

Sampling bias, gradual extinction patterns and catastrophes in the fossil record

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ABSTRACT

Catastrophic hypotheses for mass extinctions are commonly criticized because many taxa gradually disappear from the fossil record prior to the extinction. Presumably, a geologically instantaneous catastrophe would not cause a reduction in diversity or a series of minor extinctions before the actual mass extinction. Two types of sampling effects, however, could cause taxa to appear to decline before their actual biotic extinction. The first of these is reduced sample size provided in the sedimentary record and the second, which we examine in greater detail, is artificial range truncation. The fossil record is discontinuous in time and the recorded ranges of species or of higher taxa can only extend to their last known occurrence in the fossil record. If the distribution of last occurrences is random with respect to actual biotic extinction, then apparent extinctions will begin well before a mass extinction and will gradually increase in frequency until the mass extinction event, thus giving the appearance of a gradual extinction. Other factors, such as regressions, can exacerbate the bias toward gradual disappearance of taxa from the fossil record. Hence, gradual extinction patterns prior to a mass extinction do not necessarily eliminate catastrophic extinction hypotheses. The recorded ranges of fossils, especially of uncommon taxa or taxa in habitats not represented by a continuous record, may be inadequate to test either gradual or catastrophic hypotheses.

INTRODUCTION

The asteroid-impact hypothesis, recently proposed by Alvarez and others (1980) to account for the terminal Cretaceous extinction, has stimulated the interest of scientists in many disciplines; not unexpectedly, it has generated some criticism (e.g. Surlyk, 1980; Clemens and others 1981) as well as enthusiasm (Hsü, 1980; Ganapathy, 1980). Paleontological criticism of the asteroid-impact hypothesis, or any hypothesis invoking a catastrophic mechanism, focuses chiefly on the gradual extinctions of some taxa recorded in the fossil record prior to the actual extinction event (e.g. Hancock, 1967; Kennedy, 1977; Kauffman, 1979; Archibald, 1981; others, 1981; Clemens and others, 1981). Several taxa appear to decline in diversity prior to the Cretaceous-Tertiary mass extinction; the three best known examples are the ammonites (Hancock, 1967; Weidmann, 1969; Kennedy, 1977), the rudistid bivalves (Kauffman, 1979), and the dinosaurs (Russell, 1975, 1977; Van Valen and Sloan, 1977). No mechanism has been pos-

tulated whereby a catastrophe, such as a large-body impact on the earth, could cause extinctions prior to the actual event. If the fossil record accurately reflects the evolutionary history of these groups then catastrophic impact hypotheses are clearly questionable. Herein we consider whether or not the fossil record of the Cretaceous-Tertiary mass extinction must be accepted at face value and, if not, whether the evidence is compatible with a catastrophic extinction event.

The apparent decline of taxa prior to a mass extinction may simply reflect sampling effects and not actual diversity trends. Therefore, the apparent record of decline in diversity of various taxa prior to the Cretaceous-Tertiary extinction need not be considered evidence for a gradual extinction mechanism. Our arguments do not eliminate the possibilities that the Cretaceous-Tertiary extinction was gradual or catastrophic, but indicate that more rigorous tests are required to eliminate either hypothesis. If the sam-

pling problems cannot be surmounted, then the occurrences of species in the geologic record may not provide a conclusive test, and other paleontological approaches may be required.

SAMPLING AND THE FOSSIL RECORD

Numerous authors have discussed the importance of sampling effects in altering the fossil record of plants and animals (e.g. Gregory, 1955; Williams, 1957; Newell, 1959a, b; Simpson, 1960; Durham, 1967; Valentine, 1970; Raup, 1972, 1976b; Russell, 1975, 1977; Carroll, 1977; Sheehan, 1977; Koch, 1978; Signor, 1978; Knoll and others, 1979; Berger, 1979). Sampling effects can modify diversity patterns on both local (Koch, 1978) and global levels (Raup, 1972, 1976b; Signor, 1978) and can completely obscure original patterns of faunal abundance. Variations in ratios between species and higher taxa can be expected solely as a result of sampling effects (Raup, 1972, 1976a, b). Sampling biases can generate patterns in the fossil record which appear to reveal biologically significant phenomena where, in fact, none exist.

One important sampling problem is the effect of variation in sample size on apparent diversity. Raup (1972, 1976b) and Signor (1978) examined some of the difficulties inherent in comparing samples of unequal size, and Raup (1975) introduced rarefaction into the paleobiological literature in an attempt to provide a means to compensate for varying sample sizes (also see Tipper, 1979).

