Detritus feeding as a buffer to extinction at the end of the Cretaceous

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ABSTRACT

At the end of the Cretaceous the principal animals that became extinct, such as dinosaurs, marine animals that lived in the water column, and benthic filter feeders, were in food chains tied directly to living plant matter. Animal groups less affected by extinction, including marine benthic scavengers and deposit feeders, small insectivorous mammals, and members of stream communities, were in food chains dependent on dead plant material. The proposal that an asteroid or comet impact at the end of the Cretaceous produced a dust cloud that cut off photosynthesis for several months is consistent with this pattern of extinction. Food chains dependent on living plant matter crashed, while food chains based on detritus were buffered from extinction because there was a food supply adequate for the interval when photosynthesis was halted.

INTRODUCTION

The hypothesis that an extraterrestrial impact caused the terminal Cretaceous extinction (Alvarez et al., 1980) has been tested by the paleontological community primarily by studying the prediction that such an extinction would be an abrupt event. The impact hypothesis has also been countered by construction of alternative models to explain the extinction events. One line of paleontologic inquiry that has not been pursued is to devise and test a model of the ecologic effects that impact-related events would have on the ecosystem.

The primary global effect proposed for an asteroid impact is a dust cloud that cut off sunlight and interrupted photosynthesis for several months, which caused collapse of food chains (Alvarez et al., 1980; Milne and McKay, 1982). There is substantial agreement that the dust cloud would have interrupted photosynthesis for three to six months (Toon et al., 1982; Pollack et al., 1983; Gerstl and Zardecki, 1982). During this interval of darkness, primary production would have been halted. The time necessary for refoliation after darkness would have increased the length of time that primary production was unavailable to herbivores.

Given these conditions, an impact model can be constructed in which animals in food webs relying upon living plant material would be in immediate danger because they depend on constant replenishment of the standing crop of plants. Animals in food webs relying on detritus would be little affected by cessation of photosynthesis because there would be a substantial food reservoir that would not be depleted immediately. The death of plants and many animals might actually have increased the amount of detritus available.

Although the model requires that plant foliage and the standing crop of phytoplankton be killed, it does not presume plant extinctions, because species could survive as cysts, spores, and seeds and through regeneration of defoliated plants (Knoll, 1984). Evidence for massive disruption of marine phytoplankton at the boundary is substantial (Thierstein, 1982). Palynofloral studies of local sections across the boundary are consistent with massive defoliation, but not necessarily extinction of the terrestrial flora (Knoll, 1984; Tschudy et al., 1984).

This impact model may be tested by examining the hypothesis that the Cretaceous extinction would be concentrated on animals in food chains relying on living plant foliage, while animals in food chains relying on detritus would face substantially less severe extinction. After the extinction, communities relying on detritus would be more common and communities relying on living plant material would be less common than before the extinction. The hypothesis is examined first in marine and then in terrestrial environments.

MARINE

Marine (Fig. 1A) primary production is dominated by phytoplankton. In contrast to terrestrial ecosystems, the Eltonian food pyramid is inverted at any given time, the marine animal biomass exceeding plant biomass (Fig. 1A). However, rapid turnover and asexual production of new plant cells produce a normal food pyramid over a full year (Tait, 1968). The small standing crop and short life span of phytoplankton make marine ecosystems particularly vulnerable to interruption of sunlight (Milne and McKay, 1982). Animals in food chains directly dependent on living phytoplankton include animals living in the water column and benthic filter feeders that rely on organisms living in the water column (Tait, 1968). Detritus-feeding animals that do not rely directly on living plant matter include benthic invertebrates such as scavengers and deposit feeders (Gray, 1981).

At the Cretaceous/Tertiary boundary, phytoplankton-dependent marine animals living in the water column were affected drastically by the extinction. Extinction of planktonic foraminifera is correlated closely with the iridium anomaly (Alvarez et al., 1980; Smit, 1982). The extinction of ammonites, belemnites, and marine reptiles correlates well, and marine bony fishes were reduced significantly (Russell, 1979). Benthic filter feeders, including many bryozoans, crinoids, corals, articulate brachiopods, oysters, and other filter-feeding bivalves, experienced substantial extinction (Newell, 1967; Van Valen and Sloan, 1977; Russell, 1979; Emiliani et al., 1981; Jablonski and Bottjer, 1983; Van Valen, 1984; Alvarez et al., 1984; Hansen et al., 1984). On the other hand, detritus-based benthos, including bottom-dwelling predators and detritus feeders, experienced little loss (Van Valen and Sloan, 1977; Van Valen, 1984). Kauffman (1984) stressed the survival of generalists and extinction of stenotopic groups at the K/T boundary, but his examples (p. 168–176) are strongly biased toward survival of deposit feeders and extinction of suspension feeders and animals dependent directly on phytoplankton-based food chains.

