



The palaeoclimatology, palaeoecology and palaeoenvironmental analysis of mass extinction events

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Abstract

Although there is a continuum in magnitude of diversity loss between the smallest and largest biotic crisis, typically most authors refer to the largest five Phanerozoic events as “mass extinctions”. In the past 25 years the study of these mass extinction events has increased dramatically, with most focus being on the Cretaceous–Tertiary (K–T) event, although study of the end-Permian event (in terms of research output) is likely to surpass that of the K–T in the next few years. Many aspects of these events are still debated and there is no common cause or single set of climatic or environmental changes common to these five events, although all are associated with evidence for climatic change. The supposed extinction-causing environmental changes resulting from extraterrestrial impact are, at best, equivocal and are unlikely to have been of sufficient intensity or geographic extent to cause global extinction. The environmental consequences of rapid global warming (such as ocean stagnation, reduced upwelling and loss of surface productivity) are considered to have been particularly detrimental to the biosphere in the geological past. The first phase of the Late Ordovician event is clearly linked to rapid global cooling. Palaeoecological studies have demonstrated that feeding mechanism is a key trait that enhances survival chances, with selective detritivores and omnivores usually faring better than suspension feeders or grazers. This indicates that primary productivity collapse and consequent lack of food supply is a key proximate cause of extinction. Typically, this low productivity state continues for several hundred thousand years and is associated with widespread stunting of marine organisms (the Lilliput effect) and low-biomass ecosystems. Rebuilding of the marine ecosystem is an important process, and a number of models have been constructed that can be used for comparative purposes (e.g., to understand variation in rates of recovery between events, or between different regions within the same event). Understanding the extinction and recovery processes in ancient events, especially those associated with global warming, may be crucial to managing the present biodiversity crisis. Yet, as many aspects of these mass extinction events remain little understood, there is still much work to do.

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1. Introduction

Most of the species that have ever lived on Earth are extinct. Understanding the processes of extinction is therefore crucial to understanding the evolution of the biosphere. In addition, the extinction of certain fossil taxa, and their subsequent replacement by others, also makes possible the biostratigraphic correlation of sedimentary rocks, which was first proposed by William Smith more than 200 years ago and which is still the primary means of correlation and relative dating used today. Finally, an appreciation of the causes and consequences of previous extinction episodes may assist with our management of the present day biodiversity crisis.

Analysis of the fossil record indicates that extinction rates, at species, genus, or higher taxonomic level, have not been constant through time (e.g., Benton, 1995). Episodes of elevated extinction typically occur at or near period or stage boundaries: a consequence of the original biostratigraphic definitions of these time intervals and a desire to place boundaries “where something happened” (e.g., Newell, 1962; McLaren, 1970). During these events there is apparently synchronous, or near synchronous, often rapid, global extinction of

many different animal and/or plant taxa. The largest of these events are referred to as “mass” extinction events, although this is a rather poorly defined term (see discussions in Hallam and Wignall, 1997; Benton, 2003). Most authors accept five such mass extinction events: the Late Ordovician, Late Devonian (Frasnian–Famennian), Late Permian, Late Triassic and end-Cretaceous (K–T) events (e.g., McGhee et al., 2004). However, some have long referred to an episode of “mass extinction” in the Cambrian (e.g., Newell, 1962), whereas others refer to the present day biotic crisis as the “sixth” mass extinction event (e.g., Benton, 2003, p. 284). In terms of the magnitude of diversity loss, a clear continuum exists between the smallest biotic crisis and the largest “mass” extinction event (Raup, 1991). The term “mass” extinction is thus arbitrary and somewhat redundant. Herein, it is used sparingly and only for those five ancient extinction events listed above.

Today, extinction studies encompass a wide spectrum of geological activity, including palaeontological, sedimentological, geochemical, geophysical and stratigraphic analysis, as well as palaeoclimatology and other studies involving numerical (computer) modelling. The aim of this present work is to provide an overview of

some recent advances in mass extinction studies provided by palaeoclimate, palaeoenvironmental and palaeoecological data, and an outline of where such studies may lead us in the near future. Many substantial volumes have been written in recent years detailing the individual events themselves, such as Alvarez (1997), Benton (2003), Erwin (1993), and McGhee (1996). Herein, the focus will be broader, outlining general similarities and differences between the events, rather than providing a detailed description of each.

2. Brief history of mass extinction studies

The earliest representation of the diversity of life through the Phanerozoic, including (possibly) some of

the major mass extinction events, is a figure from Phillips (1860). The general increase of diversity through time is shown, punctuated by a major decrease at the Palaeozoic–Mesozoic boundary and a similarly severe, but more rapid, drop at the Mesozoic–Cenozoic boundary; both are followed by rapid diversity increases. Smaller, temporary, decreases in diversity are shown within the Mesozoic and within the Palaeozoic. Some authors (e.g., Benton, 2003, pp. 47–49) have argued, based the actual text of Phillips (1860), that John Phillips was, in fact, not representing the extinction events nor his view of Phanerozoic diversity, and that the similarity to our present view of the history of life on Earth is purely coincidental. Other commentators (e.g., MacLeod, 2004) feel that the coincidence is too great to ignore,

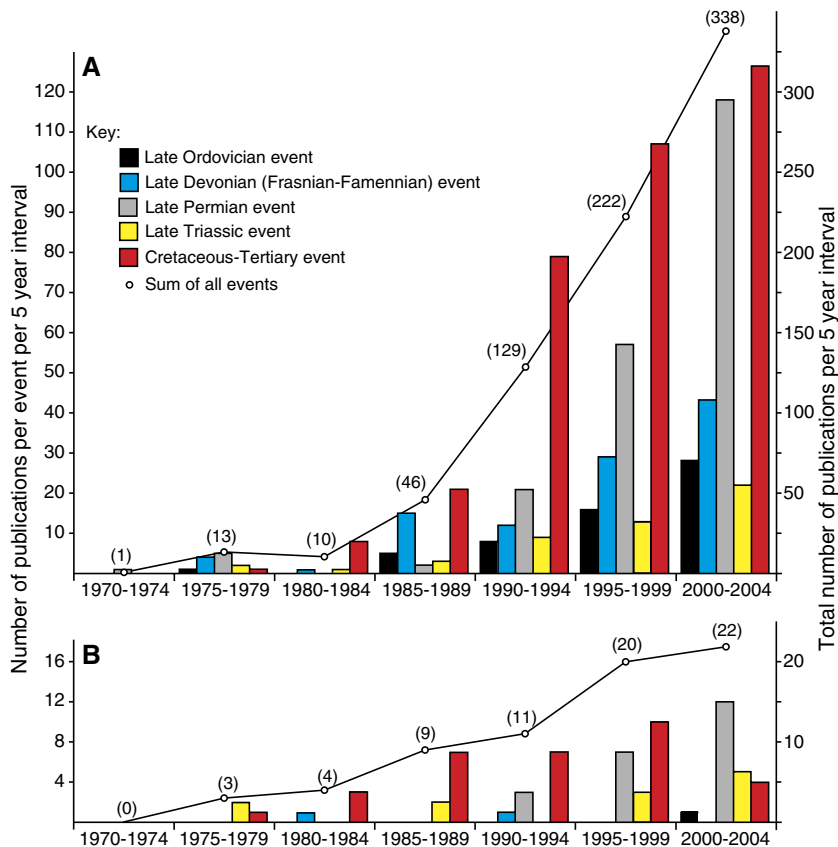


Fig. 1. Scientific interest in the mass extinction events since 1970. Data derives from an analysis of the ISI Web of Science database, and was collected via the Web of Science online search engine. For each interval of 5 years, a search was conducted using the key words <extinction> plus <the geological period in question> (i.e., namely <Ordovician>, <Devonian>, <Permian>, <Triassic>, <Cretaceous>, respectively). Results were then searched manually and papers not pertaining to the event in question were removed. A: the entire dataset. B: the journals *Science* and *Nature* only.

and that there is more to this figure than is detailed in its accompanying text.

Regardless of the true intentions behind the figure of Phillips (1860), the study of mass extinction events largely languished untouched until the 1950s and 60s, with Schindewolf's theories that catastrophic extinction could be caused by peaks in the influx of cosmic radiation (e.g., Schindewolf, 1963). This absence of scientific debate concerning extinction events is usually attributed to the prevalence of Uniformitarianism in the geological sciences, since the publication of Charles Lyell's *Principles of Geology* in the early 1830s (e.g., McLaren, 1970; Pope et al., 1998; Benton, 2003). In particular, both Lyell and Darwin (and most subsequent authors of the late 19th and early 20th centuries) considered that evolutionary change was gradual and that apparent major extinction events, such as the K–T boundary, could only be explained by significant gaps in the fossil record (Pope et al., 1998). Despite a few perceptive comments to the contrary (e.g., McLaren, 1970), this view was not seriously challenged until relatively recently: e.g., Raup (1978) showed that, if all extinction was gradual and uniform, then the time gap at the Permian–Triassic boundary must represent (an impossible) 85 million years.

