

## K-Pg extinction patterns in marine and freshwater environments: The impact winter model

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[1] The Chicxulub asteroid impact produced massive extinction in terrestrial environments most likely through an intense heat pulse and subsequent widespread fires. Aquatic environments were shielded from this heat and fire but nevertheless showed massive extinction in marine environments and, for reasons unexplained, far less extinction in freshwater environments. Extinction in marine environments resulted from the effects of an “impact winter” caused by dust and smoke in the atmosphere that extinguished sunlight at the Earth's surface for a period of months to years. The resulting cessation of photosynthesis caused a globally extensive extinction of phytoplankton taxa. Because aquatic ecosystems, unlike terrestrial environments, are strongly dependent on daily photosynthetic output by autotrophs, loss of phytoplankton likely caused catastrophic mortality and extinction in aquatic ecosystems. Other potential causes of mortality in aquatic ecosystems include lower ambient temperatures and anoxia due to the lack of photosynthetic oxygen. Inland waters, although probably subject to high mortality, showed lower proportionate extinction than marine environments probably because of the greater potential among the freshwater taxa for dormancy, the greater efficiency of reaeration by rapid flow to offset oxygen demand, abundant thermal refugia fed by groundwater at moderate temperatures, and preadaptation of freshwater taxa to a great degree of environmental variability. In addition, detrital feeders appear to have had low extinction rates in either marine or freshwater environments, but again freshwater taxa would have been favored by higher renewal rates of detrital organic matter as a result of their direct hydrologic contact with soil.

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### 1. Introduction

[2] The K-Pg extinction that followed the Chicxulub impact was one of the five great Phanerozoic marine mass extinctions in terms of both loss of genera and the restructuring of communities [Sepkoski, 2002; Rohde and Muller, 2005; McGhee *et al.*, 2004, 2013; Sheehan *et al.*, 1996]. A heat pulse and subsequent fires appear to explain terrestrial species extinctions following the asteroid impact [Melosh *et al.*, 1990; Wolbach *et al.*, 1988; Robertson *et al.*, 2004; 2013]. Those heat effects would have had little direct effect on aquatic environments because water would

provide shelter from the impact-generated heat pulse, but the subsequent “impact winter” is another matter altogether. As outlined by Alvarez *et al.* [1980], Milne and McKay [1982], Toon *et al.* [1982] and Toon *et al.* [1997], among others, the atmosphere after the impact would have had high concentrations of dust, soot, and sulfate aerosols for at least six months or possibly longer in the case of sulfates [Pope *et al.*, 1994; Pierazzo *et al.*, 2003]. This particulate matter in the atmosphere would have caused an “impact winter” with cold and darkness lasting for a period of months to years, which could have led to extinctions in aquatic environments by eliminating photosynthesis. Marine communities did show extensive extinction (approximately 50% of genera in the fossil records) [D'Hondt, 2006], but the record for freshwater biota shows low extinction rates [Sheehan and Fastovsky, 1992]. The difference in extinction rates between marine and freshwater ecosystems can be explained by differential effects of an impact winter on marine and freshwater biota, which differ in potential for use of detrital foods [Sheehan and Fastovsky, 1992; Sheehan *et al.*, 1996], as well as ecological resilience and availability of refugia, as described here. Freshwater communities were preadapted to rapidly changing environments because many of their constituent organisms were adapted to a greater degree of environmental variability than is typical of marine communities.

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[3] The catastrophic effects of heat pulse and fires on terrestrial environments in the hours to days following the Chicxulub impact were the main focus of our previous papers [Robertson *et al.*, 2004; 2013], but it is easy to show that aquatic environments provided more than adequate shelter from those effects. The calculation of Goldin and Melosh [2009, p. 1135] indicates that the downward directed radiant energy from the reentrant ejecta had an intensity of 10 kW/m<sup>2</sup> for 20 min or about  $1.2 \times 10^7$  J/m<sup>2</sup>. The specific heat of water is 4.2 J/g/°C, and the heat of vaporization of water is 2260 J/g, so about 2600 J are required to evaporate 1 g of water that is initially at 10°C. Therefore, the energy in Goldin and Melosh's calculation would be sufficient to evaporate about 4600 g of water from each square meter, or a layer of water about 0.5 cm deep. Water is essentially opaque to 1000 K blackbody infrared radiation; therefore, the heating by the incoming radiation would be concentrated in the uppermost few centimeters of water where much of it would be dissipated by evaporation. Because of the high attenuation coefficient of water for infrared radiation, all but the shallowest waters would be strongly shielded from direct thermal effects of the infrared energy burst. Stored heat could be mixed into the water column, which would raise the environmental temperature. Even so, the likelihood that waters of moderate to great depth would reach lethal temperatures for aquatic life is very low. In addition, refugia including groundwater seepage, benthic habitats, or hypolimnetic zones would shield aquatic life from mortality caused by heat, as would canopy vegetation.

## 2. Extinction in Aquatic Ecosystems

### 2.1. Marine Extinction

[4] In marine environments, the abundance of calcium carbonate microfossils produced by nanoplankton (primarily the coccolithophores) and planktonic foraminifera crashed at the impact boundary. Their abundance remained low throughout the Danian (earliest Pg) [D'Hondt, 2006]. D'Hondt notes that the CaCO<sub>3</sub> fraction of deep-sea sediments did not return to preextinction values for 3–4 Myr. The flux of organic detritus to the sea floor also declined abruptly and remained low for about 3 Myr after the impact [Zachos *et al.*, 1989; Coxall *et al.*, 2006].

[5] Marine extinction was high throughout food webs supported by plankton at the K-Pg boundary. Ammonites were the most diverse and abundant plankton feeders [Kruta *et al.*, 2011] before impact and they, along with the giant mosasaurs and sauropterygians (plesiosaurs and pliosaurs) that fed on them, became extinct. The subsequent Paleogene expansion of fishes into niches once occupied by ammonites is strikingly similar to the change from dinosaur- to mammal-dominated food chains on land. Similarly, large marine mammals eventually replaced the extinct marine reptiles and large planktivorous bony fishes.

[6] For the marine benthos, several studies have shown that postextinction faunas were greatly reduced in abundance, but the survivors did not consistently have traits such as large population sizes or species-rich clades that commonly are thought to reduce extinction rates [Lockwood, 2003; Jablonski, 2008]. One factor that appears to have enhanced the likelihood of survival during all of the

five primary mass extinctions was the wide geographic distribution of clades [Jablonski, 2008; Wendler and Willems, 2002].

