Estimates of the magnitudes of major marine mass extinctions in earth history

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Procedures introduced here make it possible, first, to show that background (piecemeal) extinction is recorded throughout geologic stages and substages (not all extinction has occurred suddenly at the ends of such intervals); second, to separate out background extinction from mass extinction for a major crisis in earth history; and third, to correct for clustering of extinctions when using the rarefaction method to estimate the percentage of species lost in a mass extinction. Also presented here is a method for estimating the magnitude of the Signor–Lipps effect, which is the incorrect assignment of extinctions that occurred during a crisis to an interval preceding the crisis because of the incompleteness of the fossil record. Estimates for the magnitudes of mass extinctions presented here are in most cases lower than those previously published. They indicate that only ~81% of marine species died out in the great terminal Permian crisis, whereas levels of 90–96% have frequently been quoted in the literature. Calculations of the latter numbers were incorrectly based on combined data for the Middle and Late Permian mass extinctions. About 90 orders and more than 220 families of marine animals survived the terminal Permian crisis, and they embodied an enormous amount of morphological, physiological, and ecological diversity. Life did not nearly disappear at the end of the Permian, as has often been claimed.

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A global mass extinction can be defined qualitatively as an event in which an unusually large percentage of higher taxa in several biological groups died out globally within a brief interval of geologic time. There is no satisfactory way to provide a universally applicable quantitative definition of a mass extinction. Major marine mass extinctions have been associated with relatively abrupt excursions of the stable carbon isotope ratio in seawater, as reflected in fossil skeletal material. Contemporaneous oxygen isotope excursions that have paralleled the carbon isotope excursions, as well as other forms of evidence, connect the biotic crises to global climate change and support other evidence that the crises were relatively sudden events (1). Most major pulses of extinction occurred at or near the ends of formally recognized geologic intervals. In fact, the resulting biotic transitions have led to the establishment of the boundaries between most geologic systems and many geologic stages. Any extinctions scattered within such an interval or within an interval not containing a mass extinction are known collectively as background extinction.

Comparing models to empirical numbers, Foote (2) considered two extreme scenarios for extinctions in the marine realm: one in which all extinctions occurred in pulses, primarily at the ends of geologic ages (the intervals representing stages) and one in which they were spread throughout ages (see also ref. 3). He found the pulsed model to be more strongly supported, which would imply that substantial backward smearing of extinctions occurred because of the incompleteness of the fossil record [the Signor–Lipps effect (4)]. As I will show here, there is evidence that this result reflects an intermediate situation: the occurrence of a large percentage of extinctions as pulses at the ends of recognized stratigraphic intervals following a considerable amount of background extinction. Another model of Foote (5) based on expected forward survivorship also produced a large Signor–Lipps effect, as well as intervals with no actual extinction whatever, but it was oversimplified in using average overall extinction rates for marine taxa. Melott and Bambach plotted percentage of extinction for marine taxa at the genus level for stages and substages against the lengths of these intervals (6). They found no correlation, and concluded that background extinction has been minimal. There were two problems here. One was that intervals exhibiting mass extinctions were not excluded. The second was that the regression was not forced through zero. When these two measures are taken, there is, in fact, a strong correlation between interval length and percentage of extinction, indicating that there has been a significant amount of background extinction during the Phanerozoic (Fig. 1*A*; see *SI Text* for excluded mass extinctions). This is not to deny that some background extinctions may have occurred in small pulses, but not necessarily simultaneously. Despite the high level of ***R*** for the regression for this plot (boldfaced to distinguish it from *R*, the symbol used here for rate of change of diversity), the variance in Fig. 1*A* is quite high (see Table 1 for definitions of symbols). A major factor here is the well-known decline for rates of extinction in the marine realm from the early Paleozoic to the late Cenozoic: a roughly threefold decline for non-mass-extinction intervals (Fig. 1*B*). In effect, these rates were collapsed onto a single axis in the production of Fig. 1*A*.

In fact, taxa such as Cambrian trilobites (7) and Triassic conodonts (8) that experienced very high extinction rates and had excellent fossil records that have been studied in detail have been clearly shown to have experienced much background extinction during formally recognized intervals (ones representing substages and stages). Furthermore, throughout the stratigraphic record many zones within substages and stages are formally defined by the disappearance of a single species or genus, not by clusters of extinctions.

Significance

This paper shows that background extinction definitely preceded mass extinctions; introduces a mathematical method for estimating the amount of this background extinction and, by subtracting it from total extinction, correcting estimates of losses in mass extinctions; presents a method for estimating the amount of erroneous backward smearing of extinctions from mass extinction intervals; and introduces a method for calculating species losses in a mass extinction that takes into account clustering of losses. It concludes that the great terminal Permian crisis eliminated only about 81% of marine species, not the frequently quoted 90–96%. Life did not almost disappear at the end of the Permian, as has often been asserted.

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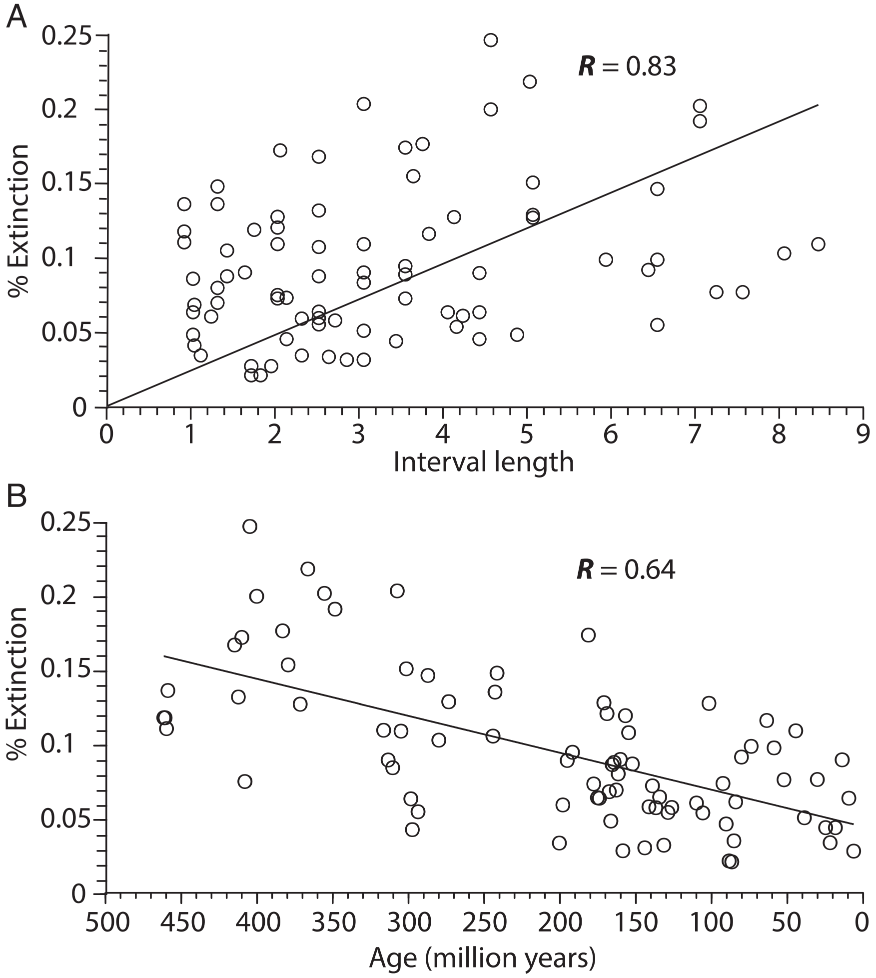


Fig. 1. Strong correlation between lengths of stratigraphic intervals and the percentages of total marine genera that became extinct within them (*A*) and Phanerozoic decline of extinction rates for marine genera (*B*). Included intervals range from the late Llanvirnian (Middle Ordovician, following the early Paleozoic interval of very high extinction rates) through the Messinian (late Miocene). Intervals characterized by mass extinctions are excluded (*SI Text*).

There is another very important point. Not all extinctions have resulted from global or regional changes in the physical environment. Adverse biotic interactions have certainly caused many piecemeal extinctions. For example, the impact of a group of highly efficient, newly evolved predators on prey that are readily accessible to them will often have caused extinctions that were not clustered but spread over millions of years. This is a matter of extinction by attrition, which is quite different in temporal pattern from the lethal impact of a sudden physical catastrophe.

The numerical size of a mass extinction has commonly been calculated as the ratio between the total number of extinctions of genera or families (e) for the mass extinction interval (MEI) and the total number of such taxa that existed during the interval (D) (9–11). This convention suffers from three errors. First, it ignores that fact that during an MEI many taxa will have died out not as part of the mass extinction but as background extinction that took place throughout the interval, as it does during intervals not characterized by mass extinctions (Fig. 1). Fig. 2 illustrates how, by including background extinction, the use of e erroneously exaggerates the number of taxa lost in a mass extinction. It also illustrates why this error is usually larger when data for the entire stage are used instead of data for only the final substage. The second error in calculating the magnitude of a mass extinction as e/D is that the appropriate number for the denominator is not total diversity for the interval (D) but the standing diversity (number of existing taxa) at the start of the mass extinction (here denoted by N). The third error of the traditional e/D calculation is that it fails to take into account the Signor–Lipps effect. The impact of this omission is also illustrated in Fig. 2.