Using the on-line ISI *Web of Science* database, the more recent surge of scientific interest in mass extinction events can be clearly demonstrated (Fig. 1). Although these data represent a small, biased sample of total scientific output over the time period in question, (e.g., they ignore published conference proceedings), several broad trends are apparent. First, with one or two minor exceptions, each event records a continuous increase in scientific interest (i.e., number of publications per five-year interval) over the past 30 years. Second, there were very low levels of interest in these events prior to the 1980s, which supports the widely held view (e.g., Benton, 2003, p. 96) that the publication of the impact hypothesis of Alvarez et al. (1980) was a key element in kick-starting the present-day interest in extinction studies. Certainly, publications concerning the end-Cretaceous extinction event have dominated output since (Fig. 1), but it's not obvious from the data that Alvarez et al. (1980) sparked interest in the other events. Other factors, such as technological advances (in the speed and power of computers, the precision of isotope analyses etc.) have also played a role. Finally, it is also clear

from the data that the different events have attracted different levels of interest through time. For example, interest in the Late Permian event remained relatively low key until the early 1990s, while (apparently) the Late Triassic event did not begin to attract significant scientific attention until the late 1990s. Of the individual events, only the K–T data seem to be recording a decline in the rate of scientific output: if these trends continue then the Late Permian event will surpass the K–T event in terms of global scientific interest in the next five years. Evidence that interest in the K–T event has already peaked is clear from the publications record of the leading scientific journals *Science* and *Nature* (Fig. 1B).

3. Palaeoclimates and extinction events

Although it is often difficult to prove a cause and effect relationship, the author considers that all major extinction episodes of the past resulted, ultimately, from changes in climate, induced by earthbound processes such as extensive volcanism, and that the case for an extraterrestrial cause of global extinction is, at best, unconvincing (see discussion below). Three types of climate change could potentially cause global extinction: rapid global cooling, rapid global warming, or rapid fluctuations of warming and cooling. However, the case for the latter mechanism as an extinction trigger is considerably weakened by data from the recent geological past, showing that no major marine extinction occurred with the advance and retreat of the Pleistocene ice caps (Newell, 1962; Valentine and Jablonski, 1991). Thus, only the first two mechanisms are considered below. The rapidity of the change is considered important, as most organisms should be able to cope with slow change over millions of years.

3.1. Global warming

Understanding the causes and consequences of ancient episodes of global warming has obvious significance for debates concerning current climate change. Global warming is associated with the second phase of the Late Ordovician event (e.g., Brenchley et al., 2003 and refs. therein), the Late Permian event (Benton and Twitchett, 2003; Kidder and Worsley, 2003), and the Triassic–Jurassic event (McElwain et al., 1999; Tanner

et al., 2004). A number of palaeo-proxies for global warming exist, and comprise (a) direct proxies of relative temperature rise and (b) indirect proxies of relative increase in known greenhouse gases such as CO₂ and CH₄. The former category includes the oxygen isotope record of seawater carbonates (e.g., Brenchley et al., 2003) and the morphology of palaeosols (e.g., Retallack, 1999). The latter category includes the stomatal index of fossil plants (e.g., McElwain et al., 1999), which may be considered a proxy for atmospheric CO₂ levels; and large negative shifts in the $\delta^{13}\text{C}$ carbonate record, which many have interpreted as indicating significant methane venting (e.g., Erwin, 1993; Krull and Retallack, 2000), although this is debatable (Kump, 1991; Berner, 2002).

It is assumed that geologically rapid global warming requires some unusual trigger, resulting in a major input of greenhouse gases into the atmosphere. The common association of mass extinction events, flood basalt eruptions and evidence for global warming have led some authors to propose that the flood basalts provide the trigger, through the venting of large amounts CO₂ (e.g., Wignall, 2001). For the Late Permian and Late Triassic events, it is further assumed that this initial phase of global warming leads to the dissociation of gas hydrates in the shallow shelf seas and/or high latitude permafrost, resulting in methane release. This exacerbates the global warming, leading to further temperature rise, further methane release, and a runaway greenhouse effect (e.g., Benton and Twitchett, 2003).

However, evidence for this scenario is circumstantial at best, relying on accurate dating of the flood basalt province and the presence of a large, otherwise unexplained, negative shift in the $\delta^{13}\text{C}$ carbonate record (as evidence of methane release). Caution is required as large negative shifts could be caused by other mechanisms, such as productivity crash (Kump, 1991) or undetected diagenesis (Mii et al., 1997) for marine carbonates. A negative shift in bulk organic matter is likely due to a change in organic matter source, such as a reduction in the relative contribution of material from higher plants (Foster et al., 1997). Volcanically vented CO₂ is also enriched in ¹²C. Recently, Berner (2002) noted that, regarding the end-Permian event, it is not possible to reject all of these other causes and the $\delta^{13}\text{C}$ record was likely driven by methane release associated with mass mor-

ality and volcanic degassing. Thus, methane venting is a possible explanation for the observed negative shift in $\delta^{13}\text{C}$. The shift itself should not be regarded as unequivocal evidence of methane flux to the atmosphere. Very large $\delta^{13}\text{C}$ excursions in the aftermath of the end-Permian event are almost certainly not the result of methane venting (Payne et al., 2004).

Although more work on understanding and modelling the triggers of catastrophic global warming are required, the environmental consequences of global warming seem to be reasonably well established, through a combination of computer modelling and direct geological evidence from the Holocene and more ancient rock records. On land, the major change is a poleward shift in climate belts. This may mean that while tropical and temperate taxa may migrate poleward and expand their ranges, high latitude taxa may become extinct as they have nowhere to go: the disappearance of the high latitude *Glossopteris* flora during the Late Permian may be one example. If the rate of warming is high enough, then lower latitude taxa with slow rates of dispersal will also be vulnerable to extinction. Increased aridity may cause extinction through water stress, and such aridity is recorded in low palaeolatitude sections through the Triassic–Jurassic interval (Tanner et al., 2004).

Temperature rise itself may, of course, adversely affect both terrestrial and marine species. Organisms can often tolerate a wide range of temperatures, but there are limits above (and indeed below) which the effect of temperature rise is lethal. Even within these lethal limits, there is usually an optimum temperature range for skeletal secretion, biochemical and physiological activity and growth. For example, in the bivalve *Phacosoma japonicum*, growth rate is fastest between 24.6 and 27.2 °C and temporarily shuts down if temperatures rise above 29 °C (Schöne et al., 2004). On land, temperature rise affects both animals and plants and in most instances adverse effects occur due to increasing water loss through transpiration and evaporation.

Global warming is accompanied by the melting of tundra permafrost, continental glaciers and sea ice, and a subsequent rise in global sea-level. Potentially, this should be good for shallow shelf faunas as they can expand their ranges, as more space becomes available. However, the overwhelming evidence is that sea-level rise is detrimental to marine ecosystems,

as many (most?) extinction events appear to coincide with transgressive episodes (Hallam and Wignall, 1997; see below).

Other oceanographic effects may also occur, largely of a detrimental nature. In the present day oceans, the temperature gradient between the tropics and poles maintains a continuous circulation as cold, nutrient and oxygen-rich water sinks at the high latitudes and travels towards the Equator. This deep water circulation keeps most of the abyssal plains well oxygenated and, where upwelling brings these nutrient-rich waters to the surface, such as along the western margin of South America, promotes high levels of surface productivity. Following severe global warming, the oceanic circulation system becomes more sluggish and large parts of the ocean become anoxic (e.g., Hotinski et al., 2001; Kidder and Worsley, 2003). This has been predicted (e.g., Wignall and Twitchett, 1996), modelled (Hotinski et al., 2001; Kidder and Worsley, 2003) and observed (e.g., Wignall and Twitchett, 2002 and refs therein) for the Late Permian mass extinction event.

Globally sluggish circulation, the generation of nutrient-poor warm saline bottom waters and reduced wind shear in coastal areas may reduce the amount of upwelling that occurs, leading to a global decrease in primary productivity (Kidder and Worsley, 2003). Certainly, there is excellent evidence that surface productivity in ocean settings declined by 50% following the warming after the end of the last Ice Age (Herguera and Berger, 1991, 1994). Later during the Holocene, episodes of temporary warming caused a shift in circulation patterns so that areas previously influenced by cold, nutrient-rich currents were then affected by warmer, nutrient-depleted currents (An, 2000). This resulted in decreased food supply and suppression of growth rate in the shallow-water fauna (Schöne et al., 2004). Increase in surface water temperatures also result in changes in the monsoon system in the low-mid latitudes, resulting in greater levels of precipitation and run-off as the summer monsoon intensifies and moves further north (An, 2000), which may also be detrimental to terrestrial and shallow water ecosystems.

Many of these Holocene changes could potentially be identified in the rock and fossil records of more ancient events, e.g., productivity collapse, reduction in molluscan growth rates, increases in run-off and sediment influx. The detrimental affects of global warming on the ocean system could explain why the

majority of extinction events, at all scales, are associated with evidence of global warming and the oceanographic changes described above. There are obvious, serious implications for the present day as well. One unresolved issue is the rates at which these oceanographic changes occur: is it possible to simply scale up linearly from Holocene data? Or, is there a threshold effect, above which temperature rise produces catastrophic, global-scale extinction-causing changes to the ocean system?

