fish extinction is poorly known, although a relatively modest ~12% extinction has been documented for fish tooth morphotypes between the Late Cretaceous and the early Paleocene (21).

Here we use ichthyoliths, the isolated teeth and dermal scales (denticles) of sharks and ray-finned fishes found in deep-sea sediments, to investigate the response of sharks and fishes to the K/Pg extinction. Calcium phosphate ichthyoliths are found in nearly all marine sediments, even red clays (22), where other microfossils have been dissolved by corrosive bottom water conditions. Therefore, ichthyoliths are relatively unaffected by the preservation biases typically found in other microfossil groups. Teeth and denticles are

Significance

Ray-finned fishes are the most diverse and ecologically dominant group of vertebrates on the planet. Previous molecular phylogenies and paleontological studies have shown that modern ray-finned fishes (crown teleosts) radiated sometime in the Late Cretaceous or early Paleogene. Our data suggest that crown teleosts came into their current dominant ecological role in pelagic ecosystems immediately following the Cretaceous–Paleogene mass extinction 66 million years ago by filling newly vacated ecological niches and marking the beginning of an “age of ray-finned fishes.” Our study is, to our knowledge, the first geographically comprehensive, high-resolution study of marine vertebrate communities across the extinction.

Author contributions: E.C.S. and R.D.N. designed research; E.C.S. performed research; E.C.S. contributed new methods; E.C.S. analyzed data; and E.C.S. and R.D.N. wrote the paper.

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reasonably common, with 10s to 100s found in a few grams of sediment, allowing studies of the fish community rather than isolated individuals. The abundance of ichthyoliths also allows for high-temporal resolution sampling similar to other microfossils. The well-resolved ichthyolith records stand in sharp contrast to those for the comparatively rare body fossil record, and can provide a complimentary analysis of abrupt biotic events such as mass extinctions or transient climate changes. In addition, the abundance, assemblage, and morphological composition of ichthyoliths record the productivity and biodiversity of the pelagic fish community.

We investigate how the pelagic fish community responded to the K/Pg extinction at six deep-sea sites in the Pacific, Atlantic, and Tethys Oceans. We use ichthyolith community metrics, including the relative abundance of microfossils from sharks and ray-finned fishes, and the size structure of the tooth assemblage to assess the changes in the pelagic fish community across the K/Pg mass extinction around the world. This represents, to our knowledge, the first geographically comprehensive, high-resolution study of pelagic marine vertebrate communities across the extinction.

Results

The K/Pg Boundary was identified in each site based on the global iridium anomaly layer, as well as the presence of tektites, impact ejecta, and slump deposits associated with the impact horizon (23–29). Site-specific chronologies were developed based on cyclostratigraphy, cobalt accumulation rates, strontium isotopes, biostratigraphy, and magnetostratigraphy, depending on the lithology at each site (see *Materials and Methods* and *SI Materials and Methods* for additional details).

Ichthyoliths are fundamentally divided into two broad taxonomic groups: teeth, which can belong to ray-finned fish as well as sharks, and dermal denticles, the tooth-like placoid scales that cover nearly all sharks and rays. We looked at the relative abundance of actinopterygian fishes to sharks before and after the extinction event, as interpreted by the relative abundance of teeth to shark denticles in an assemblage of microfossils retained on a 106- μm sieve. A tooth/denticle ratio of >1 means actinopterygian fish teeth dominated the $>106\text{-}\mu\text{m}$ ichthyolith assemblage, while a ratio of <1 means shark denticles dominated the $>106\text{-}\mu\text{m}$ ichthyolith assemblage. It is worthwhile to note that this metric considers only the numerical abundance of microfossils at a constant size fraction ($>106\text{ }\mu\text{m}$) and not individuals or biomass of these groups.

Actinopterygian fish typically have two distinct sets of teeth, oral teeth, which are found in the jaw, and the far more abundant but significantly smaller pharyngeal teeth. The $>106\text{ }\mu\text{m}$ fraction generally contains mostly oral teeth, while smaller fractions are dominated by pharyngeal teeth and tooth fragments. Rates of tooth loss and regeneration of actinopterygian fishes are poorly constrained and vary with taxon, although teeth are replaced continuously throughout the life of the individual (30). However, in at least some taxa, many teeth are resorbed, rather than shed, during tooth replacement, so the number of teeth in the sedimentary record is likely an underrepresentation of teeth produced (30, 31).

