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The Case for Sea-Level Change as a Dominant Causal Factor in Mass Extinction of Marine Invertebrates [and Discussion]

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The case for sea-level change as a dominant causal factor in mass extinction of marine invertebrates

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A correlation between global marine regressions and mass extinctions has been recognized since the last century and received explicit formulation, in a model involving habitat-area restriction, by Newell in the 1960s. Since that time attempts to apply the species–area relation to the subject have proved somewhat controversial and promoters of other extinction models have called the generality of the regression–extinction relation into question. Here, a strong relation is shown to exist between times of global or regional sea-level change inferred from stratigraphic analysis, and times of high turnover of Phanerozoic marine invertebrates, involving both extinction and radiation; this is valid on a small and large scale. In many cases the most significant factor promoting extinction was apparently not regression but spreads of anoxic bottom water associated with the subsequent transgression. The sea-level–extinction relation cannot be properly understood without an adequate ecological model, and an attempt is made to formulate one in outline.

INTRODUCTION

One of the best established results from analysis of the stratigraphic record of the continents is that they have been subjected to a succession of regionally extensive marine transgressions and regressions through the Phanerozoic. That some of these events were global in extent, and hence caused by eustatic changes of sea level, was first proposed by Suess (1906). Eustasy has been a recurrent theme among stratigraphers ever since. The application of the new technique of seismic stratigraphy by Exxon geologists (Vail *et al.* 1977; Haq *et al.* 1987) has been a major stimulus to its study. With respect to the Palaeozoic of North America, Moore (1954) perceived a relation between regressions and extinctions in the marine realm, as had Suess's contemporary, Chamberlin (1909). The idea was pursued further by Newell (1967) who recognized six episodes of Phanerozoic mass extinction, end-Cambrian, end-Ordovician, late Devonian, end-Permian, end-Triassic and end-Cretaceous. Except for the first, all of these have been subsequently accepted by the palaeontological community as genuine mass extinction events, and the end-Cambrian is also recognized as a significant event for certain groups, based on Sepkoski's (1986) analysis of family and generic turnover.

Newell (1967) put forward a qualitative argument that shrinkage of the area of epicontinental sea habitat should have a deleterious effect on neritic organisms and should therefore lead to widespread extinction. Radiation of the survivors would take place during the expansion of habitat area consequent upon a succeeding transgression. A quantitative analysis based on the ecologists' species–area relation was subsequently undertaken by Schopf (1974) and Simberloff (1974) for the biggest extinction event in the Phanerozoic, at the end of the Permian, and was held to provide support for Newell's claim of a strong relation between regression and extinction.

Within the past few years Newell's ideas, and the quantitative application of the taxon–area relation to account for mass extinctions by regression of epicontinental seas, have come under attack from palaeontologists wishing to promote alternative interpretations (McLaren 1983 and 1989; Stanley 1984 and 1986; Hansen 1987). Consequently they require further evaluation in the light of the most up-to-date information. There is also a need to take into account the inferred spread of anoxic bottom waters within epicontinental seas that is commonly associated with the early phase of transgressions; this may well prove to be more significant for mass extinction than regressions. With regard to the physical evidence of eustatic sea-level change, Haq *et al.* (1987) have argued that the correlation of major unconformities is more significant than transgressions and regressions, but Hubbard (1988) has convincingly demonstrated that many such unconformities are of regional, not global extent. It is worth bearing in mind that some episodes of mass extinction may also be regional not global. If these can be shown to correlate with corresponding regional episodes of regression or anoxic spread associated with transgression (Hallam 1986) this will strengthen the case for a relation at least with extensive epeirogeny, if not eustasy. It is always worth bearing in mind that whereas global sea-level curves are abstractions, about which there will probably always be some measure of dispute about because of inevitable uncertainties concerning the frequency, extent and rate of eustatic change, a high degree of consensus can be obtained among stratigraphers about transgressions and regressions on a regional and sometimes a global scale. Transgressions and regressions are tangible phenomena that must have had significant environmental effects on epicontinental environments.

Eustasy-extinction correlation at different scales

Notwithstanding the arguments that have been put forward against sea-level change as a dominant control on mass extinctions, it is difficult to disagree with Jablonski's (1986*a*) assessment that it shows the strongest empirical correlation of all the factors that have been proposed. This correlation is evident at large, intermediate and small scales.

The large-scale correlation can be demonstrated by plotting Newell's (1967) six marine extinction events against a sea-level curve derived from stratigraphic analysis (figure 1). Although there is no published sea-level curve that is not open to dispute, a high measure of consensus exists among stratigraphers that there were significant global regressions at the end of the Ordovician, Permian, Triassic and Cretaceous. It is also noteworthy that the biggest extinction event of all, at the end of the Permian, corresponds, according to the latest estimate, to a very substantial sea-level fall (Holser & Magaritz 1987). Another point to note in figure 1 is that the regressions were quickly followed by significant transgressions. This observation is pertinent to the common association with widespread marine anoxia, to be discussed later.