Russell (1975) reasoned that the apparent gradual decline of dinosaurs prior to the post-Mesozoic extinction results from the relatively small sample of reptiles and dinosaurs found in Maastrichtian, as compared to Campanian, rocks. Russell's analysis has been questioned on several grounds (Clemens and others, 1981) but the point remains that variations in sample size may bias the Late Cretaceous fossil record of many terrestrial taxa.

Similar biases may affect data on the diversity of marine organisms. Hallam (1971) showed that there is a decline in the areal extent of rocks deposited at the end of the Cretaceous. Ammonite diversity compiled by Kennedy (1977) is markedly parallel to Hallam's rock-area data (Fig. 1). The close correspondence between the rock-area and diversity curves suggests that sampling may exert a profound control on apparent diversity, as Raup (1976b) argued from similar data for the entire fossil record of Phanerozoic invertebrates. The area of epeiric seas could exert a primary, biological control on the diversity of marine invertebrates; indeed, Schopf (1974) and Simberloff (1974) have suggested that reductions in the area of shallow shelf seas were responsible for the Permo-Triassic extinctions. We only note that sampling could be responsible for the observed patterns and that diversity data cannot be accepted at face value.

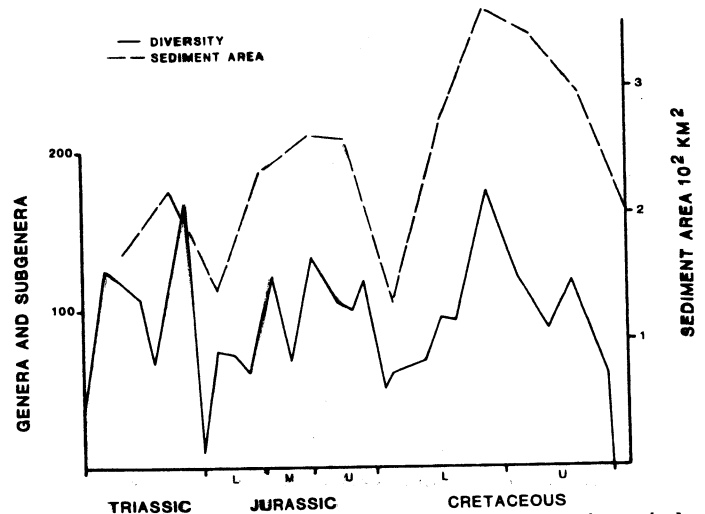


Fig. 1. Ammonite diversity and sedimentary rock area through the Mesozoic. Note that while the two data sets differ in detail, the major peaks and valleys generally correspond. Figure modified from Kennedy (1977), sediment area data is originally from Hallam (1971).

RANDOM TRUNCATION OF RANGES

A closely related but distinct sampling problem is the random truncation of stratigraphic ranges of fossil taxa. The termination of any given taxon's range is determined by the taxon's biotic extinction, or the time when the taxon is no longer available to be preserved, and by the taxon's last opportunity to be preserved and eventually discovered. Barring reworking of fossils, the last occurrence will most likely predate the taxon's extinction. How early before extinction the last occurrence of a taxon is found will depend upon the quality of the fossil record.

Occurrences of sedimentary facies within basins vary both in time and space (Ager, 1981, and references therein), and within a given habitat species occurrence may be patchy (Koch, 1978). Thus, not every taxon is found at every stratigraphic horizon and not every taxon is found each time its habitat occurs in the stratigraphic column. The range of a taxon is usually given as extending from the first occurrence to the last occurrence regardless of whether or not the taxon occurs at each intermediate stratigraphic level. Where taxa persist after their last known occurrence in the fossil record, the range will be artificially truncated.

This artificial range truncation can be treated as a more or less random process if large enough numbers of species are considered. The probability of finding the last occurrence of a taxon increases to unity as the actual extinction of the taxon is approached in time (this follows from the observation that the taxon cannot be found after its extinction but the last occurrence in the fossil record can occur before extinction). The resulting effects are illustrated in Figure 2, which shows the effect of a hypothetical catastrophic mass extinction on standing global diversity