Sharks can have 2–3 orders of magnitude more denticles—which scale numerically with body surface area—than sharks or ray-finned fish have oral or pharyngeal teeth. This means that the absolute value of the ratio of teeth to denticles in the $>106\text{-}\mu\text{m}$ size fraction, considered in this study, is not the true ratio of ray-finned fish versus shark biomass or numerical abundance. However, when considering the ratio of teeth to denticles at a constant size fraction, the metric allows for consistent comparison between assemblages, and can be interpreted as changes in relative abundances of sharks and ray-finned fish. We consider the $>106\text{ }\mu\text{m}$ fraction in this study as a uniform metric across all sample sites but note that the abundance of smaller teeth is correlated with the

abundance of larger teeth, and the absolute value of the tooth/denticle ratio increases at smaller size fractions.

An additional consideration is that teeth in the $>106\text{ }\mu\text{m}$ fraction likely include some shark teeth as well as those of ray-finned fishes. We note that shark teeth are often flattened, triangular forms with multiple cusps at the base and a cutting edge that may be ornamented with serrations. Such teeth represent $<1\%$ of the total tooth ichthyoliths in our $>106\text{ }\mu\text{m}$ samples, and were not present in a majority of assemblages. Indeed, despite constant tooth replacement, sharks will still produce several orders of magnitude more denticles in a lifetime than teeth, depending on their body size. Hence, it is unsurprising that shark teeth are rare in our assemblages, compared with the abundance of denticles. Numerical simulations show that the presence of a few shark teeth in our tooth samples does not significantly bias our results (please see *SI Materials and Methods* for more information).

We find that in the Cretaceous Pacific Ocean, the accumulation of actinopterygian teeth is consistently lower than the accumulation of shark denticles, suggesting that sharks were more dominant in the Cretaceous pelagic vertebrate community than they were in the Paleocene (Fig. 1A). The tooth to denticle ratio in the Cretaceous was $\sim 0.71:1$ in the North Pacific [Ocean Drilling Program (ODP) Site 886] Maastrichtian, and $0.76:1$ in the South Pacific [Deep Sea Drilling Project (DSDP) Site 596]. The accumulation rate of teeth increases notably after the K/Pg extinction, leading to a tooth/denticle ratio of $1:1$ at both Pacific locations in the first 500,000 y of the Paleocene before increasing toward $2:1$ by the mid-Paleocene (Fig. 1B). This change is significant at both sites (two-sided t test, $P < 0.0001$). The community change occurs at the K/Pg boundary, and cannot be explained by background variability, since the tooth/denticle ratio is nearly constant in the Cretaceous (Fig. 1B). The main reason for the increase in the tooth/denticle ratio is the increased accumulation of ray-finned fish teeth in the Paleocene, and it does not represent a large decline in sharks (Fig. 1A).

While low ichthyolith abundances $> 106\text{ }\mu\text{m}$ in the Atlantic [International Ocean Discovery Program (IODP) U1403, DSDP 386, and ODP 1262] and Tethys Sea (Gubbio) preclude similar time series analysis, grouped assemblages of ichthyoliths from the latest Cretaceous and earliest Paleocene show the same pattern as in the Pacific, with a preextinction tooth/denticle ratio between 0.7 and 1, and a postextinction ratio between 2 and 3.5 (Fig. 2). These global results suggest that the relative abundance of ray-finned fish in marine vertebrate assemblages increased dramatically at the extinction all over the world. Notably, these changes in the tooth/denticle ratio occur despite local decreases in ichthyolith accumulation in the Tethys Sea and Atlantic sites (15). In the South Pacific, we find that the ratio of ray-finned fish teeth to shark dermal denticles in the assemblage continues to rise into the Eocene, from values of $\sim 2:1$ in the earliest Paleocene to values of seven teeth per denticle in the Eocene (Fig. 3A). Hence, the increase in tooth/denticle ratio is initiated at the K/Pg boundary and continues to increase, at least in the South Pacific, for at least 24 million years after the extinction.