With regard to an intermediate scale, concerning events at intervals of the order of a few tens of millions of years apart, the ammonoids are a suitable group to study because of their high diversity through a significant portion of Phanerozoic history, and their high rate of generic turnover, implying a high rate of evolution and extinction. This implies that comparatively stenotopic organisms are sensitive to even modest environmental changes. If the taxon–area relation is valid, times of low sea level should correlate with times of low generic diversity because of increased extinction rate; and times of high sea level with high diversity because of increased origination rate, as a consequence of the correlation between sea-level stand and area

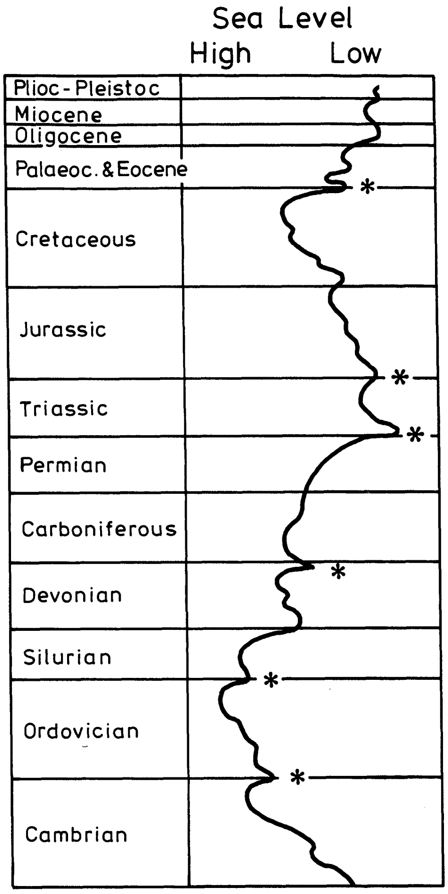

FIGURE 1. The Phanerozoic sea-level curve of Hallam (1984) with asterisks signifying the six marine mass extinction episodes recognized by Newell (1967). Adapted from fig. 6 of Hallam (1984).

of epicontinental sea. Despite the uncertainties involved in palaeogeographic reconstructions, which mean that only approximate results can be obtained, the varying degree of inundation of the continents through time (represented by the sea-level curve) can be established from stratigraphic analysis with less ambiguity than by utilizing unconformity-bound stratigraphic sequences (Vail *et al.* 1977; Haq *et al.* 1987). It has the further advantage of monitoring more directly the factor thought to be responsible for the diversity variations.

Figure 2 presents a plot of ammonoid generic diversity against two sea-level curves. Wiedmann's curve (1986) is based on data from Yanshin (1973) and Sliter (1976) on the changing area of marine inundation of the continents from the Devonian to the Cretaceous inclusive. My curve is based on a best estimate utilising both marine inundation data and data from facies changes up stratigraphic successions; this may account for some of the differences. One point, however, I will readily concede. There was a major fall of sea level in the mid-Carboniferous, as portrayed in the Wiedmann curve, which is clearly apparent from stratigraphic data in both the northern and southern hemispheres (Saunders & Ramsbottom 1986; Veevers & Powell 1987). Furthermore, I have utilized Schopf's (1974) data for the Permian without taking account of intra-Permian events such as an early late-Permian sea-level rise claimed from sequence data by Vail *et al.* (1977).

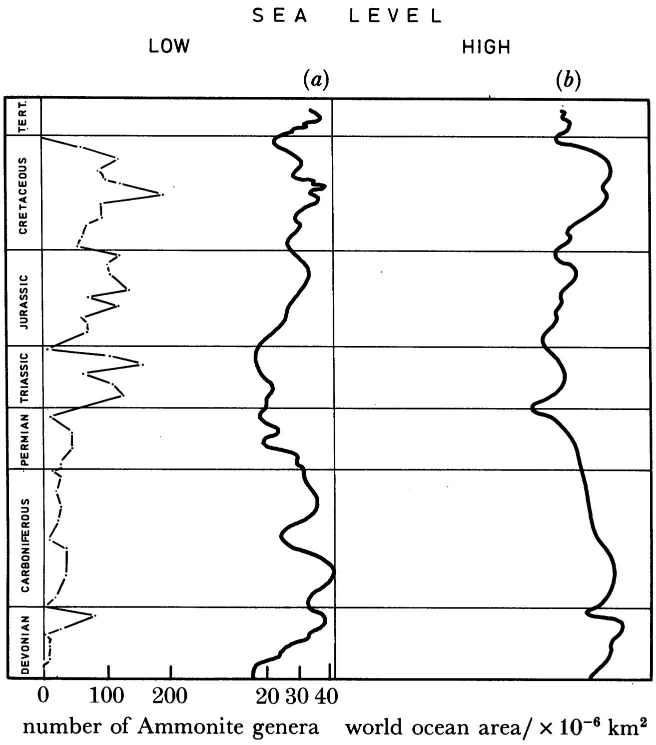

FIGURE 2. Plot of ammonoid generic diversity (broken line), based on data from House (1985), against sea-level curves (*a*) (Wiedmann 1986) and (*b*) (Hallam 1984), (solid lines.)

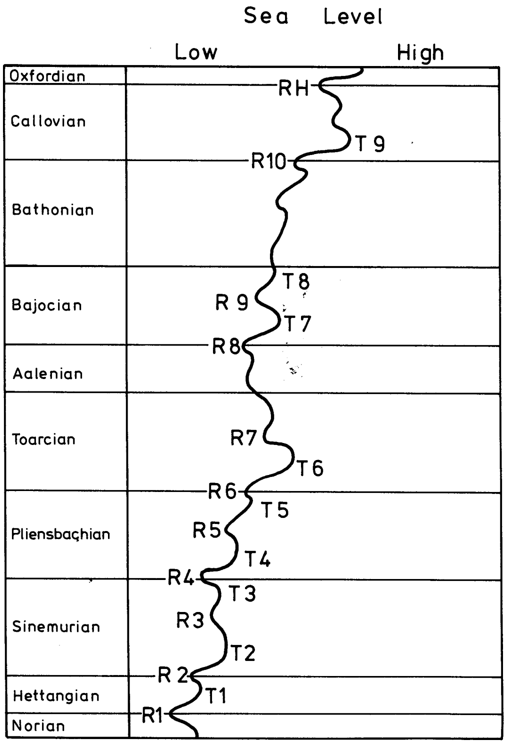

FIGURE 3. Early and Middle Jurassic sea-level curve of Hallam (1988) with succession of transgressive (T) and regressive (R) episodes enumerated. See table 1.