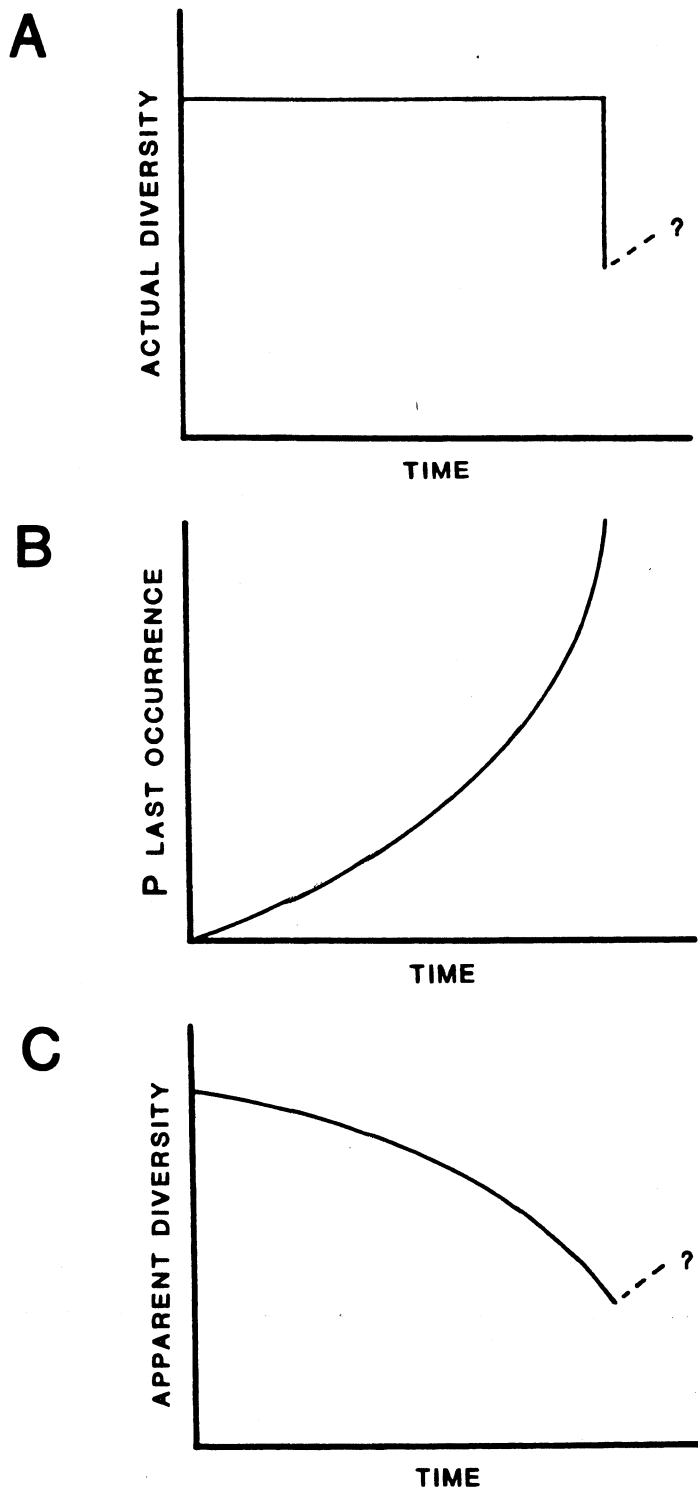


Fig. 2. Alteration of diversity patterns by artificial range truncation. In Fig. 2a we illustrate a hypothetical diversity curve, where diversity is suddenly reduced by a catastrophic extinction event. Fig. 2b presents a cumulative probability curve, showing the likelihood of different amounts of artificial range truncation. Imposing the artificial range truncation suggested in Fig. 2b on the hypothetical diversity pattern (Fig. 2a) would produce an apparent gradual decline in diversity, as shown in Fig. 2c.

(Fig. 2a). Figure 2b plots an arbitrary probability curve, giving the probabilities of different degrees of range truncation. This produces the apparent diversity curve shown in Figure 2c. Thus, the appearance of a gradual extinction can be reasonably generated by sampling effects alone even when the extinction is actually catastrophic.

The correspondence of the actual and apparent diversity curves prior to a mass extinction will vary as a function of the quality of the fossil record, with the degree of congruence increasing with increasing record completeness. This relationship can be clearly demonstrated by examining the classic example of a wooden tray, divided into compartments or cells, into which we randomly toss identical balls. The number of cells containing balls or "discovered" at the end of a given number of tosses is analogous to the number of taxa found in a sample of a given size. As the sample size decreases, the number of undiscovered cells will increase, or in paleontological terms, as increasingly shorter sections are sampled below a mass extinction, more taxa are lost from the fossil record. The missing taxa would be interpreted as having become extinct even though they would survive to the mass extinction—our reasoning here closely follows that of Raup (1972, p. 1067), except he examined the first occurrences of taxa in the fossil record and we are looking for range terminations.