3.2. *Global cooling*

In many ways, of course, the effects of global cooling are the opposite of those that occur during global warming. However, this does not mean that global cooling is necessarily less detrimental on the biosphere: Stanley (1998a,b) has argued that all mass extinction events were the result of global cooling, although much of his evidence has since been contradicted. Of the major mass extinction events, there is excellent evidence for global cooling associated with the first phase of the Late Ordovician event, including widespread glacial deposits, and changes in the oxygen isotope records of seawater carbonates (e.g., Brenchley et al., 1994, 2003). Recently, more equivocal evidence for cooling at the Frasnian–Famennian extinction horizon has also been presented, and linked to cometary impact (Sandberg et al., 2002).

Despite earlier reports (e.g., Stanley, 1998a,b) there is no evidence for cooling associated with the Late Permian event (Erwin, 1993, p. 169–170), nor for the Late Triassic event. However, extinction scenarios that involve flood basalt eruptions, such as for the Late Permian event (e.g., Renne et al., 1995), often suppose that a brief cooling episode must have initially occurred (Wignall, 2001). For the Late Cretaceous event, recent evidence shows that the climate of the Maastrichtian was rather variable: a long term cooling trend gave way to a brief interval of warming in the latest Maastrichtian, followed by the onset of cooling just before the K–T boundary (Barrera, 1994; Abramovich and Keller, 2003). Cooling is also considered to be one possible consequence of extraterrestrial impact (see below).

Global cooling should promote oceanic circulation and mixing and lead to the oxygenation of marine

ecosystems. Ocean productivity is also higher under icehouse conditions, and evidence of this is found at the Late Ordovician with a positive shift in $\delta^{13}\text{C}$ synchronous with glaciation (e.g., [Finney et al., 1999](#); [Brenchley et al., 2003](#)). While generally considered “good”, such changes could lead to extinction of a fauna that had adapted to stratified, low oxygen conditions; a hypothesis that has been invoked to explain graptolite extinction in the Late Ordovician. Also, increased upwelling and productivity may result in local/regional development of anoxia through expansion of the oxygen minimum zone. In addition, excessively low temperature can be just as lethal as excessively high temperatures. If accompanied by the development of extensive polar icesheets, then global cooling would also lead to the loss of high latitude habitats (both marine and terrestrial) and a general migration of fauna and flora towards the Equator. This could squeeze the high diversity tropics, and is one reason why authors such as [Stanley \(1998a,b\)](#) favoured cooling as a mechanism to explain all mass extinction events.

4. Palaeoenvironments and extinction events

In my opinion, there are two important aspects of palaeoenvironmental change that need to be considered when discussing ancient mass extinction events. The first, and one that most authors tend to focus on, is the record of unusual environmental change (e.g., [Ward et al., 2000](#)) that is associated with, and may be a proximate cause of, the extinction itself, or a key factor affecting post-extinction recovery. Common examples, discussed herein, include oceanic anoxia and sea-level change and the unusual and potentially devastating environmental changes associated with extraterrestrial impact. The other important aspect of palaeoenvironmental change, which is often overlooked, concerns the question of sampling bias. Specifically, are the same palaeoenvironments being sampled on either side of a supposed extinction event?

4.1. Palaeoenvironmental bias

The question of sampling bias is of paramount importance (e.g., [Smith et al., 2001](#)). Many taxa have restricted environmental distributions, controlled

by their tolerance to factors such as salinity and temperature, and are often confined to a single depositional setting such as fast-flowing rivers or the marine photic zone etc. In fossil taxa, this translates to facies dependence. It follows that, if a particular facies is sampled in time interval A, but is not sampled in the subsequent time interval B, then all those facies-dependent fossil taxa from A will have disappeared. However, it will be impossible to determine whether they suffered true biological extinction or whether their absence is merely due to facies change. The simplest scientific explanation is to accept the latter possibility.

However, in most published extinction studies, such potential palaeoenvironmental (facies) bias is largely ignored. The global databases of, for example, [Sepkoski \(1982\)](#) and [Benton \(1993\)](#) do not record facies information, although the latter makes some attempt by noting that taxa are marine, freshwater or terrestrial. Only in local or regional studies are such biases addressed. During the Triassic–Jurassic event, there is a clear facies and environmental bias in patterns of apparent extinction and recovery in the vertebrate faunas of France ([Cuny, 1995](#)) and marine bivalves ([Hallam, 2002](#)). [Brookfield et al. \(2003\)](#) showed that disappearance of the Late Permian, shallow-water, brachiopod-dominated fauna at Guryul Ravine (Kashmir) was simply the result of facies change during sea level rise: as water depths increased, shell beds containing the shallow water fauna became thinner and more sparse up section, before eventually disappearing. Finally, looking at the issue from a slightly different angle, [Briggs and Gall \(1990\)](#) considered the effects of the Permian–Triassic extinction on a single depositional environment, namely marginal marine, brackish palaeoenvironments. Although their data points were quite widely spaced on either side of the event, [Briggs and Gall \(1990\)](#) concluded that the effects of the extinction were minimal and that the community structures of late Palaeozoic and early Mesozoic marginal marine ecosystems were nearly identical.

Other potential sampling biases also exist alongside palaeoenvironmental bias, such as latitudinal bias (e.g., [Allison and Briggs, 1993](#)). This is closely related to palaeoenvironmental bias, and is important as some taxa are restricted to particular latitudes, such as the tropics or poles, depending on, for example, their

temperature tolerance. Also, the fauna and flora of high and low latitudes may respond differently during an extinction crisis and subsequent recovery (e.g., Barrera and Keller, 1994; Twitchett and Barras, 2004).

Finally, a number of studies have attempted to address such biases by simply counting the number of localities or formations sampled across an extinction horizon (e.g., Wignall and Benton, 1999; but see Twitchett, 2000). Although biases in sampling density can be addressed through counting localities, this has no bearing on the question of palaeoenvironmental bias. Facies and latitudinal biases are considered to be more important controls on the appearance or disappearance of fossil taxa. Thus, although Wignall and Benton (1999) showed that the number of sampled localities is not a problem for the Late Triassic extinction event, previous work has demonstrated that facies change during this event is very significant (e.g., Cuny, 1995). Palaeoenvironmental (facies) bias undoubtedly affects our perception of the magnitude of mass extinction events and the nature of post-extinction recovery, but, until this issue is addressed comprehensively at the global scale, the importance of this bias will remain unknown.

4.2. *Sea-level fall*

Eustatic sea-level fall, typically associated with periods of climate cooling and glaciation, has long been viewed as an important driver of extinction, especially for shelf faunas (e.g., see Tanner et al., 2004, for a discussion of the Triassic–Jurassic event). During episodes of major regression, the habitable area of shallow continental shelves will be much reduced, and, according to the species–area effect, diversity will also decline. Endemic taxa in epicontinental basins may be particularly affected as connection to the open ocean is severed and the basin dries out.

However, more recently, the role of regression alone as a major cause of extinction has been questioned. There are concerns that the species–area effect cannot be directly applied to the geological past and to marine environments (Erwin, 1993, pp. 239–242). In particular, it seems likely that the species–area effect has more to do with the heterogeneity of habitats within a particular area, rather than the absolute magnitude of the area in question. Secondly, when the

cause of major regression is global cooling and glaciation, such as with the first phase of the Late Ordovician extinction event, a reduction in water temperature, rather than loss of shelf area, may be the real proximate cause of extinction. For the Triassic–Jurassic event, while sealevel fall is recorded in some regions (e.g., Europe), no discernible change is recorded elsewhere (e.g., South America) (Tanner et al., 2004), highlighting the fact that the rock record is affected by local variations in tectonics as well as global sealevel change.

Facies change may also affect the quality of the fossil record. In shallower marine settings, sea-level fall is typically associated with exposure and the erosion of pre-existing (marine) strata, followed the subsequent deposition of non-marine sediments. Thus, there may be significant facies change (marine to non-marine) as well as loss of information (erosion of the youngest pre-event sediments), both of which may enhance the apparent magnitude of the extinction event in these proximal environments. In deeper marine settings, there is also significant facies change, with the onset of deposition of shallower facies (Paul and Donovan, 1998). In terrestrial settings, sea-level fall will cause the rivers to incise down to the new base level, creating valleys with very well drained, mature paleosols on the interfluvies between as the water table falls. One consequence of such change may be a reduction in the quality of the fossil record, as preservation potential of such environments is distinctly different to that of a marshy floodplain.

4.3. *Sea level rise*

According to a number of authors, major marine transgression has replaced major regression as a key driver of extinction (e.g., Hallam and Wignall, 1999). This change of emphasis results from detailed high resolution studies of individual geological sections through major extinction events, which tend to indicate that the extinction horizon occurs within the early phases of transgression rather than during sea-level fall. However, the mechanism by which sea-level rise alone can cause extinction is not obvious, and co-occurring marine anoxia is usually cited as being the proximate kill mechanism (e.g., Hallam and Wignall, 1999) (but see below). However, the views of Hallam and Wignall (1999) have been challenged by some

(e.g., Sandberg et al., 2002 for the Late Devonian event). If the species–area effect can indeed be extrapolated to the geological record then sea level rise should promote diversity increase in the marine realm as shelf areas expand.