Table 1. Early and Middle Jurassic ammonite radiations and extinctions in relation to transgressions and regressions

(See figure 3.)

transgressive and regressive event	radiations	extinctions
R_{11} end-Callovian	—	kosmoceratids reineckiids tulitids
T_9 early Callovian	kosmoceratids macrocephalitids	—
R_{10} end-Bathonian	—	last stephanoceratids (Cadomitinae) clydoniceratinae
T_8 late Bajocian	perisphinctids	—
R_9 mid-Bajocian	—	sonniniids
T_7 early Bajocian	sonniniids	—
R_8 end-Aalenian	—	most hildoceratids and graphoceratids
R_7 mid-Toarcian	—	dactylioceratids
	hildoceratids dactylioceratids	—
T_6 early Toarcian	(plus migration into boreal realm)	—
R_6 end-Pliensbachian	—	amaltheids
T_5 late Pliensbachian	amaltheids	—
R_5 mid-Pliensbachian	—	liparoceratids
T_4 early Pliensbachian	polymorphitids etc.	—
R_4 end-Sinemurian	—	echioceratids oxynoticeratids
T_3 late Sinemurian	echioceratids oxynoticeratids	
R_3 mid Sinemurian	—	arietitids
T_2 early Sinemurian	arietitids	
R_2 end-Hettangian	—	psiloceratids most schlotheimiids
T_1 Hettangian	psiloceratids schlotheimiids	—
R_1 end-Triassic	—	mass extinction

Regardless of their differences there is a discernible relation between sea-level curves and ammonoid diversity (figure 2). Both curves indicate a generally steady rise in sea level through the Devonian, with the time of highest stand in the late Devonian correlating closely with the peak diversity. Thereafter a sharp fall at or close to the end of the period corresponds with a marked drop in diversity to almost zero. Two diversity cycles in the Carboniferous correspond with two major eustatic cycles, with higher diversities being recorded in the early Carboniferous, when sea level stood higher. The sharp diversity fall near the end of the Permian corresponds more closely with my curve than with Wiedmann's, as does the late Triassic diversity maximum followed by a sharp fall to almost zero. Both curves correspond well with the Jurassic diversity pattern, and the mid-Cretaceous diversity peak corresponds better with Wiedmann's curve based on Sliter's (1976) data, suggesting that Cretaceous sea level reached its highest stand at that time. The late Cretaceous sea-level fall shown in both curves matches the gradual diversity decline to zero at the end of the period. It should be noted that the magnitude of sea-level change does not necessarily relate closely to the magnitude of diversity change.

Ammonoids can also be utilized to demonstrate small-scale correlation. Figure 3 is my sea-level curve for the early and mid-Jurassic, with a succession of transgressive and regressive episodes indicated at approximately 5 Ma intervals. These correspond to radiations and extinctions of ammonite families, respectively (table 1). The details of the curve are primarily based on sedimentary cycles in the exceptionally well studied European deposits, but also take into account contemporary transgressions and regressions in other continents. That the sea-level oscillations are more likely to be global than regional in extent is also indicated by the close correlation with ammonite radiation and extinction episodes. Most of the ammonites in question are cosmopolitan in distribution, and if the regressions clearly recorded in Europe were confined to that continent they could have retreated to refuges elsewhere, and returned during the subsequent transgressions, rather in the way that Quaternary organisms have followed shifting climatic belts (Coope 1979).

Bayer & McGhee (1986) confirm the relation outlined above, for the early Middle Jurassic of Central Europe, and claim a hierarchical pattern of change in the vertical sedimentary cyclic sequences corresponding with the pattern of ammonite turnover, more or less at the levels of family, genus and species. Ramsbottom (1981) came to very similar conclusions with respect to the relation of Carboniferous goniatite turnover with eustatic cycles. Other contemporary invertebrate groups such as bivalves have a much slower rate of taxonomic turnover, evidently being less vulnerable to extinction. Consequently they do not exhibit the small-scale relation so well shown by ammonoids.

Regression or anoxia?

The regression model for extinction of organisms in epicontinental seas depends upon the species–area effect being generally applicable. It does indeed appear that there is nearly always a positive correlation among living organisms in a wide range of habitats between species number and area (Connor & McCoy 1979) and study of a variety of island populations confirms the general supposition that the chances of extinction increase with decreasing habitat area (Diamond 1984). Furthermore, Sepkoski (1976) undertook a multiple-regression analysis of Phanerozoic species diversity data that appears to offer support for the species–area relation with respect to ancient epicontinental seas (see also Flessa & Sepkoski (1978)). Nevertheless, several reservations have been expressed about uncritical application of the species–area relation, whatever it may signify, to the fossil record. Thus Wise & Schopf (1981) estimated the changes in diversity of marine species between low and high stands of Quaternary sea level. They found 25% change in species, 10% in generic and less than 5% in family diversity. This agrees with the general observation that large-scale generic or family level changes are insignificant during the Quaternary. They argued accordingly that the substantial family-level drop in the late Permian was more likely to be bound up with a reduction in the number of faunal provinces (Schopf 1979). Similarly, Jablonski (1985) argued that in the modern world most marine faunas would persist in undiminished shallow water regimes around oceanic islands at times of Quaternary sea-level fall of the amount recorded, and thus, that major family-level extinction could not occur.

Stanley (1984, 1986) has observed that one of the biggest Phanerozoic sea-level falls took place, according to Vail *et al.* (1977), in the mid-Oligocene, at a time when no marine mass extinction event is recognizable. Hansen (1987) sees no relation between Palaeogene mollusc extinctions and reductions in shelf area in the Gulf Coast region of North America. More generally, Wyatt's (1987) hypsometric study has demonstrated that the response of continents to sea-level change depends upon their size, and that the global curve of shallow sea area with time that he produced does not vary in a straightforward manner with respect to sea level. Accordingly, predictions of organic diversity change with sea level should take account of their non-linear relation. A comparable point was made by Martin (1981); the species–area curve is steep for small areas but the slope becomes asymptotic as the area increases.