The number of cells expected in a sample of a given size can be calculated with the Poisson relationship:

$$C = n - ne^{-s/n} \quad (1)$$

where C is the number of cells discovered, n is the total number of cells available, and s is the sample size. The number of cells "lost" by a decrease in sample size can be calculated as:

$$E = n(e^{-(s-x)/n} - e^{-s/n}) \quad (2)$$

where x is the decrease in the sample size and E is the number of cells lost by the decrease in sample size. This loss of cells can be analogized to artificial range truncations resulting from not recovering some taxa in increasingly smaller stratigraphic sections immediately below a mass extinction. Figure 3 shows three apparent diversity curves calculated using Eq. 1. Curve **a** is arbitrarily defined as containing 1,000 taxa, with a sample size of 1,000 in each of four equal hypothetical stratigraphic units. Curves **b** and **c** are drawn assuming two and three times more sampling, respectively, than curve **a**. Clearly, the apparent diversity curves approximate the true diversity more closely as sampling improves.

The foregoing analysis is simplistic because the occurrence of taxa is not random in the stratigraphic record (species tend to occur in bunches—their respective habitats) and species are not equally abundant as we assume above (a hollow curve of distribution seems to be the general rule:

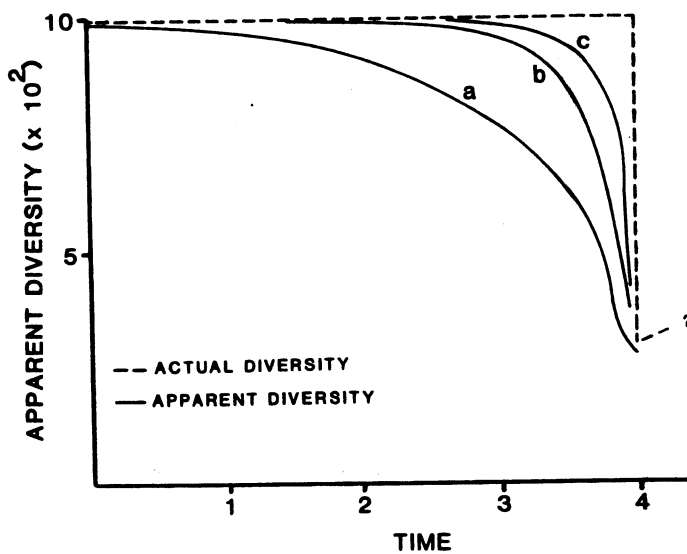


Fig. 3. Effects of improved sampling on artificial range truncation. If sampling was consistent but not thorough in each of four hypothetical time intervals the apparent diversity could appear as illustrated by curve *a*, despite the constant diversity in all four time intervals followed by a catastrophic extinction after time 4. Improved sampling, illustrated by curves *b* (twice the sampling hypothesized by curve *a*) and *c* (three times the sampling of *a*) improves the match between apparent and "actual" diversity. Different sedimentary sections must be assessed in a similar way. We expect nearshore marine and terrestrial sections to be farther from actual diversity (*a* or *b*) than the deep sea plankton record (*c*), for example.

see Anderson, 1974). The graphs demonstrate our point, and we note that similar results are obtained if we assume a lognormal distribution and that sampling is approximately random in time. Using the sampling model designed by Signor (1978), which is based on random sampling of a lognormal species-abundance distribution, we produced results similar in form to those presented in Figure 3.

The foregoing analysis assumes that the samples are distributed evenly in time. But the stratigraphic record is not continuous or uninterrupted. The likelihood of artificial range truncations will be much increased at times and places where the fossil record is particularly spotty. During periods of regression, when no deposits of marine sediments are developed on continental areas, there is no possibility of finding the last occurrences of taxa which go extinct during the regression. This will have the effect of pushing artificial range truncations further back in time to when there is a record to sample. If the regressions are gradual, they could have the effect of amplifying the apparent gradual nature of the extinctions, simply by reducing sample size as the regression progresses, at least in continental sequences.

As it happens, the Cretaceous-Tertiary mass extinction did occur in the midst of a major regression (Matsumoto,

1980). Nearly everywhere in the world the Cretaceous-Tertiary boundary is marked by an unconformity. Even sections deposited in deep water and thought to be relatively complete (e.g. the section at Gubbio, Italy) may contain gaps of unknown magnitude (see Surlyk, 1980). Hallam (1971) documented a decline in the areal extent of Late Cretaceous rocks, relative to the abundant mid-Cretaceous rock record (see Fig. 1). From this alone we would expect to find a gradual increase in apparent extinctions, regardless of the actual pattern of mass extinctions.