However, there are several reasons to be cautious. During times of sea level rise, shallow shelf sediments (containing the high diversity, shallow marine fauna) will be extensive, but will be deposited far from the basin centre, in places where they are incredibly vulnerable to erosion during subsequent sea level fall (Paul and Donovan, 1998). Thus, at times of high sea level, the fossil record should be very poor, and the magnitude of extinction may be overestimated (cf. Twitchett, 2001). In more offshore settings, sealevel rise may result in sediment starvation, non-deposition and condensation of marine deposits, which might conspire to cause an apparent truncation of many taxon ranges at a single horizon. Stratigraphic modelling by Holland (1995) also showed that sea level changes alone may cause apparent extinction events, as last occurrences tend to cluster at sequence boundaries or transgressive surfaces. All of these potential effects of sea level rise on the fossil record need to be carefully considered when proposing a cause and effect link between sea level change and mass extinction.

4.4. Oceanic anoxia

In the modern shelf seas, local anoxic (or hypoxic) events often have severe effects on the benthic community, which may last for several years (e.g., Harper et al., 1981). In the geological past, a number of global oceanwide anoxic events (OAEs) have been recognised and some authors have considered that oceanic anoxia is a potential extinction cause in most mass extinction events (Hallam and Wignall, 1997). This hypothesis derived largely from interpretations of facies and palaeoenvironmental change during the Permian–Triassic interval (e.g., Wignall and Hallam, 1992). Evidence of anoxia has also been documented in Triassic–Jurassic sections (Hallam and Wignall, 2000) and was thought to be a significant factor in this event (Hallam and Wignall, 1997). However, this is no longer the case, although anoxia has been implicated in earlier extinctions within the Late Triassic (Tanner et al., 2004) and may have affected post-extinction Hettangian recovery patterns

(Twitchett and Barras, 2004). Anoxia is associated with the second (warming) phase of the Late Ordovician event (Brenchley et al., 2003) and with warming phases through the Frasnian–Famennian interval as well (e.g., Sandberg et al., 2002).

Initially, the interpretation of anoxic conditions at the Permian–Triassic event was based solely on sedimentological and palaeoecological evidence: i.e., laminated, fine-grained, sediments lacking bioturbation and containing a depauperate bivalve epifauna (e.g., Wignall and Hallam, 1992). This interpretation was initially regarded as highly dubious, and the facies change was simply a natural consequence of the extinction event: laminated, defaunated strata appear because “most everything was dead” (Erwin, 1993, p. 246). More recent, independent, geochemical and biomarker data has since strengthened the initial interpretations (e.g., Wignall and Twitchett, 1996, 2002; Grice et al., 2005), but still this does not prove that extinction was caused by oceanic anoxia.

A critical test is to compare the relative timing of extinction and onset of anoxia. During the Permian–Triassic interval, the appearance of oceanic anoxia is highly diachronous, with shallow water regions of Neotethys remaining well oxygenated into the Early Triassic (e.g., Wignall and Twitchett, 2002). If anoxia is a kill mechanism then the extinction should be similarly diachronous. Apparent evidence of diachronous extinction was provided by Wignall et al. (1996) and Wignall and Newton (2003), but was subsequently criticised by Retallack (2004) and Twitchett et al. (2004). Although the debate remains open, it appears that the main phase of Late Permian extinction does not always coincide with the appearance of anoxia (at least in Neotethys) (cf. Brookfield et al., 2003). However, there is evidence that the extent and duration of post-extinction anoxia, probably related to global warming, did have a serious impact on the post-extinction recovery of the benthic ecosystem in the Early Triassic (Twitchett et al., 2004) and Early Jurassic (Twitchett and Barras, 2004).

4.5. Bolide impact

The impact of large extraterrestrial bodies with the Earth is viewed by some as the major driver of global extinction on this planet, although it is clear that not every large impact is associated with an extinction

event. The recent obsession with impact-related extinction seems to have begun with the Alvarez et al. (1980) publication in *Science*, although some authors had suggested this possibility much earlier (e.g., McLaren, 1970, for the Frasnian–Famennian event). In fact, Alvarez et al. (1980) really made two related, but entirely independent, hypotheses: (1) that a bolide impact occurred at the K/T boundary and, (2) that bolide impact caused the mass extinction. The former has been confirmed by numerous subsequent studies, most notably the identification of the crater itself at Chicxulub (Hildebrand et al., 1991). More recent work on new core samples has suggested that, in fact, the Chicxulub impact may have pre-dated the K/T boundary by some 300 kyr, and that at least two major impacts occurred during the Maastrichtian (e.g., Keller et al., 2004).

In order to conclude that bolide impact has caused extinction, two sets of data have been considered necessary: (1) unequivocal evidence of geologically instantaneous extinction; (2) unequivocal evidence of impact coincident with the extinction horizon. Thus, while much supposed evidence has been presented for bolide impact at the Late Permian extinction event (e.g., Becker et al., 2004 and refs. therein), most of this is seriously flawed (Renne et al., 2004) and impact is not favoured as a cause for this event (Benton and Twitchett, 2003).

However, with the exception of those unfortunate enough to be endemic to the impact site itself, species do not become extinct simply because, somewhere, a bolide has struck the Earth. It is the environmental consequences of the impact event that lead to species loss. In my view, this is a major problem with the theory that impacts cause extinction. All of the environmental consequences of impact that have been previously proposed are either (1) untestable speculation, (2) have since been disproven, or (3) may have been caused by terrestrial (i.e., non-impact related) events. Some of these are discussed herein, using the well-known end-Cretaceous impact event as the main example, although the Late Devonian crisis is also associated with some evidence for impact. If the K–T multiple impact scenario is correct, then the case against impacts as extinction triggers has already been demonstrated: extraterrestrial impacts in the early Danian and late Maastrichtian, including Chicxulub, had no discernable effect on planktonic foraminiferal

diversity (Keller, 2003; Keller et al., 2004). The plankton responded to every episode of intense volcanic activity from the Deccan Traps, but only to impact events, e.g., at the K–T boundary itself, that were coincident with a volcanic episode (Keller, 2003, p. 259).

The most commonly cited environmental consequence of impact is temporary global darkness, caused by the injection of impact-generated dust and debris high into the atmosphere (e.g., Alvarez et al., 1980), and lasting for several months (Pollack et al., 1983). In the case of the end-Cretaceous event, this darkness is hypothesised to have led to the cessation of photosynthesis and the subsequent death of primary producers on land and in the surface waters of the oceans (Alvarez et al., 1980). For a couple of months, conditions were supposed to have been so dark that animals would have been unable to forage (Pollack et al., 1983). A blanketing dust cloud would also reflect sunlight and might even trigger a short period of glaciation, as has been suggested for the Late Devonian event (McGhee, 1996, p. 163). It has been estimated that there was a maximum temperature drop of forty degrees on land a few months after the end-Cretaceous impact event (Pollack et al., 1983).

Unfortunately, there are no direct palaeo-proxies of ancient light levels or of the amount of dust in the atmosphere. The dust hypothesis can only be tested (indirectly) through numerical modelling. The productivity crash and plankton loss, or the global cooling, that occur around the K–T event may have other causes (see above), and, in any case, appear to be much longer term phenomena (e.g., Barrera, 1994; Barrera and Keller, 1994). In order to shut down photosynthesis it is calculated that a minimum of $\sim 10^{16}$ g of submicron-sized dust would be needed (Pope, 2002). However, the measured global distribution of siliciclastic debris from the end-Cretaceous impact event can be explained by the dispersal of no more than 10^{16} g of ejecta, by stratospheric winds, from the Chicxulub impact site, with less than 1% of this material being submicron-sized dust (Pope, 2002). Therefore, at most, the end-Cretaceous impact would have released just 10^{14} g of dust: two orders of magnitude less than that required to shutdown photosynthesis.

In addition, even assuming that global darkness did occur, the amount of climate cooling produced by the end-Cretaceous impact has also been overestimated.

Although it was recognised by Pollack et al. (1983) that seawater temperatures would be largely unaffected, due to the enormous heat capacity of the oceans, they underestimated the role that atmospheric circulation would play in transferring heat from the oceans to the continents. More recent modelling by Covey et al. (1990) and Luder et al. (2002) has demonstrated that only limited cooling, and no global glaciation, would have occurred. Thus, the supposed palaeoenvironmental consequences of impact-generated dust (i.e., darkness and global cooling) are unlikely to have been severe.

The triggering of continent-wide, or even global, wildfires is also viewed as a palaeoenvironmental consequence of the end-Cretaceous impact event, with devastating effects for the terrestrial biota (e.g., Melosh et al., 1990; Wolbach et al., 1990). Wildfires could potentially be triggered by the bolide's passage through the atmosphere, by the radiation from the impact plume, by the returning ejecta or by lightning strikes in the impact aftermath (see discussion in Shuvalov and Artemieva, 2002; Belcher et al., 2003).