The size structure and accumulation rate of the tooth assemblages also changed at the K/Pg boundary in the Pacific Ocean. Tooth size was measured as the longest dimension through the centroid of each tooth (Feret's Diameter) $> 106\text{ }\mu\text{m}$ using the open source image processing program ImageJ (32). Shark denticles were excluded from this analysis, as many denticles are preserved as fragments. Both Cretaceous and Paleocene tooth assemblages are dominated by small teeth, with lengths of $<0.8\text{ mm}$, and a median size of $\sim 0.43\text{ mm}$ (Fig. 1C). In the early Paleocene, the largest increases in tooth accumulation and relative abundance occur in the largest tooth size fraction ($>0.8\text{ mm}$; Fig. 1C). This increase in the abundance of large teeth begins at the K/Pg extinction in both Pacific sites, but it is most apparent in the South Pacific starting at 64 Ma and lasting until 58–59 Ma (Figs. 1C and 3B). A Cretaceous-like

from the Cretaceous to the Paleogene. There are examples of fish increasing their tooth production through changes in gene regulation, such as certain species of stickleback fish having more teeth in freshwater systems than in brackish or marine waters (35). However, the increase in tooth size and change in community structure suggest that this mechanism alone is unlikely to account for all of the changes seen in the ichthyolith community at the K/Pg boundary and maintained through the Paleocene and Eocene.

While the ratio of ray-finned fish to shark ichthyoliths appears to be relatively stable around the globe during the Cretaceous, the Paleocene ratios are more varied (Fig. 2). The productivity of pelagic ecosystems is known to have fallen abruptly in the Atlantic and Tethys Oceans while remaining relatively unchanged in the Pacific (7, 8, 12, 15). Hence, geographic variation in the fish-to-shark ratio may reflect spatial differences in dynamics of primary producers and export production in the post-K/Pg pelagic marine ecosystems (7, 8, 12) that could have supported different groups and abundances of fish in different regions (15). This is consistent with geographically heterogeneous patterns of recovery seen in other pelagic marine lineages (7).

The Paleocene increase in the size and accumulation rate of the largest teeth strongly suggests that the K/Pg event initiated a wholesale change in the fish community. Fish tooth size does not necessarily scale allometrically with body size, especially in the open ocean and deep sea: Some very large fish have only small teeth, while other very small fish have much larger teeth; hence we cannot directly interpret tooth size as a direct indication of body size. However, we suggest that the size structure of the ichthyolith assemblage does reflect the range of ecological niche space taken up by the fishes present in the system. Therefore, we infer that the large range of tooth sizes in the Paleocene indicates an expansion of the collective range of habitats and ecologies that fishes were able to exploit, somewhat analogous with the postextinction increase in the size diversity of Cenozoic mammals (36).

In addition to the increase in maximum tooth size, there is also a temporary increase in the accumulation rate, length, and relative abundance of the largest teeth (75th quartile or larger). The peak in accumulation rate and size of this largest group of teeth lasts only from the K/Pg boundary until about 60 Ma. The prominence of large teeth in the South Pacific suggests that ray-finned fishes explored a novel community structure for the first 6–7 million years of the Paleocene, in which large teeth were unusually abundant compared with those in Cretaceous and later Paleocene assemblages. The overall size structure of tooth assemblages in the later Paleocene and Eocene shows a lower relative abundance of large teeth. However, the constant presence of at least a few teeth in each sample that are significantly larger than the largest Cretaceous teeth (Fig. 3D) suggests that the decrease in relative abundance of large teeth represents a “filling in” of ecological niche space between the smallest and largest tooth sizes rather than a disappearance of large-toothed fishes in later Paleocene and Eocene fish assemblages.

A major advantage of our deep-sea ichthyolith records is that they can allow assessment of variability in marine vertebrate assemblages up to and across major events. Our Pacific records show that the latest Cretaceous vertebrate community was very stable, both in terms of the ratio of fish to sharks and the size structure of the tooth community (Fig. 3). Indeed, our South Pacific record of tooth/denticle ratios and tooth size “flatlines” for the last 10 million years of the Cretaceous. The stability of Cretaceous assemblages suggests that the changes observed at the K/Pg boundary and early Paleocene were abrupt, likely caused by the extinction event, and are not part of a background trend or the result of random chance. This change in fish community structure appears to have been caused by the Chicxulub impact (24) rather than being a long-term response to a prolonged period of volcanism during the Latest Cretaceous. Indeed, in parallel with the mammals on land (36), the K/Pg extinction event appears to have

initiated major changes in the marine vertebrate community that lead to the great diversification and ecological rise to dominance of the ray-finned fishes in our oceans today.