The approach introduced here employs a technique for estimating the number of background extinctions for a particular MEI and, from this, the standing diversity at the start of the mass extinction. These numbers make it possible to estimate the magnitude of the mass extinction appropriately. The same technique makes it possible to evaluate the magnitude of the Signor–Lipps effect at the stage or substage level. It is highly significant that the methodology is independent of the duration of the MEI. In other words, any future alteration of the estimated duration of an MEI will have no effect on the calculation of the impact of a crisis. The methodology yields estimates of percentages of genera lost in marine mass extinctions that in most cases are lower than conventional estimates.

Rarefaction curves have been used to estimate the number of species lost in the terminal Permian mass extinction (9, 12). The results exaggerated the impact of the event, however, because to conduct the analyses data for the Middle and Late Permian mass extinctions were combined (13). Failure to take into account the fact that extinctions are clustered within certain higher taxa has further exaggerated rarefaction-based estimates of the magnitude of the terminal Permian crisis. An estimate of ~81% is made here for extinction of species in this event, based on rarefaction at the genus level that is modified by a technique that

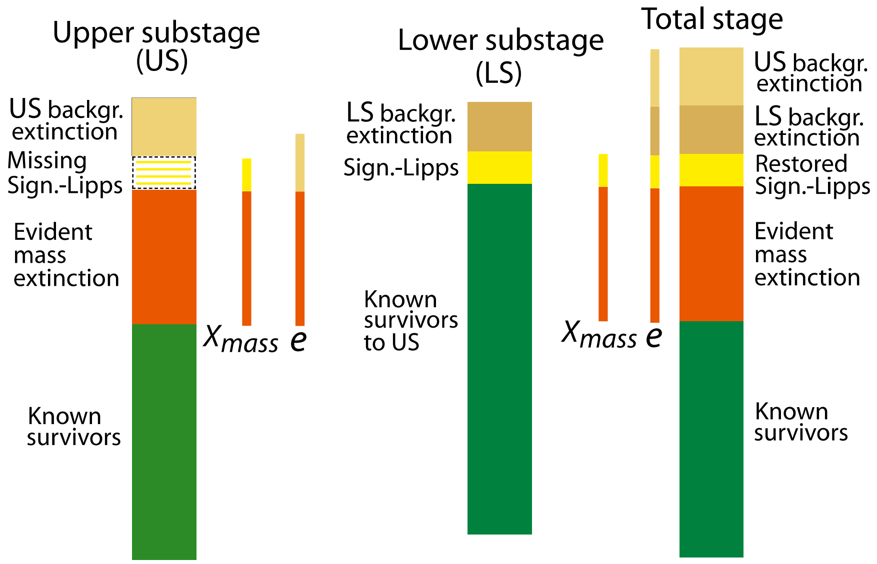


Fig. 2. Illustration of some of the ways in which calculating magnitudes of mass extinctions as *e*/*D* creates errors (vertical dimensions of all bars represent hypothetical numbers of genera). The left-hand member of each of the two pairs of small vertical bars depicts X_m, the number of genera that died out in a mass extinction, as estimated via the methodology introduced in this paper and used to calculate the percentage of genera that died out. The right-hand narrow vertical bar of each pair depicts the size of *e* used to calculate *e*/*D*. Calculation of *e*/*D* for the upper substage alone errs by leaving out Signor–Lipps extinctions recorded for the early substage and by including background extinction for the upper substage; the two errors operate in opposite directions, but usually the background extinction number is the larger of the two. Calculation of *e*/*D* for the total stage includes Signor–Lipps extinctions recorded for the early substage, but errs by including background extinction for both substages; the result is an even greater error than the one created by calculation of *e*/*D* for the upper substage alone.

compensates for clustering of extinctions. This estimate is much lower than the frequently cited estimate of 88–96% by Raup (12) that has often been rounded to 90–95% by subsequent authors, but was unknowingly based on an inappropriate body of data.

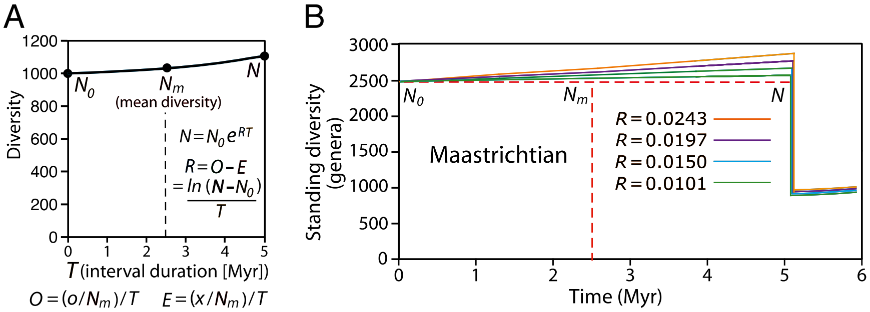
A Method for Calculating the Magnitudes of Mass Extinctions

The procedure used here to separate the background extinction that immediately preceded a mass extinction from losses in the mass extinction itself makes use of levels of background extinction for intervals preceding mass-extinction intervals (Fig. 3*A*). Relevant empirical data available for such intervals are: geologic duration (*T*), number of origins of genera (*o*), number of extinctions of genera (*e*), and total diversity (*D*). Data used here to obtain these numbers for marine animals are from the compilations of Sepkoski (14, 15) [see the Sepkoski Online Web Archive provided by Shanan Peters, University of Wisconsin (16), and Bambach's consolidation of Sepkoski's numbers (RKB Interpolation All Substages) (11)]. Dates for geologic stages and substages are from 2013 TS Creator – G & O (17).

Assuming that most singletons (taxa found in only a single interval) are products of a poor fossil record, some authors have excluded them from estimates of rates of origination and extinction or of diversity through time. I do not follow this procedure. It introduces errors for estimates of magnitudes of mass extinctions because some of the genera that arose within a mass-extinction interval will have become legitimate singletons by becoming victims of the mass extinction, yet they will be excluded from the calculations; on the other hand, those that survived will be counted. Furthermore, having appeared shortly before the crisis, genera arising during a mass extinction interval would typically have contained fewer species than more ancient genera and thus have been more likely to be eliminated by the crisis. Thus, exclusion of singletons will lead to an underestimate of the magnitude of a crisis. (For additional discussion, see *SI Text*).

Fig. 3 illustrates, step-by-step, the calculation introduced here. For an interval not including a mass extinction, the number of genera at the start (N_0) will have been *D*–*o*, and the number at the end (*N*) will have been *D*–*x*. As shown in Fig. 3*A*, rate of origination (*O*) (in units of million years) is calculated by dividing *o* by mean diversity for the interval (N_m) (which is calculated as the average of values representing exponential increase or decrease of diversity within the interval) and then dividing the resulting number by the interval duration (*T*). Rate of extinction is calculated the same way from *e*, *Nm*, and *T*. As implied above, the change in diversity within an interval will typically have been approximately exponential at some rate R (= $O - E$) and is appropriately estimated as such even though it will not have followed a perfectly exponential path (18). Fig. 3*A* depicts various levels of increase in diversity because this has been the most common condition in the absence of a mass extinction, although for some such intervals diversity has decreased or remained virtually unchanged.

Illustrating this approach by way of example, Fig. 3 *B*–*D* depict the calculation of a narrow range of estimates for the percentage of marine genera lost in the terminal Maastrichtian (Late Cretaceous) mass extinction. A special stratagem makes calculations of this kind possible by approaching them indirectly. The magnitude of *E*/*O* for one or more background intervals preceding a mass extinction is the critical metric for constraining an estimate for the magnitude of a mass extinction to a reasonable range of values. I am labeling this the extinction/origination disparity. The key initial step is to consider the hypothetical situation for an MEI in which rates of origination and background extinction are equal (horizontal dashed red line in Fig. 3*B*). With *o* and *e* equal (both in the present case being 654, which is *o* for the Maastrichtian), $R = 0$, and $n = N_0 = N_m$. This unique condition makes it possible to determine the rate of background extinction (*E*). Although *E* equals (e/Nm)/*T*, it cannot be calculated directly from this formula because *e* is not initially known. However, knowledge of *o* makes is possible to know the value of *O* (=(o/N_m)/*T* because it equals *E*. Thus, *E*/*O* obviously equals 1. These hypothetical conditions are represented by figures in the first row of Fig. 3*C*. The generic diversity reported for the start of the