Regarding the Quaternary, one important factor that should not be overlooked is the comparative rapidity of glacioeustatic sea-level change. Bearing in mind that extinction risk increases with time in a stressful environment without further diminution of area (Diamond 1984) it could be that the rapid restoration of less stressful conditions in the Quaternary has served to diminish the extinction rate owing to reduction of habitat area through sea-level fall. The slower and less spectacular sea-level falls of much of the Phanerozoic might have been environmentally more significant because they lasted longer, and quite modest falls in very extensive and extremely shallow-water epicontinental seas with no close modern analogue could have had a correspondingly major effect (Hallam 1981*a*). For both the Oligocene and Quaternary, however, an important factor might have been the presence of well aerated deep ocean as a consequence of the active circulation of cold, dense bottom water derived from the Antarctic. Thus the deep sea would have provided a refuge that might not have been in existence during the Palaeogene, Mesozoic and much of the Palaeozoic. The notion that the deep sea was more or less anaerobic for much of the geological past goes back to Murray (1895), and most of the modern deep-sea fauna may, for this reason, be no older than Neogene (Briggs 1987). A stagnant deep ocean is proposed for equable periods of earth history by Fischer & Arthur (1977) and mass extinction models invoking this factor have been put forward by Keith (1982) and Wilde & Berry (1984).

A strong empirical correlation exists between the early phases of marine transgression in epicontinental settings and the extensive spread of laminated organic-rich shales (black shales in traditional parlance), which are with good reason held to signify deposition in more or less anoxic water (Hallam & Bradshaw 1979; Hallam 1987*a*; Thickpenny & Leggett 1987). Because such transgressions normally follow quickly after major regressions, it is not always clear from analysis of extinction events what the critical causal factor was, although in both cases there would have been a reduction in benthic and nektobenthic habitable area. I briefly review the relevant evidence for several of the 29 Phanerozoic mass extinction events recognized by Sepkoski (1986) on the basis of his analysis of fossil marine genera.

Cambrian

Because of their high diversity and rate of turnover, trilobites provide the most promising material for study, and Sepkoski (1986) notes a number of extinction events, most apparently minor (Briggs *et al.* 1988). One of the more notable of these is at the end of the early Cambrian. An extensive, circum-Iapetus, regression event at this time also coincides with the extinction of the archaeocyathids (Palmer & James 1980). The most important event, at least for platform or cratonic trilobites as opposed to those that lived in deeper offshore waters, was at the end of the Cambrian. Thus at this time approximately half of North American trilobite families became extinct (Westrop & Ludvigsen 1987). To account for the extinctions these authors apply a simple biogeographic model following Schopf (1979), involving a reduction in the number of faunal provinces as a result of transgression at the beginning of the Ordovician. On the other hand Briggs *et al.* (1988) perceive a compound event, with extinction rate increasing with end-Cambrian regression prior to the extinctions associated with transgression at the beginning of the Ordovician. Westrop & Ludvigsen consider that facies data on the North American craton argue against invoking an anoxic event. Berry & Wilde (1978) and Thickpenny & Leggett (1987) single out the late Cambrian as a time of very extensive black shale deposition, so the possibility of an anoxic event cannot be excluded. Furthermore, deeper-water trilobites survive the end Cambrian event (Fortey 1983). Of these, at least the olenids and agnostids were probably adapted to cope with low oxygen concentrations.

Ordovician–Silurian

The only event of major importance in this period was at the end of the Ordovician, when one of the five most significant marine mass extinctions of the Phanerozoic took place. This has been generally associated with a regression caused by a glacioeustatic fall of sea level that was itself associated with the extension of the Saharan ice sheet. Briggs *et al.* (1988) claim to observe a compound event associated with the trilobites. A significant reduction in generic diversity is coincident with the stratigraphically well-documented regression, but the final extinction coincides with the subsequent earliest Silurian transgression that can be interpreted as glacioeustatic rebound following disappearance of the Saharan ice sheet. The earliest Silurian is marked by an exceptionally wide distribution of black shales and is a prime candidate for an oceanic anoxic event (Thickpenny & Leggett 1987).

Devonian

With regard to the ammonoids, House (1985) recognizes no fewer than eight extinction events from the early Devonian to the beginning of the Carboniferous that show a strong correlation with the widespread establishment of anoxic conditions associated with global transgressive pulses. Of these the most important, termed by House the 'Kellwasser event', took place at the Frasnian–Famennian boundary, and is one of the five biggest marine extinction events in the Phanerozoic. It is most notable for the dramatic and short-term disappearance of reef ecosystems (McLaren 1983). Whereas Johnson *et al.* (1985) agree with House that the mass extinction at this time is marked by global transgression associated with a widespread anoxic event, Goodfellow *et al.* (1989) argue for an association of the anoxic event with regression at the start of the Famennian. On the basis of conodont biofacies changes Sandberg *et al.* (1988) claim a short-term eustatic rise followed by a fall at the end of the Frasnian.

Carboniferous

According to House (1985) the correlation between widespread anoxia and ammonoid extinction is especially clear for his so-called 'Hangenberg event' at the Devonian–Carboniferous boundary. M. R. House (personal communication) also recognizes a regressive event preceding it, a pattern he compares with that at the Frasnian–Famennian boundary. Sepkoski (1986) recognizes a major mid-Carboniferous event, at the Visean–Namurian boundary, with a relatively low, although significant, extinction rate against a low rate of background extinction. The global diversity reduction at this time among ammonoids has already been noted (figure 2). As regards North America, Saunders & Swan (1984) correlate the severe goniatite diversity reduction with the major regression recorded by the widespread unconformity of the Mississippian–Pennsylvanian boundary. It should, however, be noted that, in exceptionally complete sections in Oklahoma and Texas, this boundary is marked by black shales enriched in phosphate, chalcophile and platinum group elements (Orth *et al.* 1986).