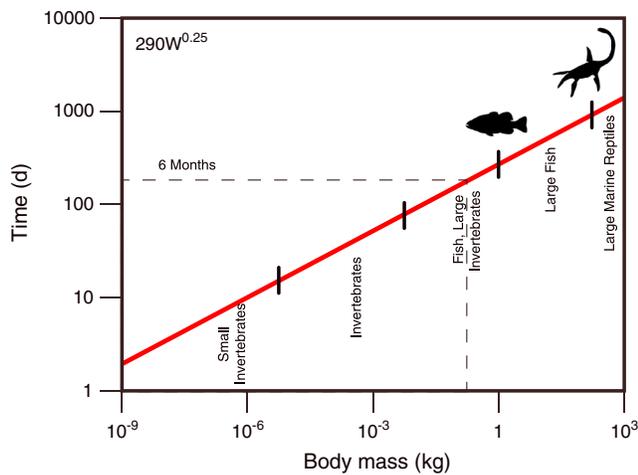
[7] Regional studies of the marine benthos show massive declines in diversity, abundance, and size of individuals. Gallagher [1991, 2003] provides a good example of changes in the benthos in New Jersey. Preextinction communities contained abundant and diverse bivalves, gastropods, ammonites, sharks, and bony fishes. A few mosasaurs, crocodiles, and brachiopods were present. Danian deposits above the extinction event show a less diverse, less abundant fauna of much smaller size than previously. The benthic faunal fossil record consists of a single species each of sponge, brachiopod, and solitary coral. The only predators in the Danian record are rare sharks and crocodiles.

[8] Studies in many other regions reveal similarly degraded benthic assemblages [Aberhan *et al.*, 2007; Stillwell, 2003]. At any given locale, the record shows diversity of higher-level taxa to be much lower after than before the extinction and lower than the general survival of the taxa across local settings. Many groups survived only in small portions of their geographic ranges and only later expanded. Recovery of local diversity through immigration of taxa that survived in other regions took much of the Danian, indicating that the refugia where survival occurred were small and probably widely dispersed.

### 2.2. Freshwater Extinction

[9] Studies of patterns of survival across the K-Pg boundary suggest that nearly all freshwater families had only minor extinction, in contrast with terrestrial or marine families. Cartilaginous fish lost about 20% of families and teleost (bony) fish lost about 10% of families [Patterson, 1993; MacLeod *et al.*, 1997]. Amphibians had little if any extinction at the family level [MacLeod *et al.*, 1997]. All six late Cretaceous turtle families survived [Novacek, 1999]. Of 10 Maastrichtian crocodylian families, five marine families became extinct, four freshwater families survived, and no freshwater species went extinct. One family in which juveniles lived in fresh water also survived the K-Pg boundary. A single family of Choristodera (including the champsosaurs) was present in the late Maastrichtian and it survived into the Miocene [MacLeod *et al.*, 1997]. No major group for which documentation is available had extinction that approached what was common in marine and terrestrial environments.

[10] The only well-studied fossil record for freshwater ecosystems across the K-Pg boundary is in western North America, where Archibald and Bryant [1990] assembled a database of all taxa in the Latest Cretaceous Hell Creek Formation and the overlying Paleogene Tullock Formation. Sheehan and Fastovsky [1992], using the database, found freshwater extinction rates of about 10% of species, while Archibald [1993] found a rate of 22%, in contrast to marine extinction rates of about 50% with total elimination of groups such as mosasaurs, sauropterygians (plesiosaurs and pliosaurs), ammonites, and heterohelicid planktonic foraminifera [D'Hondt, 2006, p 295]. Differences in the percentage of extinction between Sheehan and Fastovsky [1992] and Archibald [1993] revolved largely around criteria for deciding if various taxa became extinct, but after 15 years of additional research the low levels of extinction



**Figure 1.** Allometric relationship between body size and time to death by starvation for multicellular poikilotherms in the absence of food (red, drawn from the equation of Peters [1983, p. 42]). Names of various types of organisms are shown as an indication of body size.

have been confirmed [Archibald, 2011]. Using another criterion for freshwater extinction, Carter [2009] examined amphibians from the Hell Creek Formation and, using them because they are exceptionally sensitive indicators of environmental change, found only “muted” change across the K-Pg boundary.

[11] High-proportional survival of freshwater taxa does not necessarily indicate an absence of impact-related mortality in inland waters. The difference in relative extinction rates between marine and freshwater environments could be explained by a relatively small difference in the probability of individual survival because a small number of surviving individuals could propagate a surviving species. In other words, the extent of mortality for individual organisms in inland waters could have been only slightly less complete than in marine environments and still be consistent with differential probability of survival for marine and inland water taxa.

### 3. Mechanisms of Marine and Freshwater Survival and Extinction

[12] Three stresses associated with impact can be identified for marine and freshwater environments: (1) starvation caused by cessation of photosynthesis, (2) reduction or loss of dissolved oxygen, and (3) low temperatures. The potential of these factors to cause extinction differs for marine and freshwater environments (Figure 2).

[13] Blockage of sunlight by atmospheric particles following the Chicxulub impact was first proposed by Alvarez et al. [1980]. Toon et al. [1982] showed that particles from the impact would have eliminated sunlight at the Earth's surface for several months. Composition of the sunlight-blocking particles and gases is still under study [Pope et al., 1994; Toon et al., 1997; Schulte et al., 2010]. Even though marine and freshwater environments are both critically dependent on the near term productivity of algae, freshwater organisms may be inherently better able to survive the cessation of photosynthesis.

#### 3.1. Tolerance of Starvation

[14] Suppression of photosynthesis following impact and slow recovery of photosynthesis implicate starvation as a major cause of marine extinctions [Milne and Mckay, 1982]. Marine extinction rates were greater among pelagic than benthic organisms, suggesting greater resistance to starvation among the benthos [Sheehan et al., 1996; D'Hondt, 2006], at least partly because the food chain of pelagic organisms is almost entirely reliant on living phytoplankton, whereas on the ocean floor, dead biomass is consumed by detritivores, which are then consumed in the detritus-based food chain. Kiessling and Baron-Szabo [2004] found that photosymbiotic (zooxanthellate) corals were significantly more affected by the extinction than azooxanthellate corals, as would be expected if cessation of photosynthesis were a major cause of starvation.

[15] The ability of multicellular poikilotherms (“cold-blooded” organisms) to survive at a given temperature without nutrition is a function of body size (Figure 1: Peters [1983, p. 42]; original data gathered by Hemmingsen [1960]). Small invertebrates (10  $\mu$ g to 10 mg), including zooplankton and some benthic invertebrates, have survival times of 8 to 20 days. Large invertebrates (100 g up to 1 kg) such as large crustaceans, large mussels, and numerous other macrobenthic forms have survival times extending beyond the estimated lower boundary of the interval after which recovery of photosynthesis would have been possible (6 months). The largest poikilotherms, which include exceptionally large invertebrates, large fishes, and aquatic reptiles extending up to the very large Cretaceous reptiles [Bardet, 1994], could have withstood 1 to nearly 3 years without food. However, Bernard et al. [2010] have shown that the fast free-swimming pliosaurs and mosasaurs may have been thermoregulators with higher metabolic rates, making them more susceptible to starvation.

[16] In freshwater, large reptiles (crocodilians, choristodires, large turtles) could have been large enough to fend off extinction by starvation resistance. Smaller vertebrates, including fishes and amphibians less than about a kilogram in size, would have to resort to other survival mechanisms, especially dormancy (see the following section).