C

R	T	D	o	N_0	N	N_m	$O=(o/N_m)/T$	$E=(x/N_m)/T$	E/O
0	5.1	3127	654	2473	2473	2473	0.0519	0.0519	1.0
0.0020	5.1	3127	654	2473	2498	2485	0.0516	0.0496	0.96
0.0040	5.1	3127	654	2473	2524	2498	0.0513	0.0473	0.92
0.0051	5.1	3127	654	2473	2538	2505	0.0512	0.0461	0.90
0.0101	5.1	3127	654	2473	2604	2539	0.0505	0.0404	0.80
0.0150	5.1	3127	654	2473	2669	2571	0.0499	0.0349	0.70
0.0197	5.1	3127	654	2473	2735	2604	0.0493	0.0296	0.60
0.0243	5.1	3127	654	2473	2800	2637	0.0486	0.0243	0.50

$\downarrow E = O \downarrow - R \uparrow$

D

	T	O	E	E/O
Late Campan.	6.9	0.024	0.016	0.66
Early Campan.	6.0	0.027	0.017	0.63
Santon.	2.3	0.073	0.044	0.62

E

(E/O)	Total no. extinct. e	Total backgr. extinct. x $= EN_mT$	Mass extinct. number x_{mass} $= e-x$	Mass extinct. % (x_{mass}/N)x100
1.0	1482	654	828	33%
0.90	1482	589	894	35%
0.80	1482	523	959	37%
0.70	1482	458	1024	38%
0.60	1482	392	1090	40%
0.50	1482	327	1155	41%

Fig. 3. Method of estimating the percentage of genera lost in a mass extinction illustrated for the Maastrichtian crisis. (*A*) Calculations of values for key parameters for an interval lacking a mass extinction. Rate of change of diversity (*R*), origination rate (*O*), and extinction rate (*E*) are calculated from mean diversity (N_m), number of originations (*o*), number of extinctions (*x*), and interval duration (*T*). (*B*) Elevation of the rate of change (*R*) before the mass extinction from zero (horizontal dashed red line) to possible actual values. (*C*) First row: Calculation of *O* and *E* for the Maastrichtian before the mass extinction for the hypothetical case of $R = 0$, based on the fact that $n = N_0 = N_m = 654$; incremental elevation of *R* by 0.0020 and 0.0040 (first column) causes N_m to rise progressively so that *0* declines and *E* declines even more (arrows). Values of *R*, *O*, and *E* for four additional cases ($E/O = 0.80$, 0.70, 0.60, 0.05) are highlighted in colors matching corresponding rates of increase depicted in *B*. (*D*) Values of *E*/*O* for the three Cretaceous stages that immediately preceded the Maastrichtian and were not characterized by mass extinction. (*E*) Calculations of possible magnitudes for the Maastrichtian mass extinction. Highlighted in red are maximum and minimum estimates of 38% and 40% that are favored because they are based on $E/O = 0.70$ and 0.60, which bracket the values for the earlier stages illustrated in *D*. Highlighted in blue are less likely values for losses in the mass extinction.

Maastrichtian (N_0) is 2,473. At issue is, starting with this number, which of the possible rates of change (*R*) depicted in Fig. 3*B* may approximate the actual rate before the mass extinction.

In rows below the first row of Fig. 3*C*, *R* is increased incrementally to provide calculations representing the various possible levels of increased diversity before the crisis. The color-coded numbers in Fig. 3*C* represent values of *R* that have produced the hypothetical diversification curves of Fig. 3*B*. For each value of *R* in Fig.3*C*, *O* can be calculated. Then *E* can be calculated from *R* and *O* because $R = E/O$. Because N_m increases progressively with *R* but *o* remains at 654, *O* decreases progressively, and *E* decreases even more rapidly, equaling $O - R$ (arrows). Thus, *E*/*O* decreases. Increases in hypothetical values of *R* shown in the left-hand column of Fig. 3*C*, produce initial small reductions for *E*/*O* to 0.96 and then 0.92, followed by round-number values ranging from 0.90 to 0.5 (right-hand column). Note that this series of calculations is anchored by *o*, which remains unchanged throughout.

From the value of *E* representing a particular value of *R* in Fig. 3*C*, the number of background extinctions (x_b) is easily calculated as EN_mT (Fig. 3*E*). The critical number for losses in the mass extinction (x_m) equals $x - x_b$. An appropriate range for *E*/*O* in this case can be estimated from the *E*/*O* values for the three intervals that preceded the Maastrichtian: the Santonian and early and late Campanian, because the composition of the global marine fauna during these intervals was quite similar to that of the Maastrichtian before the crisis. Values of *E*/*O* for the three earlier intervals encompass a very small range of values (0.62–0.66) (Fig. 3*D*). These numbers justify conservatively favoring the rates of origination and extinction for the precrisis Maastrichtian that are associated with an *E*/*O* in the slightly larger 0.60–0.70 range. As shown in Fig. 3*E*, the values of x_b and *x* for this range provide a preferred estimate of 38–40% for the magnitude of the Maastrichtian mass extinction (see also Fig. 4, red bar). Arbitrarily lowering *E*/*O* for the late Maastrichtian to 0.50 only elevates the estimate for the event to 41%, and elevating *E*/*O* to 0.80 only reduces the estimate to 37%. These percentages are taken to represent possible but less likely valid estimates (see also Fig. 4, blue bars). The modest effect of these substantial alterations of *E*/*O* illustrates that the estimate of this ratio for a mass-extinction interval need not be close to perfect to obtain a reasonably good estimate of the size of a mass extinction.

Actually, the origination and extinction rates for the Santonian are both relatively high (Fig. 3*D*), but these rates are possibly elevated artificially because the Santonian may actually be longer than the short span of 2.3 My now allotted to it. In fact, an advantage of using *E*/*O* to constrain mass-extinction calculations is that errors of interval length have very little effect on it because the two rates it entails both shift up or down with any change of estimated interval duration. In addition, the calculation of X_m is independent of the duration of the MEI. This condition exists because *T* appears first in the denominator of one of the series of

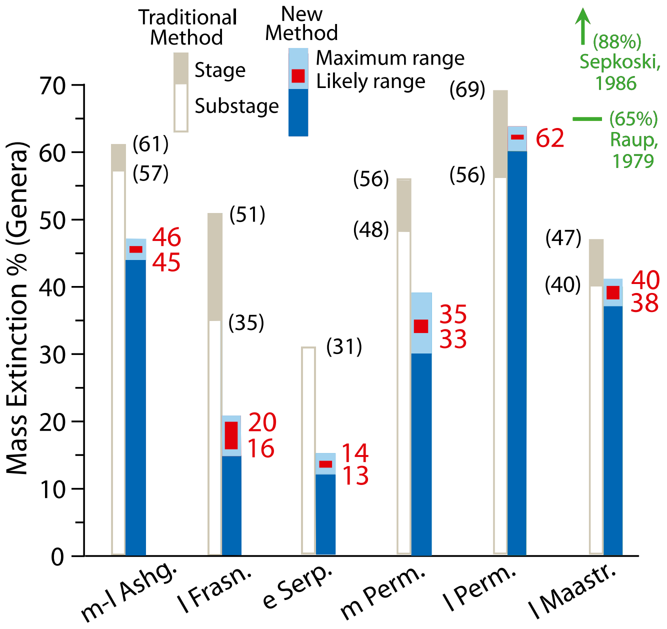


Fig. 4. Bar diagram illustrating estimates for magnitudes of major mass extinctions. Red numbers correspond to maxima and minima for losses of genera, also depicted by red bars, which represent favored estimates via the methods of this study. Blue portions of bars depict ranges considered less likely to be valid.

calculations [$E = (e/N_m)/T$ of Fig. 3*C*] and later as a multiplier in another calculation in the series (EN_mT of Fig. 3*E*): the two cancel out. This means that the estimates of magnitudes of mass extinctions via this approach will be unaffected by future changes in estimated durations for mass-extinction intervals.

The technique I have described will produce the same result whether applied to the final substage of a stage marked by a mass extinction or applied to the entire stage. This conclusion is evident from the nature of the calculation, and I have used it to make certain that calculations via both approaches match and thus are without errors.

It also turns out that the occurrence of a mass extinction within an interval, rather than at the end, has a relatively small effect on the calculation. For example, although it is not clear when heavy extinction began during the Serpukhovian, early in the late Paleozoic ice age, an arbitrary shift of the timing of the crisis in the calculation from the end of the Serpukhovian to ∼2 My earlier elevates the estimated magnitude of the mass extinction by only about 0.3 of a percentage point. Total background extinction remains the same, simply being divided between two intervals, one preceding and one following the mass extinction.