Supposed geological evidence for post-impact wildfires at the Cretaceous–Tertiary boundary is provided by the high levels of soot recorded in the sediments (Wolbach et al., 1990). However, soot can derive from a variety of sources (Belcher et al., 2003) and does not, on its own, constitute unequivocal evidence for wildfires. A recent test of the wildfire hypothesis was provided by Belcher et al. (2003), who measured in situ abundance of inertinite (charcoal fragments that can only be produced by the combustion of higher plants) at six K–T sites across North America. Their study demonstrated that wildfires were common both before and after the K/T boundary, and that abundances of inertinite at the impact horizon and in its immediate aftermath were no higher than background levels (in most cases, they were actually less). The presence of common, but unburned, plant remains in the K–T boundary beds shows that the lack of charcoal is not due to the absence of terrestrial flora nor to the non-preservation of plant remains (Belcher et al., 2003). Thus, wildfires (on either a global or continental scale) were seemingly not a palaeoenvironmental consequence of the end-Cretaceous impact.

Other supposed environmental consequences of the end-Cretaceous impact include the generation of giant tsunamis. Although not a mechanism for producing

global extinction (but see McLaren, 1970), these could have had serious consequences for the shallow marine and coastal floodplain ecosystems in the vicinity of the impact site. They might also be expected to leave some trace in the geological record, and indeed several supposed K–T tsunamites have been described from the Caribbean and Gulf of Mexico, interpreted as relating to the Chicxulub impact event (e.g., Bourgeois et al., 1988).

However, palaeoenvironmental studies of, in particular, the trace fossil record of these units, have demonstrated unequivocally, that the so-called tsunami beds of Alabama (Savrda, 1993) and north-eastern Mexico (Ekdale and Stinnesbeck, 1998) were not deposited catastrophically in a few hours. Several erosive events in the sandstone successions, and multiple horizons where different suites of trace fossils are found, indicate that deposition was episodic with significant breaks allowing the benthos time to colonise and construct complex burrows, such as *Thalassinoides* (Savrda, 1993; Ekdale and Stinnesbeck, 1998). The trace fossil record is proving a powerful tool for investigating mass extinction events, and yet has still not been analysed at all of the so-called K–T tsunamites (Twitchett and Barras, 2004). The sedimentological and ichnological data indicate that the so-called K–T tsunamites (of Alabama and Mexico at least) represent, instead, the normal transgressive fill of incised valleys, which were probably cut during an episode of sea-level fall in the latest Cretaceous (e.g., Savrda, 1993). Evidence for brief sea level fall prior to the impact horizon, can be found at many K–T sections and is itself associated with apparent extinction.

Other hypotheses (see Wolbach et al., 1990 for one such list) include the generation of devastating amounts of acid rain, which would have stripped the terrestrial vegetation and turned the surface of the oceans acidic. However, numerical models show that only a very large (1.25×10^{16} kg), fast moving (65 km/s), comet could have potentially caused truly global acid rain; in all other cases just local effects would occur (Prinn and Fegley, 1987). In addition, many of the proposed predictions for the acid rain hypothesis are not unique to this scenario, and so the theory is difficult (impossible) to test from geological data. Other untestable speculations include lethal increase in the levels of cosmic radiation striking the surface of the Earth, or widespread trace metal poisoning etc.

Science progresses through the testing of hypotheses, and theories that cannot be tested by geological data are no more than idle speculation and have no place in the scientific study of extinction and global change: a point first raised by Charles Lyell in his 1830s *Principles of Geology*. Pope et al. (1998) wrote of the K–T event: “It should be emphasized that the devastation described above is largely theoretical, although there is some independent evidence for global acid rain, fires and cooling”. The independent evidence for global palaeoenvironmental changes directly caused by the K–T impact event remains either unconvincing or has been contradicted by more recent work (e.g., Pope, 2002; Belcher et al., 2003).

The problem remains the plethora of other changes (sea level, climate and the eruption of the Deccan Traps) that were ongoing around the same time as the K–T extinctions and impact(s) (e.g., Keller, 2003). How can the cause and effect of each be untangled? What global palaeoenvironmental changes, if any, are really caused by extraterrestrial impact? One solution may be to seek evidence of local, or regional, environmental changes associated with a (large), well-dated impact event that was not contemporaneous with flood basalt eruptions.

5. Palaeoecology of extinction events

The compilation of global taxonomic databases (e.g., Sepkoski, 1982; Benton, 1993), and the subsequent statistical analysis of these data has dominated palaeontological studies of extinction events. Hypotheses such as the supposed periodicity of extinction events (Raup and Sepkoski, 1984), now regarded as highly doubtful (Stigler and Wagner, 1987, 1988; Patterson and Smith, 1987), have sprung directly from this ‘taxon counting’ effort. Palaeoecological studies have, for the most part, been an underrepresented aspect of mass extinction studies.

However, this is all beginning to change. On the one hand, problems of the taxon-counting methodology (e.g., the reliance on outdated, often flawed, taxonomic and range data) have been shown up by recent detailed cladistic analyses. For example, the study of Jeffery (2001) of echinoids through the Cretaceous–Tertiary extinction event demonstrated unequivocally that a literal reading of the fossil record

leads to a significant overestimation of extinction magnitude (65% generic loss vs. 33%), and that phylogeny is an absolutely necessary part of extinction studies. Additionally, the importance of palaeoecology in mass extinction studies has itself been recently highlighted. Studies by Droser et al. (2000) and McGhee et al. (2004) demonstrate that one cannot assess the impact of an extinction event on the evolution of the biosphere by simply calculating the magnitude of taxon loss: ecological severity is at least as important. These latter two studies, and others detailed below, demonstrate that both semi-quantitative and quantitative palaeoecological analyses of the fossil record can greatly increase our understanding of mass extinction events.

5.1. Selectivity

Understanding the selectivity of mass extinction events has been, and still is, a fundamental question. Theoretically, there are a number of different hypotheses and this is a complex subject area that deserves a more thorough analysis than is possible here. Some authors (e.g., Benton, 2003, p. 152) note that mass extinction events should, by definition, be non-selective: a completely random catastrophe where chance is the pure reason for survival (see also Raup, 1991). Others (e.g., Jablonski, 1986) have supposed that mass extinction events are selective, but that the selection pressures are fundamentally different to those affecting individual organisms during background times and operate at a higher (macroevolutionary) level. Selection pressures in extinction and background times are thus different, and traits that confer advantage at one time may not be so useful during the other. The long-realised fact that not all groups suffer equally (e.g., Newell, 1952, 1962; McLaren, 1970) is a priori evidence for some sort of selection during extinction events. Are similar traits selected for in all the major mass extinction events?

Recent studies have demonstrated that relatively few traits enhance the probability of survival during mass extinction events. However, the number of quantitative studies that have actually been undertaken is also relatively low, mostly involving analysis of the K–T record and/or benthic molluscs, and there is room for more work. In a comprehensive study of generic level extinction in K–T bivalves, Jablonski and Raup

(1995) found that there was no selectivity for body size, life habit (i.e., infaunal vs. epifaunal), or bathymetric position. However, geographically widespread genera did have significantly lower rates of extinction than those taxa with narrow geographic ranges (measured by the occupancy of different provinces). A study of Permian–Triassic gastropods also showed that broad geographic range, as well as species richness, increased the probability of survival (Erwin, 1989).

Jablonski and Raup (1995) also found that deposit feeders suffered much lower rates of extinction (30%) compared with suspension feeders (61%), but this was attributed to the extinction-resistant Nuculoida and Lucinoidea biasing the data (other deposit feeding groups had much higher rates of extinction, up to 76%). However, in detailed studies of K–T echinoids, Jeffery (2001) and Smith and Jeffrey (1998) also found that feeding strategy was the only significant factor that enhanced the probability of survival: other traits such as geographic range, life habit, bathymetric position, larval strategies etc. had little or no effect on survival. Among the irregular echinoids, deposit-feeders possessing penicillate tube feet, which allow for more efficient feeding on fine detritus, had higher probability of survival, whereas in regular echinoids omnivores fared better than specialist herbivores and grazers (Smith and Jeffrey, 1998). These studies (Smith and Jeffrey, 1998; Jeffery, 2001) are particularly important as the taxa were subjected to complete taxonomic revision and placed in a rigorous phylogenetic (cladistic) framework, thus avoiding potential problems related to taxonomy.