[17] Starvation resistance related to size may have promoted survival in some groups of marine organisms. For example, brachiopods, which increased in relative abundance across the boundary in New Jersey and Denmark, can survive for months without food [Rhodes and Thayer, 1991; Gallagher, 1991; Aberhan et al., 2007; James et al., 1992]. Brachiopods feed on phytoplankton, bacteria, organic detritus, and organic molecules adsorbed onto inorganic particles [James et al., 1992; Peck et al., 1997]. They may have been adapted to life in environments where food is scarce, as indicated by their dominance in the marine benthos during the Paleozoic when primary production was low [Bambach, 1993]. Brachiopods had declined during the Mesozoic and were replaced by other organisms as primary production increased.

[18] Having successful ways of avoiding extinction, however, did not guarantee long-term success. Although brachiopods may have expanded briefly in some places following the extinction, their success was short lived possibly because the increasing food supply allowed a rapid increase in predation in the Paleogene when many attached

filter feeders declined while mobile filter feeders expanded [Huntley and Kowalewski, 2007; Bush et al., 2007; Kelly and Hansen, 2006]. Other preferential survivors, for example, those that benefited from deposit feeding during the extinction, such as bivalves and echinoids, expanded during the massive reorganization following the extinction, in this case, probably partly because their infaunal habitat provided refuge from increased surface predation in the Paleogene [Bambach, 2002; Huntley and Kowalewski, 2007; Sessa et al., 2012].

[19] Unicells, including algae and protozoa, also show an allometric relationship based on body mass for projected mortality in the absence of nutrition (light in the case of algae, organic particles in the case of protozoans). The relationship differs from the one for multicellular poikilotherms in that unicells are more efficient in their use of energy. Thus, a median survival time for a unicell of 10 ng mass might be as high as 7 days [Peters, 1983]. Thus, starvation of unicells due to loss of sunlight over an interval of several months would involve tens of generations unless they were capable of dormancy.

[20] In the marine realm, loss of sunlight for months had an immediate effect on phytoplankton, but phytoplankton production recovered quickly thereafter [D'Hondt et al., 1998; Coxall et al., 2006]. Unlike on land, where most rooted vegetation has generation times from a year to decades, phytoplankton have biomass turnover times measured in days. At the base of the food chain, zooplankton herbivores that were poorly adapted for dormancy would have been at risk for extinction. For example, Milne and McKay [1982] estimate that zooplankton would have died of starvation within 4 months following impact (see also Figure 1). The ripple of extinction caused by darkness-induced starvation would have extended up the food chain to the margin of starvation tolerance as indicated in Figure 1. Darkness for 3 to 6 months would have induced starvation of organisms up to about 100 g (about 10 cm long) in the absence of any behavioral (e.g., detrital feeding) or physiological (e.g., dormancy) hedge against starvation. Pierazzo et al. [2003] suggest photosynthesis might have been suppressed for as long as 2 years by atmospheric sulfates. Starvation thresholds could have been extended by low temperatures if the temperatures themselves were tolerable (see below).

[21] Following a wave of phytoplankton loss caused by the short-term effects of darkness approaching 2 years, large animals would still have been protected by their body size (Figure 1), provided other conditions were suitable. Until photosynthesis resumed, a recovery of the drastically reduced zooplankton could not begin. When sunlight returned to levels that supported photosynthesis, phytoplankton biomass recovered rapidly [D'Hondt, 2006]. However, higher in the food web, each step upward required the step below to first reestablish their biomass. Recovery of the lowest animals in the marine food chain, the zooplankton, appears to have been significantly delayed, and the absence of abundant zooplankton may have increased the interval of starvation higher in the food web, thus explaining why large marine organisms also succumbed. In other words, the complete food webs would not have regenerated immediately upon the return of sunlight. Thus, the immediate effects of the impact explain the rapid loss followed by recovery of phytoplankton biomass,

but the slow recovery of zooplankton may have further delayed recovery of all other animals in the ecosystem.

[22] The large size of the Maastrichtian planktivorous fish (>5 m long and >400 kg) along with the morphology of their feeding structures suggest that as in modern planktivorous mammals, they probably fed on zooplankton and krill, but not phytoplankton [Friedman et al., 2010; Friedman, 2012]. Thus, these giant planktivores were dependent on recovery of only zooplankton and krill to survive, not recovery of the many tiers of animals upon which other giant animals were dependent. Their large size could have allowed them to survive well over 2 years of impact winter (Figure 1) and live into the time when sunlight returned and phytoplankton rebounded in surficial waters. However, their extinction provides another indication that it was the slow recovery of zooplankton and krill that feed on the phytoplankton that were unable to provide sufficient biomass to support these filter feeders following the impact winter.

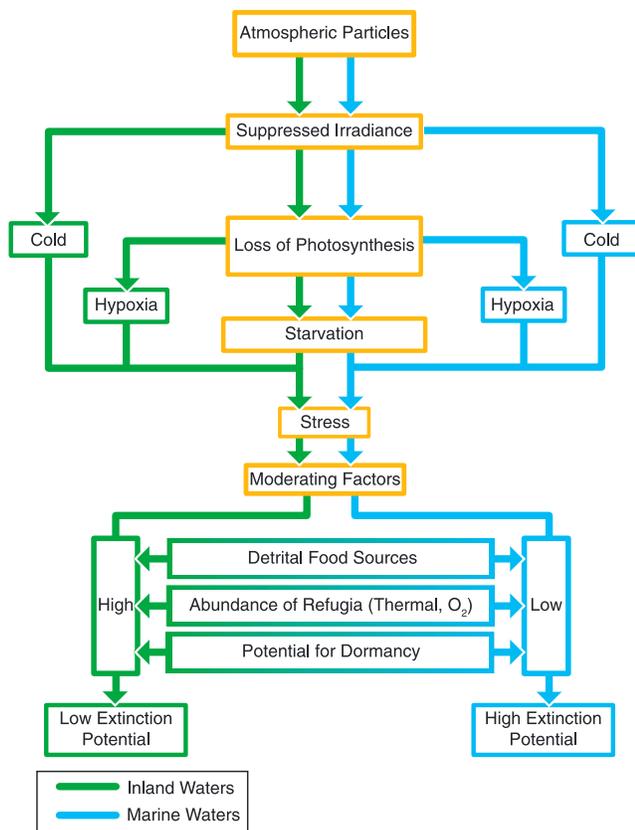
[23] The ammonites were among of the most significant groups of animals lost during the K-Pg extinction. And among the ammonites, the aptychophorans were specialized for feeding on zooplankton, and there again loss of zooplankton is a likely cause of their extinction [Kruta, et al., 2011]. The largest aptychophoran ammonites lived in the late Maastrichtian [Olivero and Zinsmeister, 1989] and had a body chamber about 1.1 m long, with an estimated size of the living animal of about 6 kg, placing it near the 2 year limit for starvation survival (Figure 1).

[24] All ammonites also had planktotrophic larvae which, because they needed to feed on phytoplankton and zooplankton, could have been affected by loss of zooplankton. Non-ptychophoran ammonites fed on animals larger than zooplankton, as did the related nautiloid cephalopods, which survived. The important difference may have been that nautiloid cephalopods had nonplanktotrophic larvae which carried a yolk sack that provided the larvae with a self-contained nutritional source [Valentine and Jablonski, 1986; Sheehan et al., 1996]. Similarly, some spatangoid echinoids evolved nonplanktotrophic larvae, and although both groups survived into the Danian, spatangoids with nonplanktotrophic larvae had less severe extinction [Cunningham and Abt, 2009].