If calculations like those in Fig. 3 are applied to an interval preceding an MEI and reveal what appears to be excess extinction, when in fact there was no mass extinction, the excess number can instead be attributed to the Signor–Lipps effect. This number calculated for the early Maastrichtian, when added to the total number of recognized late Maastrichtian extinctions, turns out to represents 10–12% of the total mass-extinction number. The Signor–Lipps effect here is almost entirely confined to the early Maastrichtian; none is apparent for the early or late Campanian. As a result, in this case calculation of the magnitude of the mass extinction using the entire Maastrichtian (Fig. 3) eliminates the Signor–Lipps effect because extinctions smeared backward from the mass extinction to the early Maastrichtian are restored in the calculation: they are part of the excess number that remains after background extinction has been subtracted: they represent part of the mass extinction. Thus, calculation of the magnitude of this event using data only for the late Maastrichtian, with the Signor–Lipps numbers for the early Maastrichtian added in, produces the same result as the calculation using the entire Maastrichtian.

Calculation of the magnitude of the Maastrichtian via the conventional method, as e/D, provides an estimate of 40%, which closely resembles that produced here (Fig. 3). This is purely fortuitous, however: failure to include Signor–Lipps extinctions from the early Maastrichtian happens approximately to offset the inclusion of late Maastrichtian background extinctions (Fig. 2). However, this coincidence is not observed for most other mass extinctions (Fig. 4). Also, application of the erroneous conventional metric (E/O) to the entire Maastrichtian elevates the estimate to 47% because this procedure increases the total error by assigning to the mass extinction background extinction of the early Maastrichtian along with that of the late Maastrichtian.

Magnitudes of Other Major Extinctions

Fig. 4 compares results of calculations like those of Fig. 3 to conventional calculations (e/D) for six additional crises traditionally considered to constitute significant mass extinctions. (See Dataset S1 and summary in Dataset S2 for E/O values used to estimate background extinction numbers for each MEI.) Three decades ago, Raup and Sepkoski (19) identified as the "big five" mass extinctions the Late Ordovician (Ashgillian), Late Devonian (Frasnian), Late Permian (Changhsingian), Late Triassic (Rhaetian), and Late Cretaceous (Maastrichtian). Bambach's more recent appraisal recognizes only three major mass extinctions, the Late Ordovician, Late Permian, and Late Cretaceous (11). All five events recognized by Raup and Sepkoski except that of the Late Triassic are evaluated here; the latter is excluded because its timing and list of marine victims remain controversial (20, 21). Sizeable Cambrian and Silurian crises (7, 22, 23) are also omitted because they remain to be studied in detail. I have, however, included the early Serpukhovian event, which occurred during the onset of the late Paleozoic ice age, and the Guadalupian (Middle Permian) event.

The event at the end of the Changhsingian remains the largest of all Phanerozoic mass extinctions (Fig. 4). Because the number of Signor–Lipps misassignments of generic extinctions to the preceding Wuchiapingian Stage (early Late Permian) is quite large, the traditional metric ($x_m = e/D$) produces what turns our to be an erroneously low estimate of 56% for the event when it is calculated for the Changhsingian alone. Because the Guadalupian, which immediately preceded the Wuchiapingian, was marked by a mass extinction, it cannot be used to estimate E/O for the Changhsingian before the terminal Permian crisis. The Leonardian and late Sakmarian intervals, which preceded the Guadalupian, yield E/O ratios of 0.95 and 0.97, respectively. The similarity of these numbers suggests that they are likely to resemble the E/O ratio for the Changhsingian, as does the fact that E/O ratios for the intervals of the ∼40 My-long late Paleozoic ice age was also very similar, averaging ∼1.0. Furthermore, because of the similar E/O ratio of 0.95 for the Leonardian, it appears that few Signor–Lipps age misassignments for genera extend back to this stage (back beyond ∼18 My). Assuming that Signor–Lipps misassignments decline more-or-less exponentially backward in the fossil record, it seems reasonable to supplement the Wuchiapingian number with one about one-third its size to represent the percentage of Changhsingian Signor–Lipps losses to the Guadalupian. Calculations based on E/O = 1.0 and 0.95 then produce best estimates of 61.8% and 62.4% (average ∼62%) for generic extinctions in the terminal Permian event. Even if E/O for the Changsingian before the crisis were as low as 0.8, this number would be elevated only to ∼64% (Fig. 3). Once again, it is apparent that there is little effect on the final calculation for an estimate of E/O that happens so be somewhat

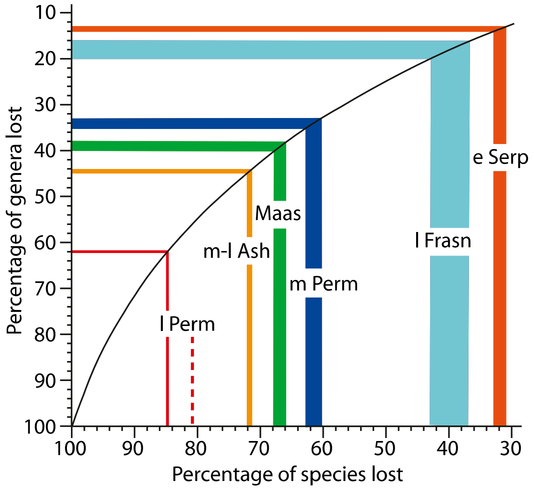


Fig. 5. Estimates via a genus-level rarefaction curve for species losses in major mass extinctions. The estimate for the Late Permian is shifted downward by 4 percentage points, to 80.5–81.5% (dashed line), to account for clustering of extinctions within certain taxa. The estimates for other MEIs should be shifted downward by approximately the same fractional amount (~5%).

inaccurate (in this hypothetical example, ~20–25% too high). About 32% of the Changhsingian mass extinction numbers are attributed to the Wuchiapingian and Guadalupian stages via the Signor–Lipps effect.

Although my best estimate of the percentage of genera lost in the late Guadalupian crisis (33–35%) is only slightly more than half the percentage estimated for the Changhsingian crisis (Fig. 4), ~80% as many genera were lost in the earlier event because the standing diversity when the terminal Permian crisis occurred was quite low; there had been only a modest rebound following the Guadalupian crisis. This calculation entails removal of the Signor–Lipps numbers restored to the Changhsingian. Possibly the Guadalupian event began before the end of the late Guadalupian (24, 25), but close to the end of this interval there was heavy extinction of fusulinidoidean foraminiferans (13, 25–27). A recent thorough study of this group found that 88% its species that existed within the last million years of the Guadalupian became extinct by the end of this brief interval (27). My Signor–Lipps estimate for erroneous transfers for the entire fauna from the late Guadalupian to the early Guadalupian is 26–29%. The previously noted similarity among E/O values for the Leonardian, late Sakmarian, and intervals of the late Paleozoic ice age suggests that very few Signor–Lipps missassignments for the late Guadalupian extend back to the Leonardian, and application to the late Leonardian of the procedures illustrated in Fig. 2 reveals no excess extinction during this interval.

On the basis of a unique database, Clapham et al. (28) concluded that there was no major mass extinction late in the Guadalupian, but a gradual decline of diversity throughout the interval. However, this analysis excluded singletons, a procedure I have already argued to be improper, especially for a mass-extinction interval (see also *SI Text*). Also, the Clapham et al. analysis did not restore Signor–Lipps numbers, which, as noted above, my approach shows to have been considerable.

The early Serpukhovian (Late Mississippian) mass extinction, associated with the onset of the late Paleozoic ice age, was of relatively small magnitude: my range of best estimates is 13–15% (Fig. 4). This number would undoubtedly have been much larger had the fragile reef-building community rebounded substantially after its Late Devonian decimation and then contributed substantially to the mass extinction numbers. Although an initial phase of ice age glaciation began late in the Visean (29), I find no excess extinction above background levels for the upper Visean substage, and there was no disruption of marine faunas in the Illinois Basin at the time of late Visean glacial eustasy (30). It seems likely that Visean glaciation preceded the major climatic shift that occurred a bit later but still early in the ice age; no large global oxygen or carbon isotope excursion has been reported for the Visean.

There were two pulses of mass extinction in the Late Devonian that were both relatively small in numerical terms (though not in ecological terms, as I will note below). The first of these is recorded at the end of the penultimate Devonian stage (Frasnian) and the second at the end of the final Devonian stage (Famennian) (Fig. 4). Each of these events was associated with global cooling (31–35). My best estimates for generic losses in the Frasnian crisis are relatively small (16–20%) (Fig. 4). The calculations for this event include no Signor–Lipps additions because the recorded extinction percentages for the middle Frasnian resemble background extinction levels for the preceding early Frasnian and Middle Devonian. The use of the extinction/origination disparity for this event is problematical because several origination rates for the Middle and Late Devonian are unusually low. As a result, I have used the origination rate for the late Frasnian itself as a denominator to produce an appropriate X/O, and for the numerator I have used extinction rates for the early Eifelian, early Givetian, and early Frasnian, which are all quite similar (0.109, 0.090, and 0.092 My^{-1}, respectively). The late Eifelian and late Givetian are inappropriate for use here because they were characterized by pulses of extinction (21).