Permian

The largest extinction event of all, which significantly affected nearly all marine groups, correlates with an equally dramatic global regression. According to the most recent estimate, the fall of sea level might have been as much as 280 m, at a rate of 60 m per Ma. It was immediately followed at the start of the Triassic by an even more rapid sea-level rise (Holser & Magaritz 1987). No widespread black shales have been reported for the earliest Triassic, but account should be taken of the fact that stratigraphically continuous sections across the Permian–Triassic boundary are very rare as a consequence of the end-Permian regression. The sections in the Lower Yangtze region near Nanjing, China, are the most complete in the world (Sheng *et al.* 1984); I have observed that the oldest Triassic limestones, though not evidently organic-rich, are finely laminated and almost entirely benthos-free, both features characteristics of anoxic deposits. The only benthic megafossils present are a few thin horizons rich in the bivalve *Claraia*; this is considered to be an opportunistic genus well adapted to dysaerobic conditions (P. Wignall, personal communication). Similar deposits with restricted, probably dysaerobic, faunas, are recorded from basal Triassic deposits in other parts of the world, such as the Caucasus, Kashmir and the southern Alps (Logan & Hills 1973).

Triassic

The only significant Triassic event recognized by Sepkoski (1986) is at the end of the period, when conodonts completely disappeared and ammonites almost completely disappeared. Many other groups were severely affected, including reef communities (Fagerstrom 1987). There is a strong correlation with widespread and substantial regression, but it is also noteworthy that the oldest Jurassic strata in western Europe include extensively distributed laminated black shales and organic-rich limestones signifying anoxic conditions; these correlate with a global transgression (Hallam 1981*b*). Personal observations in Western Nevada and northern Chile indicate barren, laminated black shales and limestones at the Triassic–Jurassic boundary, anoxic conditions having been established shortly before the end of the Triassic. I saw no evidence of end-Triassic regression. The same is true for northern Peru (Prinz 1985).

Jurassic

Two Jurassic extinction peaks are revealed by Sepkoski's generic data, Pliensbachian–Toarcian and Tithonian. The former can be pinpointed more accurately as an early Toarcian extinction event in Europe affecting the majority of the benthos and nektobenthos at species level, but not the plankton. In global terms, it correlates precisely with a transgression and an oceanic anoxic event as indicated by both facies and carbon isotope data (Hallam 1987*b*; Jenkyns 1988). This event is significant for more general interpretation because it is not immediately preceded by a globally extensive late Pliensbachian regression (though such a regression is recognizable in western Europe) that points to bottom-water anoxia as the only factor that need be invoked (Hallam 1987*b*). Whereas Jenkyns (1988) wants the anoxic event and concomitant extinctions to be global, evidence from Andean South America does not appear to accord with this (Hallam 1986); this matter clearly requires further investigation. The Tithonian event is also regional rather than global in extent. Where it is recognizable, in Europe, it correlates with evidence of widespread regression, but not anoxia during the subsequent transgression. In South America there is no evidence of regression or anoxia across the Jurassic–Cretaceous boundary (Hallam 1986).

Cretaceous

Two extinction events are clearly recognizable for this period, at the Cenomanian–Turonian boundary and at the end of the Maastrichtian. The Cenomanian–Turonian boundary event, which severely affected both the benthos and plankton (Elder 1987; Jarvis *et al.* 1988), correlates precisely with a major sea-level rise, perhaps to its highest point in the Cretaceous, and to an oceanic anoxic event clearly recorded by sedimentary facies and carbon isotope data (Schlanger *et al.* 1987; Arthur *et al.* 1987). Jarvis *et al.* (1988) recognize a series of extinction steps successively affecting the microbenthos, inferred deeper-water planktonic foraminifera and intermediate water groups. At the height of the event, the benthic fauna was extremely impoverished and the planktonic fauna consisted only of the shallowest water groups. These successive changes are correlated with a rapid rise of the oxygen minimum zone in the latest Cenomanian, and its progressive penetration into epicontinental sea environments. As with the Toarcian anoxic event, there is no evidence that this mid-Cretaceous event was preceded by a global fall of sea level.

With regard to the much discussed end-Cretaceous event, there is no need here to do more than point out that there is a strong correlation with significant global regression, which is likely to be implicated in many of the extinctions, if not with the plankton (Hallam 1987*c*) and that locally the basal Tertiary strata are organic-rich shales indicative of anoxic conditions. This is the case, for instance, in the Fish Clay of Denmark. Surlyk & Johanssen (1984) invoke bottom-water anoxia as one of the factors responsible for brachiopod extinctions in that country. It is worth noting that the highest iridium anomalies yet recorded from the K–T boundary come from organic-rich deposits at Stevns Klint, Denmark; Caravaca, Spain and Woodside Creek, New Zealand. A black clay, free of bioturbation also marks the base of the Tertiary at El Kef, Tunisia (Keller 1988*b*).

Tertiary

The most important extinction event is across the Eocene–Oligocene boundary but it has become evident from close study of the excellent marine record that the extinctions were spread out over several million years, though whether they were gradual (Corliss *et al.* 1984) or stepwise (Hut *et al.* 1987) remains debatable. Though temperature decline is commonly invoked as the prime causal factor, Dockery (1986) finds a good correlation between major benthic extinction events and marine regressions in the Gulf of Mexico coastal plain (see also Dockery & Hansen 1987).