[25] Regeneration of detectable populations was much more rapid for inland waters. The fossil record in North Dakota includes submerged leaf deposits of wetland and stream margin plants, turtles, fish, crocodylians, and re-deposited mammals in stream and pond deposits within 1 to 3 m above the impact layer [Bercovici et al., 2008, 2009; Johnson, 2002; Labandeira et al., 2002; Hunter et al., 2003]. This indicates rapid recovery of the freshwater biota. Large poikilotherms in inland waters (e.g., crocodylians and even filter feeding paddle fish that still survive in Montana today) evidently benefited from partial recovery of production that may have been underway on time scales of months after sunlight returned.

### 3.2. Dormancy

[26] Starvation could have had radically different effects on marine and freshwater ecosystems in that freshwater organisms are more likely to have dormant stages. Dormancy occurs among bacteria in all environments [Madsen, 2008]; it is also common but not universal among



**Figure 2.** Diagram of contrasts between freshwater and marine environments for factors potentially causing extinction in aquatic environments after the Chicxulub impact.

algae [Reynolds, 2006], protozoans, and small invertebrates [Hand, 1991; Caceres, 1997]. Dormancy can be explained evolutionarily as a response to environmental instability, which is a strong selective factor in inland waters. Dormancy likely was a major factor preventing sustained collapse of food webs in inland waters, but was less important in marine environments.

[27] Some important taxa of marine environments are capable of dormancy. Their selective survival is evidence of the importance of dormancy in general. Preferentially surviving marine plankton, such as dinoflagellates, commonly have the ability to form cysts and resting stages [Brinkhuis *et al.*, 1998; Kitchell *et al.*, 1986; Gedl, 2004; Wendler and Willems, 2002]. Plankton such as foraminifera and coccolithophores commonly lack cysts or resting stages; these had the highest extinction rates among the fossilized marine plankton.

### 3.3. Detrital Feeding and Dissolved Organic Matter

[28] Benthic communities rely heavily on the phytoplankton in both marine and freshwater environments. Some benthic species are able to use detritus derived from phytoplankton (with attached bacteria) as an alternative to living phytoplankton cells. For these taxa, loss of living phytoplankton might not have been an immediate threat, although exhaustion of such detritus could be expected over a matter of months without renewal of photosynthesis. Sheehan and Hansen [1986] and Arthur *et al.* [1987] propose that detritus-feeding

marine organisms were less susceptible than other organisms to end-Cretaceous extinction. Hansen *et al.* [2004] note that upper Cretaceous sediments in Texas contain a diverse (approximately 40 species) molluscan fauna dominated by suspension feeders and that the earliest Paleocene sediments contain an impoverished fauna dominated by deposit (bottom) feeders. Smith and Jeffery [1998] and Jeffery [2001] found that omnivorous fine particle deposit feeders among the echinoids were most likely to survive. Lockwood [2003] assembled data on bivalves across the boundary in the Atlantic coastal plain and found that all deposit feeding bivalves survived while other bivalves (carnivores and suspension feeders) showed 38 to 58% extinction of species. Stillwell [2003] found a similar pattern in the southern hemisphere bivalves. Many benthic foraminifera feed on detritus (nonliving organic particles) [Lipps, 1983], and others may have been able to switch from dependence on living biomass.

[29] Aquatic ecosystems also contain dissolved organic matter. Although this potential source of energy is strongly dispersed ( $<1$  mg/L in oceans, 1–20 mg/L in inland waters) [Thurman, 1985], it supports a microbial component of aquatic food webs. Eukaryotic organisms, in contrast to bacteria, are unable to take up sufficient amounts of dissolved organic matter to support metabolism. Bacteria growing on dissolved organic matter, when consumed by particle feeders such as flagellates or certain filter-feeding invertebrates, provide a link between otherwise inaccessible dissolved organic carbon and the broader food web, which is largely supported by aquatic photosynthetic output or to some extent by terrestrial organic matter (in nearshore or inland waters). This connection is referred to as the “microbial loop” in that dissolved organic carbon finds its way through microbes back to the main autotrophically supported part of the food web, which in turn produces more dissolved organic carbon [Fenchel, 2008].

[30] Although the microbial loop is a prospective source of support for organisms that can capture bacteria (protozoans, some autotrophic flagellates, and some multicellular filter feeders such as brachiopods), the efficiency of energy transfer from one consumer level to the next (typically 5–15%) dictates that the multiple transfers necessary to bring microbially derived energy to a high-level consumer could not account for much metabolic support at the upper levels of the food web [Pace and Orcutt, 1981].

[31] Perhaps the most interesting feature of dissolved and particulate organic matter in the absence of aquatic photosynthesis is its renewability from an external source (terrestrial environments), even after impact. While the energy burst of the impact and subsequent fires could have burned all exposed carbon, soils contain very large inventories of subsurface organic carbon that can be transported in particulate or dissolved form to aquatic ecosystems. This source is mostly available to inland waters, although it does reach nearshore portions of marine waters. The importance of the source for oceans is compromised, however, by its probable unavailability to many kinds of aquatic organisms that are not found in the nearshore environment. Beneficial effects of this source of organic matter would likely favor survival of freshwater taxa over marine taxa.

[32] Proximity of some marine vertebrates to the successful freshwater biota may have provided a food source that

promoted survival. Extinction of sharks at the K-Pg increases along a gradual gradient from no extinction in freshwater to 45% in the open ocean [Kriwet and Benton, 2004]. A similar pattern is found among marine reptiles surviving into the Danian where coastal forms, including dyrosaurid crocodiles, osteopygid and bothremydid turtles, and paleophid snakes had low extinction compared with open marine forms [Bardet, 1994].

### 3.4. Reduction in Dissolved Oxygen

[33] Suppression of photosynthesis for extended intervals could have had drastic effects on concentrations of dissolved oxygen in some aquatic environments. Most eukaryotic aquatic organisms (invertebrates, fish) [United States Environmental Protection Agency, 1986] require minimum concentrations of oxygen ranging from 3 mg/L (acute) to 6 mg/L (chronic). Saturation concentrations of dissolved oxygen generally are between 6 and 12 mg/L, depending on temperature, elevation, and salinity. The oxygen concentration in an aquatic environment at any given moment is explained largely by the balance between respiration, which removes oxygen, and a combination of photosynthesis and reaeration (gas exchange at the atmosphere-water interface), both of which provide oxygen. In fertile waters that contain abundant organic matter, the photosynthetic source is critical because high respiration rates are capable of drawing down oxygen to low concentrations in the absence of photosynthesis. In environments that have low supplies of organic matter, reaeration alone often is sufficient to maintain oxygen supplies sufficient to support aquatic life.