The Famennian event was too small to have contributed a substantial number of extinctions erroneously to the Frasnian total. In fact, it has proven impossible to evaluate the Famennian mass extinction by the methodology used here. Because it followed shortly after the Frasnian event, using previous intervals to obtain reasonable values of the extinction/origination for it is problematical. What is evident, nonetheless, is that this event entailed the loss of a very small percentage of marine genera. Although the use of the metric assessing the total rate of extinction for a mass extinction interval (e/D) is meaningless as a measure of the impact of a mass extinction, in this case it can be useful for a qualitative comparison. For the late Frasnian crisis interval e/D was 0.203 My^{-1}, but for the late Famennian interval it was only 0.075 My^{-1}. The difference between the two numbers must primarily reflect a much greater impact for the first event. My estimate that only 16–20% of genera were lost in the Frasnian crisis implies the Famennian event was indeed quite small in numerical terms, although I will note below that it had a significant ecological impact.

The mass extinction recorded in the Ashgillian, the final stage of the Ordovician Period, included two phases, which have reasonably been considered to constitute a single crisis because they were associated with a single glacial episode (11). The first pulse, at the end of the middle Ashgillian, coincided with glacial expansion, global cooling, and sea-level decline; many taxa migrated equatorward (36). Just ~1.9 My later, at the end of the late Ashgillian (Hirnantian substage), the second pulse preferentially eliminated cold-adapted taxa as the ice age ended and climates warmed (37). The two pulses of extinction can be combined to estimate an Ashgillian rate for the total ice age according to the following logic. First, by way of comparison, we can recognize that O and E both declined to very low levels during the late Paleozoic ice age because the survivors of the mass extinction at the start were primarily wide-ranging, broadly adapted taxa (38, 39). For the late Ashgillian ice age, O (0.041 My^{-1}) was nearly identical to the mean for the late Paleozoic ice age (0.044 My^{-1}). The mean E/O for the late Paleozoic ice age intervals was ~1.0, so that $e \sim o$, and there was

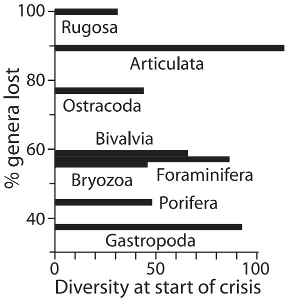


Fig. 6. Variation among higher taxa in percentage of genera estimated to have died out in the terminal Permian mass extinction. Included are taxa that contained more than 30 genera at the start of the crisis.

very little change in global marine diversity. It is reasonable to assume that R was also close to zero during the late Ashgillian ice age, so that $e \sim o = 77$. Subtraction of this number from the total number of extinctions reported for the late Ashgillian yields an estimate of the number of genera that died out in the Hirnantian crisis: 321–77 = 244. Because, it is probable that during the late Ashgillian diversity changed very little, to calculate the magnitude of the combined mass extinction, we can treat the Hirnantian as being numerically nonexistent and compress the two mass extinction events into one. This procedure, in which the late Ashgillian losses are added to the more than twice as many middle Ashgillian losses, produces a best estimate of 42–43% for the total Ashgillian event (Fig. 4). It is possible that the recorded number of 77 generic originations for the late Ashgillian is actually inflated slightly because some taxa recorded as having originated in late Ashgillian time actually originated earlier at high latitudes and simply migrated equatorward as the climate warmed. Arbitrarily reducing the number of late Ashgillian background extinctions from 77 to 60 elevates the estimate for the total extinction only slightly, to ∼43–44%. Here again, we see the robustness of the techniques used here.

Analysis at the Species Level

A detailed field study has concluded that 94% of marine species disappeared from the known fossil record at the terminal Permian boundary at the Meishan locality in China (40). However, local disappearances at or near a mass-extinction boundary cannot all represent extinctions. Some species that survived in the Meishan region after the crisis must remain undiscovered at the Meishan locality because of facies changes or the inevitable incompleteness of the local fossil record. Some species must have survived this event at greatly reduced population sizes, which would have reduced the probability of their discovery in strata above the extinction level. Furthermore, the rich Meishan fauna occupied a region near the equator where shallow seas have been estimated to have warmed suddenly to 35 °C at the time of the crisis (41). Some Meishan species are likely to have survived by persisting in or being forced into cooler regions at higher latitudes where they happen to have failed to produce recognized Early Triassic fossil records. The magnitudes of global pulses of extinction simply cannot be assessed accurately from recorded stratigraphic occurrences of species. The problem is exacerbated if records are restricted to a single site.

To estimate losses at the species level for mass extinctions, David Raup (12) made ingenious use of the rarefaction curve, borrowing it from the field of ecology, where it is used to estimate species diversities for particular localities or regions by accumulating a list of species through random collection of a large number of individuals. To adapt this kind of approach for the assessment of species losses in mass extinctions, a different kind of rarefaction curve is produced in the following way. For a species-rich group of one or more major taxa all species are pooled. Species are selected at random from this pool and, at their first appearance, genera, families, or orders to which species belong are tallied until all species are chosen. Accumulated numbers of species and numbers of higher taxa that each number of species represents are then converted to percentages of the total numbers and plotted against each other to produce a taxonomic rarefaction curve. A mass extinction can be viewed as operating in the opposite direction, removing species and, in the process, higher taxa. The curve then provides an estimate of the percentage of species that would have been lost to produce the percentage of higher taxa calculated to have died out in any mass extinction (Fig. 5).

Raup (12) used rarefaction curves for extant genera, families, and orders of the class Echinoidea (sea urchins) to estimate the magnitude of the terminal Permian crisis at the species level. He began by estimating this magnitude via the observation that numbers of orders and families of marine taxa declined progressively after the Leonardian. He concluded that this pattern likely reflected what later became known as the Signor–Lipps effect (4), but he implied that it might also in part have resulted from a single protracted crisis. In any event, he attributed this decline to a single mass extinction. To estimate the number of higher taxa lost in this event, Raup subtracted the standing diversity of orders and families for the final stage of the Permian from the larger numbers recorded for the entire Leonardian. Actually, the standing diversity at the end of the Leonardian should have been the starting number, but here Raup was correct in principle in removing an estimated amount of background extinction from the terminal Permian event. Raup calculated that 52% of families and 16.8% of orders died out, and both of these percentages yielded an estimate of 96% for the loss of species. His genus-level curve produced the lower estimate of 88% for species losses, based on the extinction of 64.8% of genera. Actually, because of the relatively small numbers they entail, family- and order-level rarefaction plots are less reliable than genus-level plots for estimating losses of species. Subsequently, however, using the same approach, Sepkoski (42) used the higher number of 83% for generic losses and obtained numbers for species losses (94–96%) that were similar to Raup's numbers based on families and orders. The lower number yielded by Raup's genus-level estimate reflected his use of survivorship analysis, which he himself stated that he considered to be dubious, to estimate the level of generic extinction at a time when Sepkoski's generic database was not yet available.

Why Previous Estimates for the Terminal Permian Crisis Have Been Too High

The rarefaction-based estimates of species losses produced by Raup (12) and Sepkoski (42) for the terminal Permian crisis were artificially elevated because these workers combined data for the Guadalupian and terminal Permian crises. This approach, though reasonable at the time, was rendered inappropriate when the Guadalupian event was brought to light in 1994 (13, 43). Tallies from Sepkoski's compendia (14–16) indicate much smaller losses for the Late Permian alone than the estimates of Raup (12) and Sepkoski (42) for the entire Middle and Late Permian.

The shape of a rarefaction curve depends on the frequency distributions of numbers of species within the higher taxa used to produce it, and these vary among higher taxa. To address this issue, Yang and I (13) produced a composite rarefaction curve at the genus level that was the average for 12 extant higher taxa of marine animals, but it turned out to be nearly coincident with Raup's generic curve for the Echinoidea. Using the composite rarefaction curve for genera and a global database of fossil occurrences (13), we obtained much lower estimates than those of Raup (12) and Sepkoski (42) the percentage of species lost in the

Table 1. Variables used in calculations and their symbols

Symbol	Definition
T	Duration of an interval lacking a mass extinction or of an episode of background extinction preceding a mass extinction (i.e., duration of an episode of exponential change of diversity)
D	Total number of genera in an interval
N	Number of genera at the end of an interval lacking a mass extinction or at the start of a mass extinction (i.e., number of genera at the end of an episode of exponential change of diversity)
N_0	Number of genera at the start of an interval (i.e., number of genera at the start of an episode of exponential change of diversity)
N_m	Mean number of genera for an episode of exponential change of diversity
o	Number originations in an interval
x	Total number of extinctions for an interval lacking a mass extinction, or number of background extinctions for a mass extinction interval (i.e., number of extinctions during an episode of exponential change of diversity)
e	Total number of extinctions for a mass extinction interval
x_{mass}	Number of genera lost in a mass extinction
O	Rate of origination
E	Rate of extinction

"Interval" refers to a formally recognized stage or substage for which calculations are made.

terminal Permian event: 76–84%, with the average of 80% being favored (the range of estimates here reflected subtraction of a range of estimates for background extinction).