As I have already stated, Stanley's (1984, 1986) argument that the spectacular mid-Oligocene sea-level fall recorded by Vail *et al.* (1977) does not correlate with an extinction event can be countered to some extent by invoking the concept of a well aerated deep ocean. A further point is that the approximately 400 m fall inferred by Vail *et al.* (1977) is a vast overestimate. The latest best estimate based on a variety of data is between 30 and 90 m (Miller *et al.* 1987).

In summary, of the 13 extinction events reviewed above, which include all the most important Phanerozoic events, regression seems to be definitely correlated in 10 cases and more doubtfully in 1, and anoxia definitely associated with transgression in 6 cases and more doubtfully in 4 (table 2). Only for the late Eocene has no correlation been yet established with either regression or anoxia, though following Dockery's (1986) work this remains a possibility.

Table 2. Correlation of marine regression and anoxic episodes with major Phanerozoic extinction events

major extinction event	regression	anoxia
late Eocene	?	–
end-Cretaceous	+	?
mid-Cretaceous (Cenomamian–Turonian)	–	+
end-Jurassic	+	–
early Jurassic (Toarcian)	–	+
end-Triassic	+	+
end-Permian	+	?
mid-Carboniferous (Visean–Namurian)	+	?
end-Devonian	+	+
late Devonian (Frasnian–Famennian)	+	+
end-Ordovician	+	+
end-Cambrian	+	?
end-Lower Cambrian	+	–

Discussion

Whereas many factors have been responsible for extinctions of particular species, there are only a few that can plausibly be invoked to account for more or less simultaneous mass extinctions of different types of marine organisms on a global scale. Although this can be considered an advantage in attempting to understand causes it should be noted at the outset that there is an interaction between environmental changes involving climate, volcanicity and sea level, so that determining the critical factor may not prove to be straightforward. Furthermore, it is important to distinguish between proximate and ultimate causes, particularly when evaluating the relative plausibility of extraterrestrial, as opposed to terrestrial, controlling factors.

Bolide impact

To have any kind of plausibility as a cause for extinctions as opposed to more conventional explanations based on changes confined to our own planet, bolide impact theories must satisfy at least two conditions. The extinctions must be demonstrated, by means of the best available stratigraphic evidence, to have been on a spectacular scale and to have taken place over geologically negligible periods of time (McLaren 1983). Secondly, there should be independent physical and chemical evidence, such as tektites, shocked quartz and platinum-group metal anomalies. After nearly a decade of intensive research such evidence remains weak to non-existent for all major extinction events except for that at the Cretaceous–Tertiary boundary (Donovan 1987; Orth & Attrep 1988; Orth 1989). Late Eocene deposits contain two regionally extensive tektite horizons, but neither correlate with a mass extinction (Glass 1988; Keller *et al.* 1987). Even for the Cretaceous–Tertiary extinction, some argue that the evidence can be explained with a purely terrestrial scenario (Hallam 1987*c*). There have undoubtedly been many bolide impacts during the Phanerozoic but the only persuasive case for an association with mass extinctions is the K–T event, which may therefore be unique in this respect. Even assuming the evidence for impact to be conclusive, it is still by no means clear how many of the end-Cretaceous extinctions relate to it, and no really plausible, exclusively impact-based 'killing scenario' has yet been proposed. The finest time resolution allowable from stratigraphic analysis is rarely less than several thousand years and usually much more. For the end-Cretaceous extinctions it has been argued that even for the more spectacular events, such as those affecting calcareous plankton, timescales of at least thousands of years must be invoked (Keller 1988*a*; Brinkhuis & Zachariasse 1988), though this view has been disputed by Smit *et al.* (1988). To propose a series of stepwise extinctions involving multiple impact by comets (Hut *et al.* 1987), is a scientifically weak response to the problem in the absence of independent evidence, requiring acceptance of a dubious astronomical hypothesis (Hallam 1987*c*). Furthermore, a recent analysis by Raup (this symposium) has thrown into doubt the possibility of distinguishing stepwise extinctions from more gradual or catastrophic events.

Climate

Climate can have an indirect affect on sea-level fluctuations at times of substantial polar icecaps as a consequence of glacioeustasy. A more direct influence for climate on Phanerozoic extinctions has been argued by Stanley (1984, 1986, 1988). His general hypothesis, that episodes of cooling, rather than of falling sea-level, have promoted mass extinctions in the marine realm, appears to be well-supported for the western North Atlantic regime in Plio-Pleistocene times. It is debatable whether it can be applied to extinctions earlier in the Tertiary. Whereas the increase in extinction rate across the Eocene–Oligocene boundary appears to correlate well with independent evidence of fall in oceanic temperatures (as determined by oxygen isotope analysis of foraminiferal shells), Shackleton (1986) points out that the main climatic change so determined, followed, rather than preceded, the biostratigraphic events that are generally taken as defining the Eocene–Oligocene boundary; this excludes a causal relation between the climatic and faunal changes. Dockery (1986) has perceived, for Gulf Coast molluscs, a close relation between extinctions and regressive events. For pre-Tertiary extinctions, evidence for the climatic cooling hypothesis is decidedly weak, if not non-existent. Thus the biggest extinction event of all, at the end of the Permian, coincides with a time of climatic amelioration following the disappearance of the last remnants of the Gondwana ice sheet (Veevers & Powell 1987.) Stanley (1988) holds a contrary opinion. Extinctions at the end of the early Carboniferous and Ordovician could be related to growth of ice sheets, but the key factor in these cases could be the regressions not the climatic cooling (Brenchley 1984; Powell & Veevers 1987). Stanley's principal argument in favour of his climatic control hypothesis is that organisms with a tropical distribution have been more subject to extinction than higher latitude organisms. This is indecisive because tropical organisms are generally stenotopic and therefore relatively vulnerable to a variety of environmental changes (cf. Jablonski 1986*b*).