[34] Molecular biomarkers preserved in sedimentary organic matter provide evidence of anoxia immediately above the boundary in El Kef, Morocco, and Geulhemmerber, Netherlands [Yamamoto et al., 1996], consistent with a major loss of photosynthetic oxygen at that time. Only a limited number of marine organisms, including brachiopods [Peck et al., 1997], have evolved the ability to survive short intervals of anoxia or sustained life in anoxic or hypoxic environments. Thus, anoxia may explain some losses of marine taxa, although complete anoxia of oceans is unlikely because of low respiratory demand in relation to high oxygen inventory in deep waters.

[35] Elimination of the photosynthetic oxygen source as a byproduct of atmospheric shading would be most likely to cause critical deficiency of oxygen in waters that have weak reaeration rates caused by stagnation combined with high amounts of organic matter per unit water volume or high sediment surface area per unit water volume. Many streams and rivers reaerate efficiently, but ice cover and low flow caused by suppression of runoff at temperatures below freezing could have impaired reaeration following impact. Shallow lakes, wetlands, and nearshore marine environments are the most likely places for prolonged and extreme oxygen deficiency in the absence of photosynthesis. It is common for shallow lakes and wetlands to become anoxic under ice because of low or negligible photosynthetic rates; many of the organisms within these environments are adapted to periodic anoxia, which may have served them well during this crisis. Also, oxic refugia (e.g., oxygenated inflows) often prevent complete mortality under anoxia, in which case anoxia may cause mortality without causing extinction.

Such refugia are predominant in inland waters, and thus would tend to favor freshwater over marine taxa.

[36] Low solar irradiance after impact may have led to loss of thermal structure in oceans, which would have allowed more extensive deep mixing than before impact. Deep waters of oceans are oxygenated, however, so deeper mixing would not have caused anoxia. Respiration, augmented by mortality of organisms dependent on photosynthesis, would have caused depletion of oxygen not offset by photosynthesis, but maximum depletion would have been small because of the small amount of biomass per unit volume in most of the ocean surface waters. Concentrations of total organic carbon (TOC) in offshore marine waters average about 50  $\mu\text{mol/L}$ , or 0.6 mg/L C. The origin of this TOC is marine photosynthesis. The ratio of particulate organic carbon (POC) to dissolved organic carbon (DOC) is approximately 40:1. The POC component includes both living organisms (e.g., phytoplankton, bacteria) plus inorganic debris (detritus). The origin of both DOC and POC in offshore regions is photosynthesis in the upper 150 m of the water column, but both POC and DOC are exported to deeper waters. [Hansell and Carlson, 2001].

[37] Given 0.6 mg/L TOC and the conservative assumption that all of this organic material would decay in several days, the total resulting oxygen demand would be approximately 1.6 mg/L. Marine waters hold an amount of oxygen reflecting primarily water temperature, but 7.5 mg/L can be taken as a representative concentration. Thus, an impact winter might result in depletion of dissolved oxygen to approximately 6 mg/L. The depletion process, however, would be offset by reaeration, which supplies oxygen from the atmosphere to the ocean surface as long as the surface is subsaturated. It seems unlikely that oxygen concentrations would move below 6 mg/L, a concentration that is unlikely to be physiologically challenging to marine organisms.

### 3.5. Low Temperature

[38] Cooling caused by atmospheric particles probably would have been sufficiently extreme to account for extensive snow and ice cover on terrestrial and inland water surfaces [Toon et al., 1997]. The depression of freezing point caused by salinity in seawater is only about 2°C at current ocean salinities, but the generally greater depth of marine waters and vigorous horizontal exchange of nearshore waters with offshore waters would have acted against formation of ice cover or severe depression of marine temperatures; inland waters would have been most vulnerable to thermal stress. Robock et al.'s [2007] climate simulations for soot in the atmosphere (about 0.1% of that which followed the K-Pg) [Robertson et al., 2013] impact do show sea ice expansion (assuming current climate initial conditions), but only at high latitudes.

[39] Because the late Cretaceous climate was warm [Coxall et al., 2006], a major challenge for aquatic organisms, especially in inland waters, may have been the persistence of temperatures well below the temperature range at which organisms of this period had evolved. Temperatures below the adaptive range of life for large organisms may have compromised their ability to move or maintain physiological functions. Thus, although the metabolic rates of large organisms might be consistent with

their survival in the absence of food over one or even more years of complete darkness, temperatures below the adaptive range might well have caused the mortality of many organisms, including air breathers, through prolonged impairment of essential physiological functions. Brachiopods provide an example of organisms with mitigating physiology. During the Paleozoic, brachiopods were among the most abundant marine benthic organisms and were common from the tropics to the poles. During the ascent of the modern marine fauna, brachiopods became a minor component of the biota, and they retreated to primarily coldwater regions. Adaptations to cold may have enhanced their survival during the impact winter. *Cunningham and Abt* [2009] suggest that during the latest Cretaceous, some spatangoid echinoids evolved adaptations to cool temperatures that may have preadapted them for the impact winter.

[40] One special characteristic of inland waters that probably had particular significance in preventing extinction caused by prolonged cold is the presence of thermal refugia in the drainage networks of inland waters. Refugia derive not only from geothermal waters, but also from perennially emerging groundwater. Groundwater originating from the upper aquifers of watersheds generally has a temperature close to the mean ambient air temperature at depths of 3 m or more below the soil surface [*Brady and Weil*, 1996]. Thus, the inland water fauna may have escaped extinction partly due to presence of thermal refugia that are common in inland waters but rare and even potentially lethal (as fresh water) in the marine environment. Therefore, although low atmospheric temperatures would have been generally unfavorable to freshwater organisms, the presence of thermal refugia would have ameliorated this threat. It might be thought that the heat pulse and fires that followed the impact [*Robertson et al.*, 2004; 2013] might heat up freshwater and eliminate the effects of cold, but the calculation in the introduction shows that only the top few centimeters or so of bodies of water would be affected by the heat. That minimal effect would be completely dissipated in the weeks to months before the impact winter took hold, after which the effects of thermal refugia would come into play.

#### 4. Conclusions

[41] Atmospheric particles consisting of dust, soot, and sulfate aerosols were sufficiently abundant following the Chicxulub impact to suppress or even eliminate photosynthesis in both marine and freshwater environments. Absence of autotrophic organic carbon production must have stressed food webs in both freshwater and marine environments. Even so, the amount of extinction indicated by the fossil record was far greater in the marine environment than in fresh waters. Reasonable explanations of the differences in extinction rates between these two environments require consideration of freshwater-marine contrasts in environmental features and in the adaptive characteristics of resident organisms.

[42] Starvation (in the broad sense, applicable to both autotrophs and heterotrophs) is the most obvious stress that resulted from lack of solar irradiance over extended intervals. Body size could provide an innate resistance to starvation, but estimates of the duration of the impact winter (6 months to 2 years) put all but the largest cold-blooded

organisms in either marine or freshwater environments within the range of expected starvation for organisms that lack specialized defensive responses to starvation.

[43] Absence of new photosynthate raises the question of alternate food sources not dependent in the short term on photosynthesis. In both marine and freshwater environments, detrital foods can support certain taxa in the absence of photosynthesis. The potential duration of this support is difficult to quantify. While both marine and freshwater environments have abundant detrital carbon, especially associated with sediments, freshwater environments have the advantage of detrital renewal from particulate carbon that moves from soil to flowing waters continuously through hydrologic processes, whereas marine environments lack this feature. Thus, detrital feeders may have been favored during extended intervals of darkness in inland waters as contrasted with marine waters.