The new estimate of ~62% provided here for terminal Permian extinction at the genus level (Fig. 4) yields an estimate of ~85% for loss of species based on the composite rarefaction curve of Stanley and Yang (13) (Fig. 5). Fig. 5 also includes a genus-level rarefaction curve for each of the other major crises considered here. The range of values for each event reflects the range of extinction/origination ratios considered most appropriate for each calculation (red bars of Fig. 4) (Dataset S1 and Dataset S2).

Actually, all of these estimates of species losses in Fig. 5 are too high because they are based on the false assumption that extinction struck all taxa with equal probability. Raup (12) acknowledged that clustering of species-level extinctions within certain higher taxa would usually produce a rarefaction-based overestimate of the percentage of species lost, but he expressed skepticism about the idea that mass extinctions actually struck nonrandomly. (In fact, extreme clustering could lead to an underestimate of species losses if a few higher taxa included a huge percentage of all species and species losses were concentrated within them.) It is by now common knowledge that certain higher taxa have repeatedly been struck harder than others by mass extinctions, and this pattern is illustrated in Fig. 6. Taxa with characteristically high rates of background extinction usually suffer relatively heavy losses in mass extinctions because background rates are multiplied in these crises (44, 45). Even within orders and classes, there is evidence of clustering (46, 47).

The effects of clustering on the entire marine fauna can be circumvented by conducting a rarefaction estimate of the percentage of species lost for each major higher taxon individually and then giving each of these groups its proper contribution to losses for the total fauna by calculating a weighted average, based on diversities of groups at the start of the mass extinction (Dataset S3).

I have calculated what generic losses in the terminal Permian mass extinction would have been using the approach illustrated in Fig. 3 for taxa containing >30 genera at the start of this mass extinction. Taxa with fewer genera (mean ~10) represented only ~18% of the total, and these minor groups were simply assigned losses in the mass extinction by assuming that their background losses were of the same magnitude as those for earlier late Paleozoic intervals not characterized by mass extinction. Of course, the composite rarefaction curve used could not be perfectly accurate for all of these taxa, but I have assumed that the inaccuracies would approximately cancel each other out. Taxa containing <5 genera at the start of the mass extinction were judged inappropriate for the final calculation, but the total number of genera used amounted to ~90% of those actually present the start of the mass extinction. This sample produced an unweighted extinction magnitude of 84%, virtually identical to the ~85% estimate for the entire fauna.

To produce numbers for the weighted average, the approach illustrated in Fig. 3 produced high and low estimates of generic losses for individual taxa. To deal with this, either the high or the low number for each taxon that contained >30 genera at the start of the mass extinction was selected randomly 20 times to produce a series of 20 sets of estimated species-level losses for these taxa via the rarefaction method; estimated losses for the minor taxa were not varied in the same way but simply added to each set (Dataset S4). The mean of the weighted average for the 20 resulting species-level estimates was 80.2% ($\sigma = 0.29$) for loss of species in the terminal Permian event. This weighted average was ~4% below the unweighted number of 84%. When applied to the entire fauna, this estimate produces a reduction of the calculated losses of marine species in the terminal Permian event from ~85% to ~81% (Fig. 5).

In Fig. 5, an adjustment for clustering has been made only for the Late Permian curve. Comparable adjustments for the other curves would reduce estimated losses of species in other crises to about 95% of the figured values. Furthermore, it should be noted that additional clustering at lower taxonomic levels than the orders and classes considered here would, at least slightly, further reduce estimates of losses at the species level.

Discussion

The calculations presented here for genus-level losses in mass extinctions (Fig. 4) were devised to improve on previous estimates by incorporating estimates of background extinction, standing diversity at the start of a crisis, and the size of the Signor–Lipps effect. The resulting numbers produced by the particular techniques used here are of course only as accurate as the data used for the calculations. Nonetheless, my estimates have resilience in the sense they will be unaffected by future changes in the perceived durations of MEIs and will be little altered by changes in the perceived durations of the intervals preceding the MEIs used to make the calculations. Furthermore, moderate raising and lowering of seemingly appropriate values for the key parameters (in effect, conducting sensitivity tests) has had only a minor effect on the results.

I have avoided presenting what are sometimes termed "rates of extinction" for major biotic crises, meaning percentages of extinction per unit time during these events. These "rates" are often calculated as $(e/D)/T$ (%/My). The employment of e and D instead of x_m and N are inappropriate here, just as they are when the magnitude of a mass extinction is calculated as e/D. Calculation of the actual rate at which taxa are lost during a mass extinction requires a value of T for a crisis. This is often impossible to estimate accurately because of stratigraphic uncertainties, including the need for interpolations or the assumption of constant rates of deposition. Also, the use of $(e/D)/T$ or e/D can disguise minor but significant mass extinctions if it is deemed necessary that, for an interval to be recognized as harboring a mass extinction, one or another of the resulting numbers must stand well above the equivalent numbers for adjacent intervals (10, 11, 19, 41). Many small events that should qualify as global mass extinctions do not meet such criteria even though paleontologists have detected their elimination of several percent of marine genera globally. Of course it is unnecessary to try to calculate actual rates of extinction to identify major mass extinctions because these events were so large that they are obvious to us. If the terminal Cretaceous crisis occurred within a few days, or even a few years, its rate of global extinction may well have been by far the largest of all time. This kind of rate interests us to the degree that it reflects the cause of a mass extinction, but what interests us more in comparing mass extinctions is their overall impact on biodiversity, which is to say the percentages and types of taxa they eliminated. The terminal Cretaceous crisis may have occurred at an astounding rate, but the terminal Permian crisis had a greater impact on global diversity.

It is important to recognize that the ecological consequences of mass extinctions have not always reflected their magnitudes (48, 49). For example, the Ashgillian crisis, which ranks second numerically in the group of crises considered here (Fig. 4), had a relatively minor ecological impact because, of the major groups that were heavily affected, only the trilobites failed to recover substantially in the aftermath of the event. On the other hand, the Frasnian event, which was not nearly so severe in numerical losses, resulted in a permanent decline for the coral/stromatoporoid reef community and inflicted permanent damage on pelagic life and certain articulate brachiopod taxa. The Famennian event, which was very small in overall percentage of genera lost, nonetheless entailed the virtual disappearance of placoderm fishes, which previously had been voracious top predators in the ocean. Food webs in the ocean must have been profoundly altered by this event.

An analysis comparing the numerical magnitudes of mass extinctions with their ecological impact has ranked the great Changhsingian crisis first in both categories, and the Cretaceous crisis also ranks high in both (49). Nonetheless, numbers belie the frequent Armageddon-like claim that life in the ocean nearly disappeared at the end of the Permian, as exemplified by the subtitles given to two books on the terminal Permian crisis (50, 51), perhaps in both cases under the strong influence of publishers. Because in this event the losses were unequally distributed among taxa (there was clustering), some orders and classes absorbed a disproportionate percentage of species losses, and others did not even come close to disappearing. In fact, of the marine higher animal taxa present in the Late Permian, ∼90 orders (∼90% of those that had been present) and more than 220 families survived the crisis (14). Considerable morphological, physiological, and ecological diversity was conserved via the survival of so many higher taxa, a large number of which went on to diversify substantially in the Mesozoic. For example, the articulate brachiopods and crinoids, starting from very low diversity after the Permian, soon radiated substantially along with the mollusks. The terminal Permian crisis by no means sealed the brachiopods' and crinoids' fate, but in 1977 I pointed out that the expansions of these two groups were eventually stifled because of their vulnerability to predation by the newly radiating crabs, predaceous gastropods, and teleost fishes (52). Citing my paper, Vermeij labeled this the Mesozoic marine revolution (53). The new marine carnivores clearly produced the kinds of protracted extinctions by attrition that I have already discussed. Had these predators never appeared, articulate brachiopods and crinoids would undoubtedly be much better represented than they are in shallow seas today.

As already noted, when the Guadalupian mass extinction came to light in 1994 (13, 54), my former student Xiangning Yang and I showed that Raup and Sepkoski's estimates for the loss of species in the terminal Permian event (12, 42) were clearly too high because they included extinctions for the entire Middle and Late Permian (13). Our best estimate for species losses in this crisis was ∼80%. This turns out to be nearly identical to the new estimate of ∼81% presented here, which is based on a more sophisticated approach. Although our 1994 article has received nearly 400 citations, Raup's estimates of 88–96% (often rounded to 90–95%) have been quoted inappropriately at least 65 times in scientific articles since our article's appearance, sometimes alongside our lower estimate. Although the high numbers are dramatic and therefore appealing, the present paper underscores the point that they are unquestionably wrong. They should not be quoted, even as possibly being correct.