These data led to the conclusion that the proximate cause of the K–T extinction event was a decrease in productivity and phytoplankton abundance, leading to lower food supply reaching the seafloor (Smith and Jeffrey, 1998). Other studies have also demonstrated that plankton productivity declined dramatically at the K/T boundary, with greater loss in the low latitudes (e.g., Barrera and Keller, 1994). It is clear that the plankton were suffering brief intervals of dramatic ecological change before, during and after the K/T boundary, but only at the boundary did significant taxon extinction occur (Keller, 2003). Selectivity against suspension-feeders during both the K–T and second phase of the Late Ordovician event has also been interpreted as indicating a reduction of primary

productivity (Sheehan et al., 1996). Shallow marine bivalve faunas prior to the K–T event were dominated by suspension feeders, but, in the immediate aftermath deposit feeders dominated the benthic communities (Hansen et al., 2004). Likewise in the aftermath of the Late Permian event, there is a temporary loss of soft-bodied, infaunal suspension feeders, as recorded in the trace fossil data (Twitchett and Wignall, 1996; Twitchett and Barras, 2004) and high tier suspension feeders such as crinoids (Twitchett, 1999). However, it should be noted that within Permian–Triassic echinoids, it is the specialist deposit-feeding clade that becomes extinct (Andrew Smith pers. comm. 2004). For the K–T event, low productivity levels lasted for a few hundred thousand years before the restoration of ‘normal’ ecosystems (Barrera and Keller, 1994) and a return of suspension feeding (Hansen et al., 2004).

Thus, from the current, albeit limited, data available it appears that two main traits may enhance survivability during the major mass extinction events: (1) wide geographic range and (2) feeding strategy (namely, selective deposit feeding or omnivory). These data may indicate that reduced primary productivity in the surface waters was a main cause of these events, with corresponding reduction in food supply for animals at higher trophic levels that lasted for a few hundred thousand years.

5.2. Biotic recovery

Prior to the 1990s, most research effort was directed towards the extinction events themselves, particularly from the point of view of taxonomic loss and possible causation. However, this is now changing and understanding how ecosystems, clades and the global biosphere responds and recovers from extinction events is becoming a major research objective.

Two main lines of research are being pursued. Firstly, detailed palaeoecological studies of individual regions, or clades, in the aftermath of a particular mass extinction event (e.g., Schubert and Bottjer, 1995; Hansen et al., 2004). However, there are still surprisingly few such studies and there is much scope for more (quantitative) work in this field. Secondly, attempts are being made to look at the broader, global recovery patterns and to develop methods of comparing the rates and patterns of recovery between different events.

5.2.1. The *Kauffman–Erwin (1995) model*

In many ways the IGCP project 335 (*Biotic recovery from mass extinction events*) and the resultant edited volumes (e.g., [Hart, 1996](#)), can be viewed as the trigger of the recent interest in post extinction recovery. Near the beginning of this project, [Kauffman and Erwin \(1995\)](#) proposed a model for describing post-extinction recovery, which was later refined by [Kauffman and Harries \(1996\)](#) and which has since been applied to a number of events of differing magnitude. The model ([Fig. 2](#)) is based on the application of theoretical concepts of survivorship to the fossil record. In particular, a number of possible survival mechanisms were proposed (see for example, [Harries et al., 1996](#)), and taxa in the extinction aftermath were interpreted as having survived by virtue of one or other survival mechanism, based on characteristics of their stratigraphic range ([Fig. 2](#)).

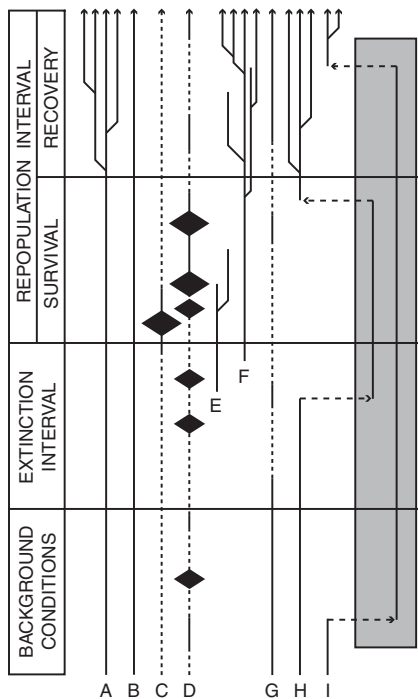


Fig. 2. The *Kauffman–Erwin* model of recovery after mass extinction events (modified from [Kauffman and Erwin, 1995](#)). A=pre-adapted survivors; B=ecological generalists; C=disaster species; D=opportunistic species; E=failed crisis progenitors; F=crisis progenitors; G=stranded populations; H=short-term refugia species; I=long-term refugia species. Grey shaded area represents refugia, outside the normal geographic range of the refugia species. For definitions of taxa see [Kauffman and Harries \(1996\)](#).

This over-emphasis on interpretations based on literal reading of the stratigraphic ranges of fossil taxa, has led to criticism of some aspects of the model. For example, Lazarus taxa (those taxa that temporarily disappear from the fossil record) are termed instead “Refugia taxa”, of which two types (Short Term Refugia Species and Long Term Refugia Species) have been identified ([Kauffman and Harries, 1996](#)). The key stratigraphic characteristic is a temporary absence from the fossil record, during which time the species in question emigrated to some unknown refugium, outside of their normal geographical range ([Harries et al., 1996](#)), before returning to help seed the subsequent post-event radiation. This interpretation of Lazarus taxa is easy to criticise on several grounds, biological and geological, including the fact that changes in facies or preservation potential is an alternative, far more plausible, reason for temporary absence from the fossil record (e.g., [Erwin, 1996](#); [Twitchett, 2000](#)). Biologically, it is highly unlikely that species could successfully colonise a novel habitat or region, just in time to escape the biotic crisis, yet were unable to colonise that area prior to the event ([Wignall, 1994](#)). More likely, shrinkage of the original range to a core area would happen during the crisis, with subsequent re-colonisation of the previous range once conditions improve; a pattern observed in modern taxa ([Twitchett, 2001](#), p. 347).

Regardless of these difficulties with the [Kauffman and Erwin \(1995\)](#) and [Kauffman and Harries \(1996\)](#) interpretations, several aspects of their model have been incorporated into the study of post-extinction recovery. One is the twofold division of the post-extinction “Repopulation Interval” into an initial “Survival Interval” and a later “Recovery Interval” ([Fig. 2](#)). The boundary is marked by the onset of significant post-extinction radiation, and comparing the duration of Survival Intervals is one possible method of comparing the rates of recovery after different events (e.g., [Erwin, 1998, 2001](#)). There is a minor issue of nomenclature here: many authors prefer to use the common term “recovery interval” when referring to the whole of the post-extinction aftermath, rather than the *Kauffman and Erwin* term “repopulation interval”.

Additionally, terms like “Disaster species”, or “Disaster taxa” have subsequently become commonplace in studies of mass extinction events. During

background times, disaster taxa (as defined) are geographically restricted, often to marginal, high stress environments. This is supposedly due to their exclusion from other (by inference, more “normal”) habitats through competition from other organisms (Kauffman and Harries, 1996, p. 20). In the immediate aftermath of the extinction event (early Survival Interval), disaster species are briefly widespread and abundant, with a larger geographic range that includes these more “normal” habitats, before retreating into relative obscurity once more. This post-extinction bloom of disaster species is interpreted as being due to the extinction of their competitors (i.e., relaxation of biotic control), but, alternatively, could simply indicate a temporary expansion, into these other environments, of the deleterious environmental conditions to which they are adapted (i.e., abiotic control).

In the aftermath of the Late Permian event, the inarticulate brachiopod *Lingula* is interpreted as a disaster taxon (e.g., Schubert and Bottjer, 1995; Rodland and Bottjer, 2001). Rare in pre-extinction shallow marine assemblages, *Lingula* often, though not always, dominates assemblages in the immediate post-extinction aftermath (specifically the first one or two conodont zones of the Induan) and is globally widespread in shallow subtidal environments (Rodland and Bottjer, 2001). In the aftermath of the K–T event, blooms of the small opportunistic disaster taxon *Guembelitria* have been documented (Keller and Pardo, in press). Similarly, post-extinction stromatolites, or other microbial structures, are typically interpreted as disaster ‘taxa’, or ‘disaster forms’ (e.g., Schubert and Bottjer, 1992, 1995; Whalen et al., 2002).

At the global, Phanerozoic-level scale, stromatolites seem an archetypal disaster ‘taxon’, having enjoyed former glory throughout the shallow subtidal environments of the Proterozoic, before being restricted to marginal, hypersaline settings in the Phanerozoic. Only after the mass extinction events of the Phanerozoic, primarily the Late Permian (e.g., Schubert and Bottjer, 1992) but also the Late Devonian (Whalen et al., 2002), were they able to colonise other subtidal settings and become, temporarily, common in the fossil record once more. This was made possible by the widespread extinction of the metazoan infauna and/or continuation of deleterious environmental conditions unsuitable for burrowing benthos, which led to

the return of Proterozoic-like substrate conditions (Pruss et al., 2004).

However, there are problems with this scenario. Firstly, regarding the Late Devonian event, Shen and Webb (2004) have recently cast doubt on the interpretation of Whalen et al. (2002) on Famennian stromatolite reefs as disaster forms. They note that salinity, nutrient availability and sediment influx may be the primary controls on stromatolite distribution, and that stromatolite reefs and other microbial build-ups are common throughout the Late Devonian (before, during and after the extinction crisis) and may be associated with a diverse fauna (Shen and Webb, 2004). Secondly, according to the Kauffman–Erwin model (Fig. 2), the definition of disaster taxa is that they only bloom in the very earliest part of the Survival Interval. In the aftermath of the Late Permian event, stromatolites and other microbial structures, such as wrinkle structures (Pruss et al., 2004), are encountered at various horizons and in various depositional settings throughout the Early Triassic, including the late Olenekian (Spathian) where there is unequivocal evidence of increasing diversity and recovery.