The apparent sudden termination of oceanic microplankton at the Cretaceous-Tertiary boundary stands in marked contrast to the seemingly gradual decline of larger marine and terrestrial biotas. In general, oceanic microplankton have a more complete record because the very sediment itself is composed of their innumerable skeletal remains. This is particularly true of biogenic sediments deposited above the carbonate compensation depth (Berger, 1979). Wherever pelagic calcareous or siliceous oozes occur, there is a fossil record of microplankton. While hiatuses are common in this record (Moore and others, 1978), it is nevertheless very complete in comparison to terrestrial or marginal marine deposits. We expect, then, that the abundance of oceanic microplankton insures improved sampling and that the sampling bias introduced by sporadic occurrence in the sedimentary record would be reduced. That is, of course, what has been documented for a number of sections (see Percival and Fischer, 1977; Smit and Hertogen, 1980; Herm, 1963; Thierstein, 1981). Yet even in this case, smaller scale gradual extinctions and radiations seem to occur (Perch-Nielsen and others, 1982) that may also be attributed to sampling bias, as hiatuses could be present, sediment mixing occurs, preservation may be selective (Thierstein, 1981), and the numbers of microfossils decline at the Cretaceous-Tertiary boundary (Percival and Fischer, 1977).

DISCUSSION

Commonly, fossil groups which suffer dramatic mass extinctions appear to decline in diversity so early before the mass extinction that artificial range truncation can hardly seem a plausible hypothesis. For example, Hancock (1967), Weidmann (1969) and Kennedy (1977) have noted that the ammonites were declining in taxonomic diversity well before the Maastrichtian, with most of the decline occurring before the Santonian. Yet, these declines cannot be accepted uncritically as support for either catastrophic or gradualistic hypotheses for mass extinctions. Clades wax and wane through time (see Sepkoski, 1981, Fig. 1 for a particularly striking illustration of the phenomenon) for a variety of reasons and no certain link exists between the pre-Santonian decline of ammonites and the post-Maastrichtian mass extinction. Similarly, the decline of other

taxa before the end of the Cretaceous might only be "background noise" and not related to the actual mass extinction.

Artificial range truncations will alter the shape of diversity curves after a mass extinction in much the same way that diversity curves are altered before a mass extinction. In earlier papers, Raup (1972) and Derstler (1981) have shown that a rapid rise in diversity can be masked by sampling problems resulting from a poor fossil record, which would delay the appearance of new taxa in the record. Diversifications of surviving clades, following a mass extinction, could be much more spectacular than is apparent in the fossil record.

Evidence contradicting a catastrophic mass extinction might not be derivable from fossil range data alone. Because the disappearance of taxa from the fossil record may not be due to simultaneous extinction, the range data must be supplemented with other information, for example the existence of numerous deposits where the taxa should be found but are not.

An alternative test needing further documentation is the gradual *replacement* of pre-extinction by post-extinction taxa. Patterns in the terrestrial deposits, where Tertiary mammals gradually replace Cretaceous reptiles (see Archibald, 1981; Clemens and Archibald, 1980), and in oceanic sedimentary rocks, where Tertiary species replace Cretaceous species of microplankton (Thierstein, 1981), could not be generated by a catastrophic event. However, mixing mechanisms, for example, bioturbation in marine sediments (Thierstein, 1981) and reworking in terrestrial deposits (Russell, 1977), might cause the apparent gradual replacement.

Our arguments should not be interpreted as support for the impact hypothesis or any other theory invoking a catastrophe as the extinction mechanism. The evidence at hand for most environments is as compatible with a gradual extinction event as with a catastrophic one. We emphasize, however, that catastrophic hypotheses can not be discarded on the basis of presently available fossil range data. Indeed, Thierstein (1982) presents reliable data that plankton extinctions were geologically instantaneous, after consideration of biases. Additional evidence should be developed in other environments as well.

CONCLUSIONS

Two separate sampling biases will act in concert to cause diversity to appear to decline prior to the post-Mesozoic mass extinction. These biases—reduced sample size in the Maastrichtian and artificial range truncation—will modify diversity patterns by making them appear gradual in nature, regardless of the actual mode of extinction. Until methods of removing these biases are utilized,

hypotheses invoking a sudden mass extinction at the Cretaceous-Tertiary boundary cannot be discarded.

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