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1. Stanley SM (2010) Relation of Phanerozoic stable isotope excursions to climate, bacterial metabolism, and major extinctions. *Proc Natl Acad Sci USA* 107(45):19185–19189.
2. Foote M (2005) Pulsed origination and extinction in the marine realm. *Paleobiology* 31:6–20.
3. Foote M (2003) Origination and extinction through the Phanerozoic: A new approach. *J Geol* 111:125–148.
4. Signor PW III, Lipps JH (1982) Sampling bias, gradual extinction patterns, and catastrophes in the fossil record. *Spec Pap Geol Soc Am* 190:291–296.
5. Foote M (2007) Extinction and quiescence in marine animal genera. *Paleobiology* 33: 261–272.
6. Melott AL, Bambach RK (2014) Analysis of periodicity of extinction using the 2012 geological timescale. *Paleobiology* 40:177–196.
7. Stitt JH (1971) Repeating evolutionary patterns in Late Cambrian trilobite biomeres. *J Paleontol* 45:178–181.
8. Orchard MJ (2007) Conodont diversity and evolution through the latest Permian and Early Triassic upheavals. *Palaeogeogr Palaeoclimatol Palaeoecol* 252:93–117.
9. Sepkoski JJ, Jr (1984) A kinetic model of Phanerozoic taxonomic diversity. III. Post-Paleozoic families and mass extinctions. *Paleobiology* 10(2):246–267.
10. Sepkoski JJ, Jr (1996) Patterns of Phanerozoic extinction: A perspective from global data bases. *Global Events and Event Stratigraphy*, ed Walliser OH (Springer, Berlin), pp 35–51.
11. Bambach RK (2006) Phanerozoic biodiversity mass extinctions. *Annu Rev Earth Planet Sci* 34:127–155.
12. Raup DM (1979) Size of the Permo-Triassic bottleneck and its evolutionary implications. *Science* 206:217–218.
13. Stanley SM, Yang X (1994) A double mass extinction at the end of the Paleozoic Era. *Science* 266:1340–1344.
14. Sepkoski JJ, Jr (1982) A compendium of fossil marine families. *Milwaukee Pub Mus Contr Biol Geol* 51:1–125.
15. Sepkoski JJ, Jr (2002) A compendium of fossil marine animal genera. *Bull Am Paleontol* 363:1–560.
16. Sepkoski JJ, Jr (2002) Sepkoski's Online Genus Database, ed Peters SE. Available at strata.geology.wisc.edu/jack/. Accessed September 15, 2016.
17. Ogg J, Gradstein F (2013) *TimeScale Creator (TSCreator) 6.0* (Geologic TimeScale Foundation, Purdue University, West Lafayette, IN).
18. Foote M (2000) Origination and extinction components of taxonomic diversity: General problems. *Paleobiology* 26(4, Supplement):74–102.
19. Raup DM, Sepkoski JJ, Jr (1982) Mass extinctions in the marine fossil record. *Science* 215:1501–1503.
20. Hallam A (2002) How catastrophic was the end-Triassic mass extinction? *Lethaia* 35: 147–157.

21. Tanner LH, Lucas SG, Chapman MG (2004) Assessing the record and causes of Late Triassic extinctions. *Earth Sci Rev* 65:103–139.
22. House MR (2002) Strength, timing, setting and cause of mid-Palaeozoic extinctions. *Palaeogeogr Palaeoclimatol Palaeoecol* 181:5–25.
23. Loydell DK (2007) Early Silurian positive δ13C excursions and their relationship to glaciations, sea-level changes and extinction events. *Geol J* 42:531–546.
24. Wignall PB, et al. (2009) Volcanism, mass extinction, and carbon isotope fluctuations in the Middle Permian of China. *Science* 324:1179–1182.
25. Bond DPG, et al. (2010) The mid-Capitanian (Middle Permian) mass extinction and carbon isotope record of South China. *Palaeogeogr Palaeoclimatol Palaeoecol* 292: 282–294.
26. Kasuya A, Isozaki Y, Igo H (2012) Constraining paleo-latitude of a biogeographic boundary in mid-Panthalassa: Fusuline province shift on the Late Guadalupian (Permian) migrating seamount. *Gondwana Res* 21:611–623.
27. Groves JR, Wang Y (2013) Timing and size selectivity of the Guadalupian (Middle Permian) fusulinoidean extinction. *J Paleontol* 87:183–196.
28. Clapham ME, Shen S, Bottjer DJ (2009) The double mass extinction revisited: Reassessing the severity, selectivity, and causes of the end-Guadalupian biotic crisis (Late Permian). *Paleobiology* 35:32–50.
29. Smith LB, Jr, Read JF (2000) Rapid onset of late Paleozoic glaciation on Gondwana: Evidence from Upper Mississippian strata of the Midcontinent, United States. *Geology* 28:279–282.
30. Bonelli JR, Patzkowsky ME (2011) Taxonomic and ecologic persistence across the onset of the Late Paleozoic ice age: Evidence from the Upper Mississippian (Chesterian Series), Illinois Basin, United States. *Palaios* 26:5–17.
31. McGhee GR (1982) The Frasnian-Famennian extinction event: A preliminary analysis of Appalachian marine ecosystems. *Spec Pap Geol Soc Am* 190:491–500.
32. Copper P (1986) Frasnian/Famennian mass extinction and cold-water oceans. *Geology* 14:835–839.
33. Streel M, Caputo MV, Loboziak S, Melo JHG (2000) Late Frasnian-Famennian climates based on palynomorph analyses and the question of the Late Devonian glaciations. *Earth Sci Rev* 52:121–173.
34. Buggisch W, Joachimski MM (2006) Carbon isotope stratigraphy of the Devonian of Central and Southern Europe. *Palaeogeogr Palaeoclimatol Palaeoecol* 240:68–88.
35. Brezinski DK, Cecil CB, Skema VW, Stamm R (2008) Late Devonian glacial deposits from the eastern United States signal an end of the mid-Paleozoic warm period. *Palaeogeogr Palaeoclimatol Palaeoecol* 268:143–151.
36. Sheehan PM (1973) The relation of Late Ordovician glaciation to the Ordovician-Silurian changeover in North American brachiopod faunas. *Lethaia* 6:147–154.
37. Sheehan PM, Coorough PJ (1990) Brachiopod zoogeography across the Ordovician-Silurian extinction event. *Palaeozoic Palaeogeography and Biogeography*, eds McKerrow WS, Scotese CR (Geological Society Memoir, Boulder, CO), Vol 12, pp 181–187.
38. Stanley SM, Powell MG (2003) Depressed rates of origination and extinction during the late Paleozoic ice age: A new state for the global marine ecosystem. *Geology* 31: 877–880.
39. Powell MG (2005) Climatic basis for sluggish macroevolution during the Late Paleozoic ice age. *Geology* 33:381–384.
40. Jin YG, et al. (2000) Pattern of marine mass extinction near the Permian-Triassic boundary in South China. *Science* 289:432–436.
41. Sun Y, et al. (2012) Lethally hot temperatures during the Early Triassic greenhouse. *Science* 338:366–370.
42. Sepkoski JJ, Jr (1986) Phanerozoic overview of mass extinction. *Patterns and Processes in the History of Life*, eds Raup DM, Jablonski D (Springer-Verlag, Heidelberg), pp 277–295.
43. Jin YG, Zhang J, Shang QH (1994) Two phases of the end-Permian mass extinction in Pangea: Global environments and resources. *Can Soc Pet Geol Mem* 17:813–822.
44. Stanley SM (1979) *Macroevolution: Pattern and Process* (W.H. Freeman & Co., San Francisco).
45. Stanley SM (2007) An analysis of the history of marine animal diversity. *Paleobiology* 33(47 Supplement):1–55.
46. McKinney ML (1995) Extinction selectivity among lower taxa: Gradational patterns and rarefaction error in extinction estimates. *Paleobiology* 21:300–313.
47. Janevski GA, Baumiller TK (2009) Evidence for extinction selectivity throughout the marine invertebrate fossil record. *Paleobiology* 35:553–564.
48. Droser ML, Bottjer DJ, Sheehan PM, McGhee GR, Jr (2000) Decoupling of taxonomic and ecologic severity of Phanerozoic marine mass extinctions. *Geology* 28:675–678.
49. McGhee GR, Jr, Sheehan PM, Bottjer DJ, Droser ML (2004) Ecological ranking of Phanerozoic biodiversity crises: Ecological and taxonomic severities are decoupled. *Palaeogeogr Palaeoclimatol Palaeoecol* 211:289–297.
50. Benton M (2003) *When Life Nearly Died: The Greatest Mass Extinction of All Time* (Thames & Hudson, London).
51. Erwin DH (2006) *Extinction: How Life on Earth Nearly Ended 250 Million Years Ago* (Princeton Univ Press, Princeton, NJ).
52. Stanley SM (1977) Trends, rates, and patterns of evolution in the Bivalvia. *Patterns of Evolution, as Illustrated by the Fossil Record*, ed Hallam A (Elsevier, Amsterdam), pp 209–250.
53. Vermeij GJ (1977) The Mesozoic marine revolution: Evidence from snails, predators, and grazers. *Paleobiology* 21:125–152.
54. Jin YG, Zhang J, Shang QH (1994) Two phases of the end-Permian mass extinctions. *Can Soc Pet Geol Mem* 17:813–822.