Part of the reason is probably that some of these records are, in fact, from marginal, salinity-stressed environments and not “normal” subtidal settings. Many of the Olenekian examples of microbial structures derive from the Moenkopi Formation of SE Nevada, USA (Schubert and Bottjer, 1992, 1995; Pruss et al., 2004), which is a very marginal setting. Stromatolites are absent from coeval strata in northern Nevada that were deposited in more open marine conditions (pers. observ.). The high abundance of microbial wrinkle structures in the Campil Member of the Werfen Formation (northern Italy) (Pruss et al., 2004) is almost certainly due to the brackish depositional environment (e.g., Twitchett, 1999). Wrinkle marks are very common in such brackish water, tide-influenced facies throughout the Phanerozoic (e.g., Mángano and Buatois, 2004) and no special evolutionary/environmental argument is necessary to explain their occurrence in equivalent facies of Early Triassic age. Indeed, the tidal flat facies of the Carboniferous Stull Shale of Kansas (Mángano and Buatois, 2004, Fig. 4b, p. 163), which contains abundant wrinkle structures, is identical to facies of the upper Moenkopi Formation of southern Nevada (Pruss et al.,

2004, Fig. 3d, p. 363); only the interpretations are different.

Even microbialites of the immediate post-Permian aftermath are not universally considered to represent disaster forms (Kershaw et al., 2002) as other abiotic factors apparently controlled their distribution (cf. Shen and Webb, 2004). These conflicts demonstrate the potential dangers of letting a model control one’s interpretations of the fossil record, without due consideration of possible alternatives. Such “hypothesis-driven interpretations” (Stinnesbeck et al., 1994) are, unfortunately, rather common in the study of extinction events. Clearly, more detailed work is needed to determine the factors controlling the distribution of so-called disaster taxa.

5.2.2. A new recovery model?

More recently, efforts have got underway to construct an alternative method of describing marine benthic recovery based on empirical data from the fossil record (Twitchett et al., 2004). The currently proposed ordinal scheme comprises four Recovery Stages, from the initial post-extinction aftermath to

the final recovery of the benthic fauna (Fig. 3) and is based on observation of fossil assemblages from Permian–Triassic shallow shelf environments. The broad aim of devising such a model is to allow comparison of the rates of recovery between different regions or localities in the aftermath of a single event, or between different events. The model incorporates data on trace fossils, which are the only records of responses of the soft-bodied biota to extinction events (Twitchett and Barras, 2004), as well as body fossils, and thus could potentially be used to compare ancient events with modern, smaller scale defaunation events and experimental work.

Several key palaeoecological criteria have been found to be most useful in the discrimination of the recovery stages: (1) tiering levels, (2) the presence/absence of key ichnotaxa, (3) body (or burrow) size and (4) dominance and evenness of shelly assemblages. Diversity also changes through the recovery interval, of course, but not necessarily in a predictable way. For example, the sudden appearance of many opportunists in the aftermath of an event may lead to a peak in local (alpha) diversity prior to final recovery

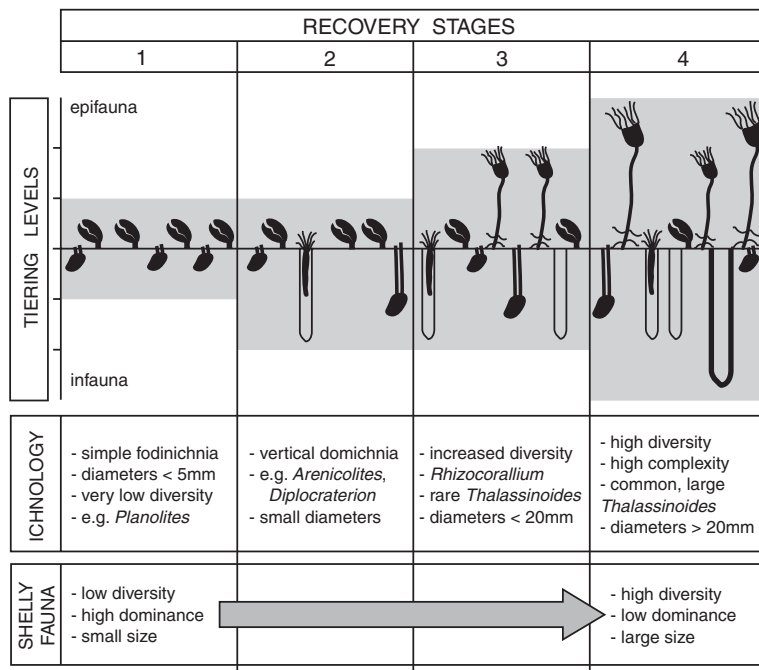


Fig. 3. Four stage palaeoecological model for recovery of benthic marine ecosystems in the aftermath of biotic crises, based on empirical observations of the fossil record of Permian–Triassic shallow shelf settings (see also Twitchett et al., 2004). See text for further details.

and has been recorded in both modern (Lu and Wu, 2000) and ancient (Looy et al., 2001) events. In addition, measured diversity may be affected by factors such as preservation, taphonomy and the scale of the study (e.g., field observations, study of museum specimens, thin section analyses etc.).

Tiering (sensu Ausich and Bottjer, 1982) is a very useful measure of ecological recovery (e.g., Twitchett, 1999). Tiering describes the vertical stratification of marine suspension feeders above and below the level of the substrate. The epifaunal and infaunal tiers appear to be decoupled, and tiering levels have changed through time (Ausich and Bottjer, 1982; Bottjer and Ausich, 1986). Recently, it has been realised that mass extinction events cause a temporary, dramatic reduction in tiering levels (e.g., Bottjer et al., 1996; Twitchett and Barras, 2004), and so the recovery of tiering back to pre-event levels can be used to assess benthic recovery (Twitchett et al., 2004; Fig. 3). In the immediate aftermath (Recovery Stage 1) epifaunal and infaunal tiering is reduced to a bare minimum. Next, infaunal tiering begins to recover (Recovery Stage 2), followed by epifaunal tiering (Recovery Stage 3). Finally, pre-extinction levels of tiering are attained (Recovery Stage 4). Infaunal tiering can be measured directly from the depth of bioturbation (e.g., Twitchett and Barras, 2004), or inferred from e.g., the morphology of the shelly, infaunal mollusca. Epifaunal tiering is measured from the shelly remains (e.g., articulated crinoids). In the absence of articulated material, the presence of a high tier can still be inferred from the presence of e.g., disarticulated crinoid ossicles. Such ossicles have a very high preservation potential, and so although absence may be due to shell bed taphonomy, this bias is considered to be minimal.

Recent work on the post-extinction trace fossil records of the early Triassic and Early Jurassic (e.g., Twitchett and Wignall, 1996; Twitchett, 1999; Twitchett and Barras, 2004) have shown that there is a stepwise reappearance in certain ichnotaxa during the post-extinction recovery. At first, Twitchett (1999) supposed that the re-appearances were globally synchronous. However, this is not the case, and although the sequence of trace fossil recovery remains similar worldwide, at least after the Late Permian and Late Triassic events (Twitchett and Barras, 2004), the timing of reappearance of specific ichnotaxa may be

globally diachronous. Thus, trace fossils can be used as a measure of relative recovery rates. The immediate extinction aftermath (Recovery Stage 1) is characterised by the presence of rare, small, simple fodinichnia (e.g., *Planolites*) of deposit feeding animals and an absence of the vertical domichnia of suspension feeders. Subsequently, these domichnia (e.g., *Arenicolites* and *Diplocraterion*) appear in Recovery Stage 2, and are themselves followed by ichnotaxa that may be attributable to burrowing crustaceans, such as *Rhizocorallium* and, sometimes, small *Thalassinoides* (Recovery Stage 3). A return to pre-extinction ichnodiversity, burrow size and amount of bioturbation characterises the final stage of recovery. The reappearance of common, large (>20 mm) diameter *Thalassinoides* and/or *Rhizocorallium* burrows are considered particularly indicative of the final stage of benthic recovery (Twitchett et al., 2004).

The combination of ichnology and tiering are viewed as particularly powerful tools for documenting benthic recovery in marine shelf settings, and can be easily applied in the field. Other useful measures include organism size (or burrow diameter), which is typically very low in the extinction aftermath and increases again through the post-extinction recovery. Changes in tiering and organism size hint at profound changes in the biomass of marine ecosystems through these events. In addition, ecological parameters such as the dominance and evenness of fossil assemblages also provide a measure of recovery, although care is required in their application, as they are particularly sensitive to changes in taphonomy and preservation. Typically, the immediate post-extinction aftermath (Recovery Stage 1) is characterised by high dominance (often also high abundance) assemblages (e.g., Schubert and Bottjer, 1995; Twitchett, 1999; Twitchett et al., 2004), whereas the final stage of recovery is characterised by a return to more 'even' communities. When the changeover occurs is not very clear, although from a theoretical point of view it should be at the boundary between the Survival and Recovery Intervals of Kauffman and Harries (1996).