[44] Starvation also can be offset by dormancy. Because dormancy is much more common among freshwater than marine organisms, reflecting inherently greater instability in the freshwater environment, dormancy also may have lowered extinction rates in inland waters compared to marine waters.

[45] Other stresses that may arise in the absence of photosynthesis are hypoxia or anoxia and low temperatures. Loss of oxygen sufficient to cause stress is more likely in inland waters than in marine waters because of higher rates of respiration combined with lower water volume in inland waters. Offsetting this advantage would be the extensive presence of refugia in inland waters caused by the presence of abundant, rapidly flowing waters that re-aerate efficiently, and thus supply oxygen at a rate that more than offsets respiration at many locations. Oxygenated inflows to standing water also would provide refugia in waters with little to no oxygen. Thus, the prospects for survival of oxygen stress seem greater in fresh waters than in marine waters.

[46] Prolonged low temperatures could impair metabolic function sufficiently to cause mortality of organisms either in marine waters or fresh waters. As in the case of oxygen, thermal stress likely would have been greater in inland waters than in marine waters, but widespread entry of groundwater into surface waters in the freshwater environment would have provided thermal refugia that would offset the greater average thermal stress in inland waters.

[47] Overall, it is likely that the abundance of refugia combined with greater likelihood of adaptation to stressful conditions through dormancy and possibly a greater detrital food supply in inland waters explain lower extinction frequencies in inland waters than in marine waters. Mortality within all taxa may have been equal to or even greater in freshwaters than in marine waters, but the factors that protect some survivors against extinction in the face of considerable general mortality are more evident in the freshwater environment.

[48] The view of aquatic extinction presented here is consistent with the terrestrial extinction mechanism discussed in *Robertson et al.* [2004; 2013]. Two separate and distinct extinctions, terrestrial and marine, were separated in time by a matter of months to years. These extinctions had a single cause (the Chicxulub impact), but two different mechanisms (an impact winter in the marine environment, and largely a heat pulse and subsequent fires

in the terrestrial environment, although an impact winter would also affect the terrestrial environment), and three separate spatial domains (terrestrial, marine, and freshwater); the latter largely avoided a mass extinction. Only when these domains and mechanisms are properly separated does a complete picture of the K-Pg extinction become clear.