In the Late Cretaceous, both benthic filter-feeding and deposit-feeding communities were common in outer-shelf, soft-substrate environments, but at the beginning of the Tertiary, deposit-feeding communities became dominant. Although not completely eliminated, the outer-shelf, filter-feeding communities persisted only locally (Jablonski and Bottjer, 1983).

An adequate field test of this theory requires a conformable K/T boundary sequence with well-preserved molluscan faunas and microfaunas so that the full range of feeding types, from suspension-feeders to detritus-feeders and carnivore-scavengers, can be compared in terms of their extinction patterns. The Brazos River, Texas section is one of the most complete K/T sequences (it has an iridium anomaly but a short early Paleocene hiatus) in that it has a full suite of aragonitic and calcitic molluscs and microfaunas (Hansen et al., 1984, 1986).

The patterns of extinction revealed in this section (Hansen et al., 1984) conform with the theory that detritus feeding is a buffer to extinction. Latest Cretaceous molluscan faunas had a diverse array of life habits, dominated by infaunal suspension feeders and including substantial numbers of epifaunal suspension feeders, infaunal deposit feeders, and infaunal and nektic carnivores. The microfauna is represented by a typical Cretaceous planktonic and benthic foraminiferal assemblage, ostracods, and nannofossils. The molluscan, planktonic foraminiferal, and nannofossil communities crashed (over 95% extinction for planktonic foraminiferal species; over 90% extinction for molluscan species) at the K/T boundary, whereas the ostracods experienced a much less severe effect, and the benthic foraminifera actually increased in diversity. Among the molluscs, suspension feeders had the greatest losses, whereas at least one species of nuculanid (the dominant deposit-feeding bivalve family) increased in relative abundance across the boundary. The molluscan assemblage immediately above the K/T contact is dominated by deposit-feeding bivalves and benthic carnivorous gastropods. The one common denominator among most of the disappearing taxa is that they lived and/or fed in the water column.

TERRESTRIAL

Modern terrestrial food chains (Fig. 1B) dependent on living plant material contain mammalian browsers. During the Cretaceous the position of modern browsing mammals was held by herbivorous dinosaurs. Food chains based on detritus feeding include the forest-soil fauna which may extend vertically well above the ground (Wallwork, 1976, p. 24). Forest-soil food chains are based on leaf litter, decaying wood, roots, branches, and fungi. The soil fauna includes protozoans, nematodes, annelids, molluscs, arthropods (including insects but also crustaceans, myriapods, and arachnids), and small mammals (Wallwork, 1976; Kuhnelt, 1976). Carnivorous mammals, which are commonly characterized as being insectivorous, actually feed on most soil fauna groups, and are thus in a system that does not rely directly on living plants.

At the K/T boundary, terrestrial extinctions were concentrated in animals, particularly dinosaurs, in food chains reliant on living plant material. Survivors, notably many mammals, were concentrated in detritus-based food chains.

Among the mammals, eutherians and deltatheridians had the least extinction and seem to have been quite clearly insectivorous (Kielan-Jaworowska et al., 1979a, 1979b). Thus, the most successful survivors among the mammals may have been buffered from extinction by belonging to detritus-based food chains.

Unfortunately, feeding methods of the other groups of latest Cretaceous mammals are much less certain than for the eutherians and deltatheridians. Multituberculates survived the Cretaceous, although with some extinction (Clemens et al., 1981). The multituberculates were probably primarily herbivorous, or in some cases omnivorous, according to Clemens and Kielan-Jaworowska (1979), but Krause (1984) believed that many small multituberculates were typically insectivorous and less herbivorous than previously thought. The latest Cretaceous marsupials included only four genera. The only surviving genus was probably an omnivore, and the feeding methods of the three genera that became extinct are speculative but may have included an herbivore, an omnivore, and a genus specialized in shell crushing (Clemens, 1979).