Volcanism

The transmission of large quantities of volcanic dust and aerosols into the atmosphere and stratosphere is known to cause lowering of air temperatures and may also give rise to substantial acidic rainfall, with environmentally deleterious consequences (Rampino *et al.* 1988). Volcanism on a massive scale over an extended period of time has been proposed as an alternative to bolide impact to account for the dramatic extinction event at the end of the Cretaceous (Officer *et al.* 1987) but it is unlikely to have been more than a contributory factor to the general pattern of extinctions (Hallam 1987*c*). There is at least one good reason why volcanism is unlikely to have been a major causal factor in Phanerozoic marine extinctions; the correlation between major extinction and volcanic events is rather poor. Although the eruption of the Siberian Traps may well coincide quite closely with the end-Permian extinctions (Holser & Magaritz 1987), just as the Deccan Traps eruption apparently coincides with the end-Cretaceous extinctions, the peak of Karoo volcanic activity was early Jurassic not end-Triassic (Fitch & Miller 1984; Aldiss *et al.* 1984). For the other major extinction events there are no correlating major eruptive events. The Paraná (early Cretaceous), North Atlantic (Palaeocene) and Columbia River flood basalts (Miocene) compare in size with the Deccan eruptions but there are no correlative major extinction events. Where a correlation does exist, as at the end of the Palaeozoic and Mesozoic, both volcanism and sea-level changes may be expressions of significant events in the mantle Loper *et al.* 1988).

Sea-level changes

As has been outlined above, a strong correlation exists between both major and minor extinction episodes in the marine realm and inferred changes of sea level, with the likeliest cause of extinction being bound up with reduction of shallow marine habitat area as a consequence either of regression or the spread of anoxic waters during the ensuing transgression. At times of significant regression the continental climates would be expected to exhibit greater seasonal extremes of temperature, a phenomenon that could well have been a major causal factor in the significant increase in extinction rates that took place among land vertebrates at the end of the Permian, Triassic and Cretaceous (Bakker 1977). It is noteworthy that an important mid-Oligocene extinction event among land mammals (Prothero 1985) appears to coincide with a major regressive event.

In seeking an adequate extinction model for Phanerozoic shallow-marine invertebrates it is inappropriate to lay too much emphasis on the comparatively abnormal circumstances of the Quaternary, with shallow ocean being represented by pericontinental seas. One should take full account of the likelihood that the environmental settings of ancient epicontinental seas were different in important respects from anything today (Hallam 1981*a*). In such seas of extreme shallowness over extensive stretches, even a modest change of sea level could have had significant environmental consequences. Johnson (1974) stressed the importance of organic adaptations to changed circumstances in understanding the likely causes of extinction of neritic invertebrates. During episodes of sustained enlargement of epicontinental seas, organisms become progressively more stenotopic and an equilibrium is established. They are in effect 'perched', subject to the continued existence of their environment. Extinctions occur to an extent proportional to the speed of regression, degree of stenotopy attained, or a combination of the two.

The ecological model proposed by Hallam (1978) to account for Jurassic ammonite extinctions bears several resemblances to that of Johnson. Evidence of progressively increasing stenotopy is recorded by data on phyletic size increase, a *K*-selected trend. Times of relatively low sea level signify times of restriction and deterioration of neritic habitat, such as increases in the variability of temperature and salinity of extremely shallow water. In familiar ecological parlance, the increased environmental stress favours *r*-selected organisms. This is recorded by the small size of new ammonite taxa that have evolved rapidly from their larger more stenotopic ancestors, often as a result of heterochronous changes (figure 4); thus speciation, involving the origin of new taxa by reproductive isolation at times of restricted connections between epicontinental seas, as well as extinction, is promoted by regression. Comparable models to those of Johnson & Hallam have been put forward for a variety of Palaeozoic and Mesozoic marine invertebrates (see Johnson & Colville 1982; Rollins *et al.* 1979; Klapper & Johnson 1980; Roberts 1981; Ramsbottom 1981; Bayer & McGhee 1985).

None of these models takes into account anoxic events associated with marine transgression as a possible cause of mass extinction, but we have seen that such phenomena may in some cases have been more significant than regression. McLaren (1983) has argued that a sudden spread