Supporting Information

Stanley 10.1073/pnas.1613094113

SI Text

Data for individual taxa were calculated from sources identified in the text specifically for analyses undertaken here. Genera of questionable identity or occurrence were included.

Genera confined to a single interval ("singletons") were also included in analyses. Excluding singletons from tallies, as some researchers have done, removes a large amount of valid information. It has an especially large negative effect for taxa characterized by high rates of extinction. Most ammonoid and nautiloid genera and a large percentage of brachiopod, trilobite, and conodont genera are known from only a single stage or substage. The mean generic durations for these groups are so short that many legitimate singletons are to be expected. So many singletons recorded for these large groups are legitimate singletons that eliminating them from databases does more harm than good by causing rates of extinction to be underestimated.

Data for the ammonoid order Clymeniida illustrate what a devastating effect singleton exclusion can have. The Clymeniida arose in the middle Famennian and radiated explosively but also suffered heavy losses during this interval (had a high turnover rate). They added a smaller number of new genera in the late Famennian, when they also suffered many extinctions, some of them recognized as having occurred in the terminal Famennian event. Here are the raw numbers compared with the numbers that result from elimination of singletons:

Famennian extinctions and originations for the Clymeniida	Raw data	Minus singletons
Late Famennian extinctions	22	7
Late Famennian diversity	22	7
Late Famennian originations	15	0
Middle Famennian extinctions	35	0
Middle Famennian diversity	42	7
Middle Famennian originations	42	7

Elimination of singletons essentially destroys the database here. With the full set of data, we can see: (*i*) that total known diversity was 57, not 7; that rates of origination and background extinction were very high (the middle Famennian data illustrate this); and (*ii*) by assessing the likely rate of background extinction and magnitude of the Signor–Lipps effect, we can estimate the number of genera lost in the terminal extinction event (the number will have been very low because of the large amount of background extinction: ~84% of all middle Famennian genera are recorded as having died out via background extinction). There is almost no question that the Clymeniida arose in the middle Famennian, so it is very unlikely that any of the genera actually ranged back to the Frasnian. We can conclude a priori that there had to be many legitimate singletons because of the high turnover rate. Because rates of origination and extinction are strongly correlated, the high origination rate implies that mean longevity for genera would have been very short. Thus, although slightly more than 7 middle Famennian genera may have survived to the late Famennian, a large majority of the 35 apparent middle Famennian singletons must be legitimate singletons. Because it appears that what few genera were present at the end of the Famennian died out en masse, it is very likely that all 15 genera that arose in the late Famennian are also legitimate singletons.

A simple thought experiment shows that the existence of a considerable number of legitimate singletons for marine life in general is inevitable. Valid genera are monophyletic, meaning that each one is initially represented by a single species. Species longevities vary among taxa, but consider a taxon in which the average species longevity is 5 My (probably about right for brachiopods). This situation means that a large fraction of all species in such a taxon will survive for less than 5 My. Mean interval duration for my dataset is close to 5 My. It follows that many new genera will die out during the interval in which they arise: they will become legitimate monospecific singleton genera. A few will die out even after having expanded to two or more species during the interval. And think what happens when one applies this thought experiment to the many taxa for which species durations are much shorter than 5 My. (e.g., Mesozoic ammonoids, for which, in addition, the modal diversity for number of recognized species per genus is one!)

Elimination of singletons also badly distorts estimates of the magnitudes of mass extinctions. The key point here is that many genera that arise during an interval terminated by a mass extinction will automatically become legitimate singletons as victims of the mass extinction (in fact, because these new genera will typically contain relatively few species, the percentage of these genera lost in the crisis will be larger than average). On the other hand, all species that have arisen during the mass extinction interval but that are found to have survived the crisis will be tallied as survivors. Clearly, excluding the legitimate singletons and including all nonsingletons will artificially reduce the calculated magnitude of the mass extinction.

Results obtained when singletons are included will not be perfect (calculations of rates and diversities never are), but on average, they will be more accurate than results obtained after exclusion of singletons, because in many cases exclusion produces extreme distortions of actual patterns. For the reason given in the preceding paragraph, exclusion of singletons is especially harmful in the estimation of magnitudes of mass extinctions.

The time scale used is from 2013 TS Creator – G & O, except for the Ordovician, for which the 2008 time scale of the International Subcommission on Ordovician Stratigraphy was used. Where no values were given for lower, middle, or upper boundaries of an epoch, the epoch was divided into equal segments.

Intervals for Which Data Were Excluded from the Regression showing the Correlation Between Interval Length and Mass Extinction (Fig. 1) **(References for documentations of mass extinctions in parentheses.)**

Late Eocene (Prothero, 1994*, The Eocene-Oligocene Transition*, D.R., Columbia University Press, New York, 291pp.; Prothero, D.R., Ivany, L. C., and Nesbitt, E.R., 2003, *From Greenhouse to Icehouse: The Marine Eocene-Oligocene Transition*, Columbia University Press, New York, 541 pp.)

Maastrichrian (Common knowledge)

Cenomanian (Elder, W.P., 1987, *Palaios* 2:24-40; Parente, et al., 2008, *Geology* 36:715-718; Monnet, C., 2009, *Palaeogeography, Palaeoclimatology, Palaeoecology* 282:88–104)

Aptian (Huber, B.T. and Leckie, R. M., 2011, *Jour. of Foraminiferal Research.* 41:53–95; Méhay, S. et al., 2009, *Geology* 37:819–822.)

Tithonian (Hallam, A., 1986, *Nature* 319:765–768.)

Pliensbachian (Hallam, A., 1986, *Nature* 319:765–768.)

Rhaetian (Common knowledge)

Norian (Hallam, A., 2002, *Lethaia* 35:47–157; Tanner, L.H., Lucas, S.G., and Chapman, M.G., 2004, *Earth-Science Reviews* 65:103–139.)

Carnian (Tanner, L.H., Lucas, S.G., and Chapman, M.G., 2004, *Earth-Science Reviews* 65:103–139.)

Ladinian (Signor-Lipps)

Induan (Stanley, S.M., 2009, *Proc. National Academy of Sciences* 106:15264-15267.)

Lopingian (Late Permian) (Common knowledge)

Guadalupian (Jin, Y.G. and hang, Q.H., 1994, Memoir Canadian Society of Petroleum Geologists 17:813–822.)

Lower Serpukhovian (Stanley, S. M. and Powell, M. G., 2003, *Geology* 31: 877–880.)

Visean (Stanley, S. M. and Powell, M. G., 2003, *Geology* 31: 877–880.)

Late Famennian (Common knowledge)

Late Frasnian (Common knowledge)

Givetian (Taghanic Event) (Talent, et al., 1993, *Palaeogeography, Palaeoclimatology, Palaeoecology* 104:139–152; House, M.R., 2002, *Palaeogeography, Palaeoclimatology, Palaeoecology* 181:5–25; Brett, C.E., et al., 2011, *Palaeogeography, Palaeoclimatology, Palaeoecology* 304:21–53.)

Eifelian (Kacek Event) (Talent, et al., 1993, *Palaeogeography, Palaeoclimatology, Palaeoecology* 104:139–152; House, M. R., 1993, Systematics Assoc. Special Vol.47:13–34; DeSantis, M. K. and Brett, C.E., 2011, *Palaeogeography, Palaeoclimatology, Palaeoecology* 304:113–135.)

Pridolian (Talent, et al., 1993, *Palaeogeography, Palaeoclimatology, Palaeoecology* 104:139–152.)

Ludlow (Lau Event) (Chatterton, B.D.E., Edgecombe, G.D., and Tuffnell, P.A., 1990, *Jour. Geological Society of London* 147:703–715; Talent, et al., 1993, *Palaeogeography, Palaeoclimatology, Palaeoecology* 104:139–152; Eeiksson, M. E, Nilsson, E.K., and Jeppsson, L. 2009, *Geology* 37:739–740.)

Wenlock (Homerian Event) Chatterton, B.D.E., Edgecombe, G.D., and Tuffnell, P.A., 1990, *Jour. Geological Society of London* 147:703–715.

Llandovery (Ireviken and Sedgwickii events) (Chatterton, B.D.E., Edgecombe, G.D., and Tuffnell, P.A., 1990, *Jour. Geological Society of London* 147:703–715; Aldridge, R.J., Jeppsson, L., and Dorning, K.J., 1993, *Jour. Geological Society of London*, 150:501–513; Talent, et al., 1993, *Palaeogeography, Palaeoclimatology, Palaeoecology* 104:139–152.)

Hirnantian (Sheehan, P.M. and Coorough, 1990, *Geological Society Memoir* 12:181–187.

Katian (Common knowledge)

Caradoc (Patzkowsky, M. E. and Holland, S.M.,1993, *Geology* 21:619–622.)

Other Supporting Information Files

Dataset S1 (XLS)
Dataset S2 (XLS)
Dataset S3 (XLS)
Dataset S4 (XLS)