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## References

- Aberhan, M., S. Weidemeyer, W. Kiessling, R. A. Scasso, and F. A. Medina (2007), Faunal evidence for reduced productivity and uncoordinated recovery in Southern Hemisphere Cretaceous-Paleogene boundary sections, *Geology*, *35*, 227–230.
- Alvarez, L. W., W. Alvarez, F. Asaro, and H. V. Michel (1980), Extraterrestrial cause for the Cretaceous-Tertiary extinction, *Science*, *208*, 1095–1108.
- Archibald, J. D. (1993), Major extinctions of land-dwelling vertebrates at the Cretaceous-Tertiary boundary, eastern Montana, Comment, *Geology*, *21*, 90–93.
- Archibald, J. D. (2011), *Extinction and Radiation: How the Death of the Dinosaurs Led to the Rise of the Mammals*, 120 pp., Johns Hopkins Univ. Press, Baltimore, Md.
- Archibald, J. D., and L. Bryant (1990), Differential Cretaceous-Tertiary extinctions of non-marine vertebrates: Evidence from northeastern Montana, in *Global Catastrophes in Earth History: An Interdisciplinary Conference on Impacts, Volcanism, and Mass Mortality*, edited by V. L. Sharpton and P. Ward, *Spec. Pap. Geol. Soc. Am.*, *247*, 549–562.
- Arthur, M. A., J. C. Zachos, and D. S. Jones (1987), Primary productivity and the Cretaceous/Tertiary boundary event in the oceans, *Cretaceous Res.*, *8*, 43–54.
- Bambach, R. K. (1993), Seafood through time, *Paleobiology*, *19*, 372–397.
- Bambach, R. K. (2002), Supporting predators: Changes in the global ecosystem inferred from changes in predator diversity, in *The Fossil Record of Predation*, edited by M. Kowalewski and P. H. Kelley, pp. 319–351, Paleontol. Soc., New Haven, Conn.
- Bardet, N. (1994), Extinction events among Mesozoic marine reptiles, *Hist. Biol.*, *7*, 13–324.
- Bercovici, A., J. Wood, and D. Pearson (2008), Detailed palaeontologic and taphonomic techniques to reconstruct an earliest Paleocene fossil flora: An example from southwestern North Dakota, USA, *Rev. Palaeobot. Palynol.*, *151*, 136–146.
- Bercovici, A., D. Pearson, D. Nichols, and J. Wood (2009), Biostratigraphy of selected K/T boundary sections in southwestern North Dakota, USA: Toward a refinement of palynological identification criteria, *Cretaceous Res.*, *30*, 632–658.
- Bernard, A., et al. (2010), Regulation of body temperature by some Mesozoic marine reptiles, *Science*, *328*, 1379–1382.
- Brady, N. C., and R. R. Weil (1996), *The Nature and Properties of Soils*, 11th ed., Prentice Hall, Upper Saddle River, N. J.
- Brinkhuis, H., J. P. Bujak, J. Smit, G. J. M. Versteegh, and H. Visscher (1998), Dinoflagellate-based sea surface temperature reconstructions across the Cretaceous-Tertiary boundary, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, *141*, 67–83.
- Bush, A. M., R. K. Bambach, and G. M. Daley (2007), Changes in theoretical ecospace utilization in marine fossil assemblages between the mid-Paleozoic and late Cenozoic, *Paleobiology*, *33*, 76–97.
- Caceres, C. E. (1997), Dormancy in invertebrates, *Invertebrate Biol.*, *116*(4), 371–383.
- Carter, G. E. (2009), Amphibian paleocommunity dynamics of the Hell Creek Formation in northeastern Montana and the Cretaceous-Tertiary extinction event, in *9th North American Paleontological Convention Abstracts, Sci. Contrib.*, *3*, pp. 331–332, Cincinnati Mus. Cent., Cincinnati, Ohio.
- Coxall, H. K., S. D'Hondt, and J. C. Zachos (2006), Pelagic evolution and environmental recovery after the Cretaceous-Paleogene mass extinction, *Geology*, *34*, 297–300.
- Cunningham, J. A., and C. H. J. Abt (2009), Coordinated shifts to non-planktotrophic development in spatangoid echinoids during the Late Cretaceous, *Biol. Lett.*, *5*, 647–650.
- D'Hondt, S. (2006), Consequences of the Cretaceous/Paleogene mass extinction for marine ecosystems, *Annu. Rev. Ecol. Evol. Syst.*, *36*, 295–317, doi:10.1146/annurev.ecolsys.35.021103.105715.
- D'Hondt, S., P. Donaghay, J. C. Zachos, D. Luttenberg, and M. Lindinger (1998), Organic carbon fluxes and ecological recovery from the Cretaceous-Tertiary mass extinction, *Science*, *282*, 276–289.
- Fenchel, T. (2008), The microbial loop—25 years later, *J. Exp. Mar. Biol. Ecol.*, *366*, 99–103.
- Friedman, M. (2012), Parallel evolutionary trajectories underlie the origin of giant suspension-feeding whales and bony fishes, *Proc. R. Soc. B*, *279*, 944–951.
- Friedman, M., K. Shimada, L. D. Martin, M. J. Everhart, J. Liston, A. Maltese, and M. Triebold (2010), 100-million-year dynasty of giant planktivorous bony fishes in the Mesozoic seas, *Science*, *327*(5968), 990–993, doi:10.1126/science.1184743.
- Gallagher, W. B. (1991), Selective extinction and survival across the Cretaceous/Tertiary boundary in the Northern Atlantic Coastal Plain, *Geology*, *19*, 967–970.
- Gallagher, W. B. (2003), Oligotrophic oceans and minimalist organisms: collapse of the Maastrichtian marine ecosystem and Paleocene recovery in the Cretaceous-Tertiary sequence of New Jersey, *Geol. Mijnbouw*, *82*(3), 225–231.
- Gedl, P. (2004), Dinoflagellate cyst record of the deep-sea Cretaceous-Tertiary boundary at Uzgru, Carpathian Mountains, Czech Republic, *Geol. Soc. Spec. Publ.*, *230*, 257–273.
- Goldin, T. J., and H. J. Melosh (2009), Self-shielding of thermal radiation by Chicxulub impact ejecta: Firestorm or fizzle?, *Geology*, *37*, 1135–1138, doi:10.1130/G30433A.1.
- Hand, S. C. (1991), Metabolic dormancy in aquatic invertebrates, in *Advances in Comparative and Environmental Physiology*, *2*, pp. 1–50, Springer, New York.
- Hansell, D. A., and C. A. Carlson (2001), Marine dissolved organic matter and the carbon cycle, *Oceanography*, *14*(2), 41–49.
- Hansen, T. A., P. H. Kelley, and D. M. Haasl (2004), Paleocological patterns in molluscan extinctions and recoveries: Comparison of the Cretaceous–Paleogene and Eocene–Oligocene extinctions in North America, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, *214*, 233–242.
- Hemmingsen, A. M. (1960), Energy metabolism as related to body size and respiratory surfaces, and its evolution, *Rep.* *9*, pp. 6–110, Steno Mem. Hosp., Copenhagen, Denmark.
- Hunter, J. P., D. A. Pearson, and J. H. Hartman (2003), Additions to the Puercan mammals of North Dakota and a framework for the study of post K/T vertebrate recovery, *J. Vertebr. Paleontol.*, *23*, 64A.
- Huntley, J. W., and M. Kowalewski (2007), Strong coupling of predation intensity and diversity in the Phanerozoic fossil record, *Proc. Natl. Acad. Sci. U. S. A.*, *104*, 15,006–15,010.
- Jablonski, D. (2008), Extinction and the spatial dynamics of biodiversity, *Proc. Natl. Acad. Sci. U. S. A.*, *105*, 11,528–11,535.
- James, M. A., A. D. Ansell, M. J. Collins, G. B. Curry, L. B. Peck, and M. C. Rhodes (1992), Biology of living brachiopods, *Adv. Mar. Biol.*, *28*, 175–387.
- Jeffery, C. H. (2001), Heart urchins at the Cretaceous/Tertiary boundary: A tale of two clades, *Paleobiology*, *27*, 140–158.
- Johnson, K. R. (2002), Megaflora of the Hell Creek and lower Fort Union Formations in the western Dakotas: Vegetational response to climate change, the Cretaceous-Tertiary boundary event, and rapid marine transgression, in *The Hell Creek Formation and the Cretaceous-Tertiary Boundary in the Northern Great Plains: An Integrated Continental Record of the End of the Cretaceous*, edited by J. H. Hartman et al., *Spec. Pap. Geol. Soc. Am.*, *361*, 329–391.
- Kelly, P. H., and T. A. Hansen (2006), Comparisons of class- and lower taxon-level patterns in naticid gastropod predation, Cretaceous to Pleistocene of the U.S. Coastal Plain, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, *236*, 302–320.
- Kiessling, W., and R. C. Baron-Szabo (2004), Extinction and recovery patterns of scleractinian corals at the Cretaceous-Tertiary boundary, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, *214*, 195–223.
- Kitchell, J. A., D. L. Clark, and A. M. Gombos (1986), Biological selectivity of extinction: A link between background and mass extinction, *Palaios*, *1*, 504–511.
- Kriwet, J., and M. J. Benton (2004), Neoselachian (Chondrichthyes, Elasmobranchii) diversity across the Cretaceous-Tertiary boundary, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, *214*, 181–194.
- Kruta, I., N. Landman, I. Rouget, F. Cecca, and P. Tafforeau (2011), The role of ammonites in the Mesozoic marine food web revealed by jaw preservation, *Science*, *331*(6013), 70–72, doi:10.1126/science.1198793.
- Labandeira, C. C., K. R. Johnson, and P. Lang (2002), Preliminary assessment of insect herbivory across the Cretaceous-Tertiary boundary: Major extinction and minimum rebound, in *The Hell Creek Formation and the Cretaceous-Tertiary Boundary in the Northern Great Plains: An Integrated Continental Record of the End of the Cretaceous*, edited