Conclusions

While there were relatively low levels of extinction of pelagic fish at the K/Pg boundary, we find that the extinction event marked an ecological turning point for the pelagic marine vertebrates. Most open ocean, gyre-inhabiting, Cretaceous fishes were likely small and relatively rare—like the terrestrial mammals of their time—compared with their counterparts of the Paleocene and Eocene. In the Paleogene, ecological changes such as the increase in relative abundance of ray-finned fish compared with sharks and the persistence of large-toothed fishes are both permanent changes in the fish community that were initiated by the extinction. The presence of a novel “disaster fauna” of large-toothed fishes, at least in the South Pacific, suggests that rapid evolution occurred in the pelagic fish community following the extinction (4), before a more delayed filling in of niche space occurred in the later Paleocene and Eocene. The extinction event changed the fundamental ecosystem structure of the pelagic marine vertebrate community, allowing the ray-finned fishes to rapidly diversify in the early Cenozoic pelagic oceans. The extreme stability of Cretaceous ichthyolith accumulation rates, assemblage structure, and tooth sizes suggests that, without the extinction, it is unlikely that the system would have reset so dramatically in favor of ray-finned fishes. The K/Pg extinction appears to have been a major driver in the rise of ray-finned fishes and the reason that they are dominant in the open oceans today.

Materials and Methods

Sample Preparation. Samples were obtained from Integrated Ocean Drilling Program (now International Ocean Discovery Program, IODP), ODP, and Deep Sea Drilling Project sites, from the North Pacific (ODP Site 886), South Pacific (DSDP Site 596), North Atlantic (IODP Site U1403), Central Atlantic (DSDP Site 386), and South Atlantic (ODP Site 1262). Gubbio samples were obtained from the limestone outcrop on Contessa Highway north of Gubbio, Italy (37). DSDP Sites 386 and 596 and ODP Site 886 are red clay, while ODP Site 1262 and IODP Site U1403 are primarily carbonate ooze. Sample processing varied based on lithology (see *SI Materials and Methods*). All samples were dried to constant weight in a 50 °C oven. Ichthyoliths were isolated from the samples by disaggregation with deionized water in the case of clays, and by dissolution in weak (5–10%) acetic acid in the case of carbonates. All particles > 38 μm were retained, and ichthyoliths > 106 μm were hand-picked from the residue using a dissection microscope and archived in cardboard micropaleontology slides using gum tragacanth glue to hold in place.

Ichthyolith Assemblage Analysis. Ichthyoliths were classified into denticles (shark scales) and teeth (assumed to be mostly ray-finned fish teeth, <1% shark teeth; see *SI Materials and Methods* for more discussion). All Pacific assemblages were photographed using a Canon Powershot S5 IS microscope-mounted camera. The resulting image was processed and analyzed using ImageJ (32) to count and measure the size and shape of the ichthyoliths. The other sites considered in this study were simply grouped into “preboundary” and “postboundary” assemblages for analysis. Size structure analysis was restricted to teeth, since about 20–40% of the denticles were partially fragmented.

Age Models and Accumulation Rates. While ichthyolith assemblage metrics are independent of age model beyond preboundary and postboundary, ichthyolith accumulation rate (reported as ichthyoliths per square centimeter per million years) is, by definition, age-model dependent, since the calculation depends on sedimentation rates and accurate age datums. The age model for DSDP Site 596 is based on a cobalt accumulation rate stratigraphy (38), and tied to the K/Pg boundary by a prominent iridium anomaly at that site (23). The age model has been shifted to hang on the Geologic Time Scale 2012 (GTS2012) K/Pg boundary age of 66.04 Ma (39). The ODP Site 886 age model is based on a compilation of radiolarian biostratigraphy and strontium isotope stratigraphy, and is also tied to the K/Pg boundary by an iridium anomaly (25) and given the GTS2012 age of 66.04 Ma. For the other sites, where accumulation rate is not considered, samples were grouped into preboundary and postboundary, based on prominent impact horizons in each location.

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