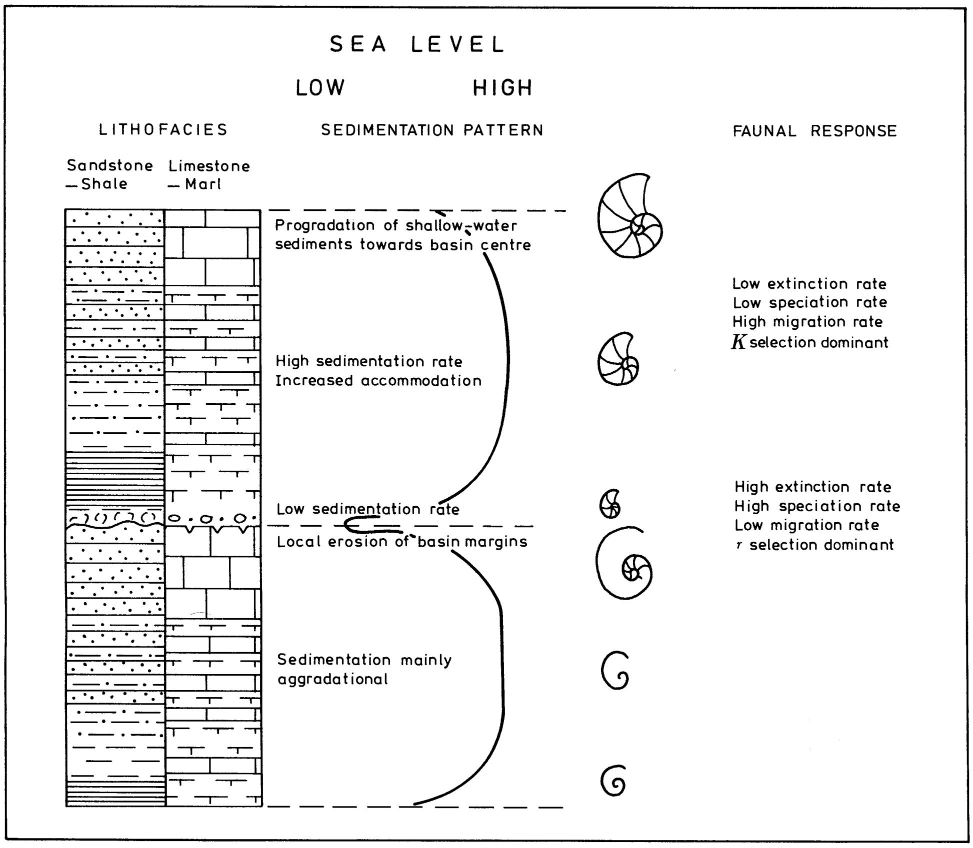

FIGURE 4. Relation of sea-level changes to major sedimentary cyclicity in the European Jurassic, and concomitant faunal response. The sea level oscillations are probably symmetrical and the curve appears cuspate because of the relatively condensed character of the 'transgressive' deposits. The changes schematically represented for the ammonite sequence are (*a*) phyletic size increase (a *K*-selected trend) and (*b*) paedomorphosis, with the ribbed juvenile character of the ancestral taxon extending into the adult of the descendent, following progenesis at a time of high environmental stress (an *r*-selected adaptation).

of anoxic bottom waters at the beginning of the Famennian could have been a consequence of oceanic overturn provoked by bolide impact, but the timescale implied seems much too short. The widespread black shales at extinction horizons normally have a thickness suggesting deposition over periods of time ranging from at least thousands to hundreds of thousands of years. Furthermore, an impact would be expected to disturb oceanic stratification and thereby act against the preservation of anoxic layers. On the other hand the initial spread of anoxic bottom water could have been geologically very rapid, with extinction horizons in the stratigraphic sequence being knife-sharp (Hallam 1987*b*). This overcomes an objection raised by McLaren (1983, 1989) that regressions were too slow to have caused mass extinctions as dramatically sudden as, for instance, those at the Frasnian–Famennian boundary. It should be evident from this that a combination of regression and subsequent transgression with concomitant spread of anoxic water provides an exceptionally powerful means of substantially increasing extinction rate among epicontinental marine organisms. That not all sea-level falls (e.g. in the early Devonian) correlate with mass extinction episodes, and that there is no simple relationship between the amount of sea-level change and the extent of extinction, probably indicates that the key factor is reduction of habitat area; this will depend on such factors as continental configuration and topography.

Much uncertainty surrounds the frequency, rate and extent of the underlying causes of sea level change (Hallam 1984). A mechanism involving volume change of ocean ridges seems inadequate to account for the frequently short-term events that many stratigraphers recognize, but the invocation by Goodwin & Anderson (1985) of numerous glacioeustatic events throughout the Phanerozoic to account for small-scale sedimentary cycles seem implausible without evidence of substantial polar icecaps for most of this time, and the evidence from flora and fauna of extended periods of equability. Although there is now evidence of some high latitude ice during equable periods such as the Jurassic and Cretaceous (Frakes & Francis 1988) this does not establish the likelihood of icecaps large enough to affect sea-level in any significant way. Furthermore, anoxic events would be difficult to explain if such icecaps had persisted through the Phanerozoic (Fischer & Arthur 1977). The most important reason for the association of black shales and transgressive episodes is that the early stages of transgression over the continents are characterized by broad stretches of poorly oxygenated shallow water, with restricted circulation with the open ocean, that provide a short transit for organic matter from productive surface water to the bottom sediments. Consequently there is less oxidation and greater retention of organic matter (Hallam 1981*a*; Arthur & Jenkyns 1981). The vertical and lateral extent of anoxic waters during a transgressive event would depend on a variety of factors, such as bottom topography, climate and rate and amount of sea-level rise. Some anoxic (perhaps more safely called hypoxic) events in epicontinental seas might have been generated by upwards expansion of the oceanic oxygen-minimum zone and others by phenomena intrinsic to the seas themselves. It may yet prove unnecessary to invoke the proposal of the lack of deep ocean refugia at times of habitat restriction in such seas.

Correlation between mass extinctions and magnetic field reversal patterns at the end of the Palaeozoic and Mesozoic, together with changes in sea level, volcanicity and climate, may be best accounted for by a model involving mantle–core interactions, such as that put forward by Loper *et al.* (1988). Major epeirogenic movements of the continents at these times could have had a more spectacular influence on sea level than, for example, changes in seafloor spreading rates. The extent to which some such model could provide an adequate causal mechanism for a greater number of mass extinction events remains uncertain, but at any rate it is likely that the extinction events indicate episodic rather than periodic control (Lutz 1987; Quinn 1987).

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Discussion

J. M. Cohen (39 *Greenhill*, *Blackwell*, *Worcestershire*, *U.K.*). How could such organisms as sharks, mid-water cephalopods and coelacanths have survived your universally anoxic deep-seas? Surely any such black-shale producing anoxias must have been local rather than global?

A. Hallam. I fear that Dr Cohen obtained an exaggerated impression from my lecture as to the extent to which I thought the deep ocean was anoxic in the past. It would be more accurate to state that there was a greater tendency towards anoxia in the past, at times when the earth's climate was more equable. Dr Cohen's point is, nevertheless, an interesting one, because it implies that at least limited refugia must have existed at times of mass extinction. Otherwise it is difficult to explain the survival of so-called Lazarus taxa. He could well be right, the anoxic events recorded from the stratigraphic record could perhaps signify relatively local phenomena. I speculate in my paper that many such events may have been confined to epicontinental seas.