- by J. H. Hartman, K. R. Johnson, and D. J. Nichols, *Spec. Pap. Geol. Soc. Am.*, 361, 297–327.
- Lipps, J. H. (1983), Biotic interactions in benthic foraminifera, in *Biotic Interactions in Recent and Fossil Benthic Communities*, edited by M. J. S. Tevesz and P. L. McCall, pp. 331–376, Plenum, New York.
- Lockwood, R. (2003), Abundance not linked to survival across the end-Cretaceous mass extinction: patterns in North American bivalves, *Natl. Acad. Sci. U. S. A.*, 100, 2478–2482.
- MacLeod, N., et al. (1997), The Cretaceous-Tertiary biotic transition, *J. Geol. Soc.*, 154, 265–292.
- Madsen, E. L. (2008), *Environmental Microbiology, From Genomes to Biogeochemistry*, Blackwell, Oxford, U. K.
- McGhee, G. R., Jr., P. M. Sheehan, D. J. Bottjer, and M. L. Droser (2004), Ecological ranking of Phanerozoic biodiversity crises: Ecological and taxonomic severities are decoupled, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 211, 289–297.
- McGhee, G. R., Jr., M. E. Clapham, P. M. Sheehan, D. J. Bottjer, and M. L. Droser (2013), A new ecological-severity ranking of major Phanerozoic biodiversity crises, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 370, 260–270.
- Melosh, H. J., N. M. Schneider, K. J. Zahnle, and D. Latham (1990), Ignition of global wildfires at the Cretaceous-Tertiary boundary, *Nature*, 343, 251–254.
- Milne, P. H., and C. McKay (1982), Response of marine plankton communities to a global atmospheric darkening, in *Geological Implications of Impacts of Large Asteroids and Comets on the Earth*, pp. 297–303, Geol. Soc. of Am., Boulder, Colo.
- Novacek, M. J. (1999), 100 million years of land vertebrate evolution: The Cretaceous-early Tertiary transition, *Ann. Mo. Bot. Gard.*, 86, 230–258.
- Olivero, E. B., and W. J. Zinsmeister (1989), Large heteromorph ammonites from the Upper Cretaceous of Seymour Island, Antarctica, *J. Paleontol.*, 63, 626–636.
- Pace, M. L., and J. D. Orcutt Jr. (1981), The relative importance of protozoans, rotifers and crustaceans in a freshwater zooplankton community, *Limnol. Oceanogr.*, 26, 822–830.
- Patterson, C. (1993), Osteichthyes: Teleostei, in *The Fossil Record 2*, edited by M. J. Benton, pp. 621–656, Springer, New York.
- Peck, L. S., M. C. Rhodes, G. B. Curry, and A. D. Ansell (1997), Physiology, in *Treatise on Invertebrate Paleontology, Part H, Revised*, edited by A. Williams and 47 others, pp. 213–242, Geol. Soc. of Am., Denver, Colo.
- Peters, R. H. (1983), *The Ecological Implications of Body Size, Cambridge Stud. in Ecol.*, vol. 2, Cambridge Univ. Press, New York.
- Pierazzo, E., A. N. Hahmann, and L. C. Sloan (2003), Chicxulub and climate: Radiative perturbations of impact-produced S-bearing gases, *Astrobiology*, 3, 99–118.
- Pope, K. O., K. H. Baines, A. C. Ocampo, and B. A. Ivanov (1994), Impact winter and the Cretaceous/Tertiary extinctions: Results of a Chicxulub asteroid impact model, *Earth Planet. Sci. Lett.*, 128, 719–725.
- Reynolds, C. S. (2006), *Ecology of Phytoplankton*, Cambridge Univ. Press, Cambridge, U. K.
- Rhodes, M. C., and C. W. Thayer (1991), Mass extinctions: Ecological selectivity and primary production, *Geology*, 19, 877–880.
- Robertson, D. S., M. C. McKenna, O. B. Toon, S. Hope, and J. A. Lillegraven (2004), Survival in the first hours of the Cenozoic, *Geol. Soc. Am. Bull.*, 116, 760–768, doi:10.1120/B25402.1.
- Robertson, D. S., W. M. Lewis, P. M. Sheehan, and O. B. Toon (2013), K/Pg Extinction: Re-evaluation of the heat/fire hypothesis, *J. Geophys. Res.*, 118, 1–8, doi:10.1029/2012JG002118.
- Robock, A., L. Oman, and G. L. Stenchikov (2007), Nuclear winter revisited with a modern climate model and current nuclear arsenals: Still catastrophic consequences, *J. Geophys. Res.*, 112, D13107, doi:10.1029/2006jd008235.
- Rohde, R. A., and R. A. Muller (2005), Cycles in fossil diversity, *Nature*, 434, 208–210.
- Schulte, P., et al. (2010), The Chicxulub asteroid impact and mass extinction at the Cretaceous-Paleogene boundary, *Science*, 327, 1214–1218, doi:10.1126/science.1177265.
- Sepkoski, J. (2002), *A Compendium of Fossil Marine Animal Genera, Bull. of Am. Paleontol.*, vol. 363, edited by D. Jablonski and M. Foote, Paleontol. Res. Inst., Ithaca, N. Y.
- Sessa, J. A., T. J. Bralower, M. E. Patzkowsky, J. C. Handley, and L. C. Ivany (2012), Environmental and biological controls on the diversity and ecology of Late Cretaceous through early Paleogene marine ecosystems in the U.S. Gulf Coastal Plain, *Paleobiology*, 38, 218–239.
- Sheehan, P. M., and D. E. Fastovsky (1992), Major extinctions of land-dwelling vertebrates at the Cretaceous-Tertiary boundary, eastern Montana, *Geology*, 20(6), 556–560.
- Sheehan, P. M., and T. A. Hansen (1986), Detritus feeding as a buffer to extinction at the end of the Cretaceous, *Geology*, 14, 868–870.
- Sheehan, P. M., P. J. Coorrough, and D. E. Fastovsky (1996), Biotic selectivity during the K/T and Late Ordovician extinction events, in *The Cretaceous-Tertiary Event and Other Catastrophes in Earth History*, edited by G. Ryder, D. Fastovsky, and S. Gartner, *Spec. Pap. Geol. Soc. Am.*, 307, 477–489.
- Smith, A. B., and C. H. Jeffery (1998), Selectivity of extinction among sea urchins at the end of the Cretaceous period, *Nature*, 392, 69–71.
- Stillwell, J. D. (2003), Patterns of biodiversity and faunal rebound following the K-T boundary extinction event in Austral Palaeocene molluscan faunas, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 195, 319–356.
- Thurman, E. M. (1985), *Developments in Biogeochemistry: Organic Geochemistry of Natural Waters*, Martin Nijhoff Junk, Dordrecht, Netherlands.
- Toon, O. B., J. P. Pollack, T. P. Ackerman, R. P. Turco, C. P. McKay, and M. S. Liu (1982), Evolution of an impact generated dust cloud and its effects on the atmosphere, in *Geological Implications of Impacts of Large Asteroids and Comets on the Earth*, edited by L. T. Silver and P. H. Schultz, *Spec. Pap. Geol. Soc. Am.*, 190, 187–200.
- Toon, O. B., K. Zahnle, D. Morrison, R. P. Turco, and C. Covey (1997), Environmental perturbations caused by the impacts of asteroids and comets, *Rev. Geophys.*, 35, 41–8.
- United States Environmental Protection Agency (1986), Ambient water quality criteria for dissolved oxygen, oxygen, Rep. EPA 440/5-86-003, Natl. Acad. Sci., Washington, D. C.
- Valentine, J. W., and D. Jablonski (1986), Mass extinctions: Sensitivity of marine larval types, *Natl. Acad. Sci. U. S. A.*, 83, 6912–6914.
- Wendler, J., and H. Willems (2002), Distribution pattern of calcareous dinoflagellate cysts across the Cretaceous-Tertiary boundary (Fish Clay, Stevns Klint, Denmark): Implications for our understanding of species-selective extinction, in *Catastrophic Events and Mass Extinctions: Impacts and Beyond*, edited by C. Koeberl and K. G. MacLeod, *Spec. Pap. Geol. Soc. Am.*, 356, 265–275.
- Wolbach, W. S., I. Gilmour, E. Anders, C. J. Orth, and R. R. Brooks (1988), Global fire at the Cretaceous-Tertiary boundary, *Nature*, 334, 665–669.
- Yamamoto, M., K. Ficken, M. Baas, H.-J. Bosch, and J. W. de Leeuw (1996), Molecular paleontology of the earliest Danian at Geulhemmerberg (the Netherlands), *Geol. Mijnbouw*, 75, 255–267.
- Zachos, J. C., M. A. Arthur, and W. E. Dean (1989), Geochemical evidence for suppression of pelagic marine productivity at the Cretaceous/Tertiary boundary, *Nature*, 337(5), 61–64.