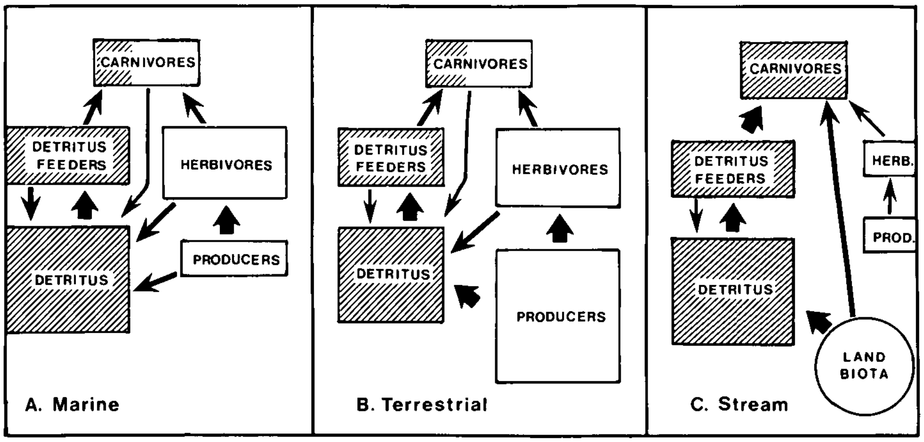

Figure 1. Simplified Eltonian food pyramids and energy flow in three environments. Diagonal-rule pattern indicates categories protected from short-term loss of sunlight by detritus buffering. Categories are assumed to be protected if most input comes from a protected category below. Relative size of standing crop is represented by size of rectangles. Arrows show direction of energy pathways. Weight of arrows indicates relative importance of pathways. A: Although standing crop of marine phytoplankton is small (small producer rectangle), rapid turnover results in high annual production. Carnivores dependent primarily on detritus feeders may have been protected. B: Dinosaurs occupied herbivore category and large-body-size section of carnivore category. Many mammals were small-body-size members of carnivore category, and those dependent on detritus feeders as prey were protected. C: Primary production is small in streams, and most food for animals is supplied from land. Most members of this community were protected.

Thus, mammalian groups that retained primitive insectivorous dentitions and presumably were in detritus-buffered systems survived the extinction. Mammalian extinctions were concentrated in groups that had evolved dental adaptations that removed them from insectivorous diets. At least some extinct groups were in food chains relying directly on living plants.

Fresh-water stream communities (Fig. 1C) are a special case of a detritus-based ecosystem because they derive their food resources primarily from the land (reviewed in Webster, 1983). Primary production is very low in stream communities.

One recurrent puzzle has been that large reptiles such as turtles and enormous crocodiles survived, while large dinosaurs became extinct (Clemens et al., 1981). Animals in fresh-water ecosystems, including crocodiles, champsosaurs, and turtles (Hutchison, 1982), generally survived the extinction. Since fresh-water ecosystems are based on detritus derived from land, they are buffered from extinction in this model.

Thus, the hypothesis is supported for terrestrial ecosystems. Animals, notably dinosaurs, in food chains dependent on living plant material became extinct. Surviving animals, such as mammals, lizards, and aquatic forms, were concentrated in detritus-buffered food chains. At the beginning of the Paleocene, herbivore diversity was low because of the loss of the dinosasurs. Fewer communities were based on primary production, and a greater proportion of communities were based on detritus feeding than in the Cretaceous. The spectacular radiation of browsing mammals was still in the future (Krause, 1982; Gingerich, 1984). Condylarths, with dentitions modified for processing living plants, rapidly expanded in the early and especially middle Paleocene (Krause, 1984; Clemens, 1984, personal commun.). This group was diversifying into ecospace vacated by the extinction of herbivorous dinosaurs. Lizards and other reptiles that are not commonly herbivores were a significant part of the Paleocene fauna (Estes, 1970, 1982), and perhaps along with birds, they challenged mammals for dominance.

DISCUSSION

Further rigorous testing of the model presented here is needed, and the model permits such tests. A particularly powerful test would be to examine the pattern of extinction within taxa of animals in which individual species have differing feeding adaptations. For example, in terrestrial environments most lineages of Late Cretaceous lizards survived into the Tertiary. One of the few groups that had severe extinctions was the Polyglyphanodontinae, which had enlarged molariform or polycuspate-spatulate teeth (Estes, 1982). The subfamily was one of the first groups of lizards to evolve omnivorous or herbivorous adaptations (Estes, 1982), which may have moved them out of detritus-based food chains. Similarly, turtles survived the K/T extinction event with very little extinction. Most were in the detritus-buffered aquatic ecosystem. Extinction in turtles was concentrated in the tortoiselike, land-dwelling dermatemydids which were herbivorous (Hutchison and Archibald, 1984) and thus not buffered from extinction.

In summary, the ecologic pattern of extinction at the K/T boundary, in both marine and terrestrial animals, fits the predictions of an impact model in which photosynthesis was interrupted for several months. Extinction was concentrated in animals dependent on living plant material rather than animals dependent on detritus. That a significant proportion of the extinctions across the wide spectrum of marine to terrestrial environments (Steele, 1985) fits the predictions of the model is strong evidence in support of the impact hypothesis.

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