As this model is applied more widely, it will no doubt be refined and probably superseded by better methods. As Erwin (1998, 2001) has noted, quantifying biotic recovery is certainly not easy. It is, however, of prime importance as we seek to more fully understand the way in which the global biosphere has

responded to extinction events in the past and how different events compare. Successful management of the present-day biodiversity crisis and its aftermath may depend upon such studies.

5.3. Size change (the Lilliput Effect)

Adam Urbanek (1993) described a “post-event syndrome” that affected Silurian graptolites, and is very applicable to the aftermath of mass extinction events as well. One aspect of this model that is particularly important is his “Lilliput effect”. This term refers to the pattern of size change through extinction events, specifically the temporary appearance of organisms with suboptimal body size (i.e., dwarfism or stunting) in the immediate aftermath. Body size is a key morphological variable, with implications for many aspects of an animal’s biology, behaviour and ecology, and so understanding the Lilliput effect may be crucial in understanding the nature of ecological, environmental and biological change during past biotic crises.

The study of Urbanek (1993) documented a size decrease in several taxa of Silurian graptolites, all of which were holdover or survivor taxa of (relatively) minor biotic crises. In the subsequent decade, the Lilliput effect has been recognised in the aftermath of the five mass extinction events and has been documented in a wide variety of animal groups (Twitchett, 2001 and refs. therein). It appears to be a factor that is common to all known extinction crises. Do animals respond in a similar (and therefore predictable) way to all biotic crises regardless of scale and forcing mechanism? If so, then this has important implications for our understanding of the response of organisms to ecological disturbance at both global and local scale, and may even allow us to predict the future response of the biosphere to present-day environmental change. Alternatively, does this commonality imply that a single proximate cause links all major extinction events of the past?

What are the possible causes of size decrease following extinction events? The simplest explanation is to invoke size selection during the extinction event itself, which causes the demise of large K-selected taxa and heralds their replacement by small, r-selected opportunists. While post-extinction size increase has been explained in terms of changes in life-history

strategy (e.g., Hallam, 1975), to date no study has demonstrated that extinctions are size selective (Jablonski, 1996; discussion above), although selection against large body size was invoked as an explanation for size changes in K–T and P–Tr bivalves (Hayami, 1997). At the K/T boundary event, while all of the large, specialist (K-selected) planktonic foraminifera disappeared, so did all the small trochospiral ecological generalist taxa (except the hedbergellids, which became extinct in the early Danian) (Keller, 2003).

The Lilliput effect of Urbanek (1993) explicitly describes temporary, within-lineage size decrease of the surviving organisms. Data collected by the author from a number of Early Triassic assemblages worldwide show that not only are surviving taxa smaller than expected, but taxa which originate in the immediate aftermath of the Late Permian extinction crisis are also significantly smaller than later forms (Fig. 4). Therefore, the Lilliput effect is not restricted to just the holdover taxa (cf. Urbanek, 1993), and may be caused by the nature of the environment in the imme-

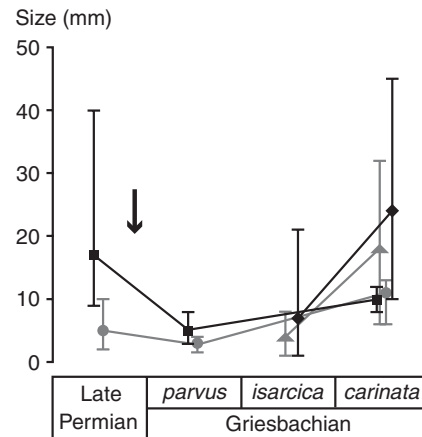


Fig. 4. Temporary size decrease (the Lilliput effect) in benthic marine invertebrates in the aftermath (Griesbachian substage) of the Permian–Triassic mass extinction event. Black square=*Bellerophon* ($n=42$); grey circle=*Lingula* ($n=195$); black diamond=*Claraia* ($n=721$); grey triangle=*Unionites* ($n=258$). Symbols show mean size, horizontal lines indicate maximum and minimum recorded sizes. Size calculated as the geometric mean of length and height. All within-taxon size changes are significant at the 5% level (Kolmogorov–Smirnov test). Data collected in the field from localities in northern Italy (Bellerophon and Werfen Formations). The Griesbachian is divided into three conodont zones: *parvus*, *isarcica* and *carinata*. Arrow indicates approximate position of extinction event. Data modified from Price-Lloyd and Twitchett (2002).

diate post-extinction aftermath. The post-Permian Lilliput effect lasted until the late Griesbachian (*carinata* Zone). As well as the short, sharp, within-lineage size decrease recorded in the immediate post-extinction aftermath (i.e., the Lilliput effect, sensu Urbanek (1993); Fig. 4), Early Triassic taxa in general are also much smaller than their modern, or Late Palaeozoic, counterparts (e.g., Fraiser and Bottjer, 2004; Payne et al., 2004), which implies that the environmental causes of size decrease were of a significant duration and/or that more than one process is operating. The incredibly low levels of atmospheric oxygen during Early Triassic may be one factor; productivity may be another. Furthermore, evidence from Permian–Triassic and Triassic–Jurassic trace fossils, indicates that the Lilliput effect is not restricted to just mineralised taxa but may affect the soft-bodied biota as well (Twitchett, 1999; Twitchett and Barras, 2004), so is probably not caused by some preservational bias or by a problem with biocalcification.

Stanley (1973) hypothesised that for any given set of environmental parameters there is an optimal body size for animals, and that size trends result from the process of attaining optimal size in the face of changing environmental conditions. If the immediate aftermath of mass extinction events represents a time when environmental conditions are such that small size is favoured, then this could explain some aspects of the Lilliput effect. There are a number of potential environmental causes of stunting in animals, including suboptimal salinity, low oxygen levels, low food supply etc. (e.g., Hallam, 1965), which have all been linked to mass extinction events. In particular, rapid global warming may result in the co-occurrence of several of these factors, e.g., productivity collapse and oceanic anoxia. Rapid dwarfing of many taxa of planktonic foraminifera is recorded in the latest Maastrichtian warm event (Abramovich and Keller, 2003).

Food shortage is one environmental factor that has long been associated with body size decrease (Hallam, 1965; Hayami, 1997) and is favoured by the author as an explanation of the Lilliput effect (Twitchett, 2001). The compelling evidence that phytoplankton collapse may be behind the selectivity of mass extinction events (see above; Hayami, 1997) is an additional reason to favour food shortage as a cause of the Lilliput effect. Certainly, within-lineage size decrease has been linked to productivity collapse and food

shortage in Frasnian–Famennian conodont taxa (Renaud and Girard, 1999), P–Tr gastropods and *Lingula* (Price-Lloyd and Twitchett, 2002) and K–T echinoids (Smith and Jeffrey, 1998). Many modern studies show that adult size is restricted by a lack of food, especially if the shortage occurs early in life history.

A critical test for the food shortage hypothesis would be to demonstrate that the Lilliput changes were synchronous with a decrease in primary production. Good proxies for marine primary productivity exist in post-Jurassic strata. For example, by comparing the $\delta^{13}\text{C}$ values of benthic and planktonic foraminifera a collapse in primary production has been demonstrated for the K–T boundary event (D'Hondt et al., 1996), which may have lasted some 500,000 years (Barrera and Keller, 1994). Data from K–T echinoids indicates that most survivors suffered dramatic size decrease through the event, and remained small until the latter half of the Danian, consistent with the duration of this shortage in nutrient supply (Smith and Jeffrey, 1998).

In pre-Jurassic rocks, proxies for marine productivity are more problematic. For example, the $\delta^{13}\text{C}$ record can be the result of several different processes such as terrestrial biomass burning, methane release or volcanic activity (see Berner, 2002 for recent discussion). When tackling these older events, testing and rejecting alternative possible causes of size change (such as temperature change and benthic oxygen levels) will be one way forward, as the proxies for these environmental changes are less equivocal than are those for productivity levels.

The study of the Lilliput Effect is currently a minor, but nevertheless important, aspect of mass extinction studies. If the fauna of an entire ecosystem really can become stunted for hundreds of thousands of years, due to environmental changes such as reduction of food supply and oceanic anoxia brought on by rapid climate warming, then there are significant implications for the present biodiversity crisis.

6. Summary

Mass extinction studies have enjoyed a surge in scientific interest of the past 30 years that shows no sign of abating. Recent areas of particular interest

include the palaeoecological study of biotic crises, and analyses of patterns of post-extinction recovery. There is good evidence of rapid climate change affecting all of the major extinction events, while the ability of extraterrestrial impact to cause extinction remains debatable. There is growing evidence that food shortage and suppression of primary productivity, lasting several hundred thousand years, may be a proximate cause of many past extinction events. Selective extinction of suspension feeders and the prevalence of dwarfed organisms in the aftermath are palaeoecological consequences of these changes. The association with rapid global warming shows that study of mass extinction events is not just an esoteric intellectual exercise, but may have implications for the present day.

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