# Size of the Permo-Triassic Bottleneck and Its Evolutionary Implications

Abstract. *Rarefaction analysis of extinctions in the Late Permian indicates that as many as 96 percent of all marine species may have died out, thus forcing the marine biosphere to pass through a small bottleneck. With such severity of extinction, chance elimination of certain biologic groups would have been probable. Some of the changes in biologic composition observed at the Permo-Triassic boundary may be explained as an evolutionary founder effect that followed the bottleneck.*

The late Permian is generally recognized as the most severe of the several mass extinctions recorded in the Phanerozoic marine fossil record, but quantitative analysis has proved difficult. Most analyses of mass extinctions are based on data from the higher taxonomic categories (families, orders, and classes) because only at these levels is sampling complete enough to bridge the gaps in the evolutionary record. Valentine noted that it would be far more appropriate biologically to analyze extinction at the species level; but the record is simply not available, and he suggested the family level as the best compromise (*1*). Several attempts have been made to interpolate extinction data from higher taxa down to the species level. Most recently Valentine *et al.* (*2*) provided estimates indicating a drop of 77 percent in standing diversity of species from the Permian to the Triassic. This suggests that marine biotas went through a diversity bottleneck.

Data on families, orders, and classes used here (Table 1) come from Sepkoski (*3*). The data set was chosen from among many because it is the most comprehensive and includes marine vertebrates as well as invertebrates. As the end of the Permian approached, numbers of taxa declined, thus departing from a steady state that had been maintained for at least 100 million years (*3*). The effect (Table 1) is seen first among families (Leonardian-Guadalupian) and then among orders and classes (Guadalupian-Dzhulfian). This sequence is to be expected on sampling grounds alone: even if the extinctions all occurred at the same time, the preserved record would be smeared out. Because of the smearing effect, the magnitude of the extinctions is calculated (right-hand column in Table 1) by comparing numbers of taxa in the Leonardian with those at the Permo-Triassic boundary. The generic data come from survivorship analysis (*4*). These data are less complete, and sampling problems abound as a result of the short half-life of genera. Thus, the generic extinction figure in Table 1 should be used with caution.

The basic question is: How many species must have died out to produce the extinction rates listed in Table 1? For living organisms, this interpolation is straightforward. For example, there are estimated to be 894 living species of echinoid echinoderms distributed among 222 genera, 40 families, and 9 orders (*5*). Of the 222 genera, 78 are monotypic, 42 have two species, and so on. The frequency distribution follows the "hollow curve" typical of all groups of organisms (*6*). If 50 percent of the echinoid species were to die out (leaving no descendents), and if the species extinctions were nonselective, one could predict the numbers of higher taxa that would go extinct just as a result of losing all their constituent species. The most straightforward technique for calculating this is rarefaction, developed originally in an ecological context to answer the question of how many species would have been found had fewer specimens been collected (*7*). When rarefaction is used in the present context, species are substituted for specimens and higher taxa are substituted for species.

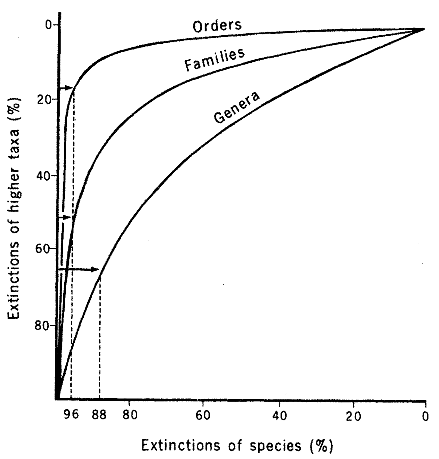

Fig. 1. Rarefaction curves based on taxon size frequencies for 894 species of living echinoids. Labeling of axes is reversed to show the relation between extinction of species and higher taxa. Complete survival (zero extinction) is at the point of convergence in the upper-right corner. Complete extinction is the convergence in the lower left. Intermediate positions indicate the number of species lost (abscissa) for a given extinction at higher taxonomic levels (ordinate). The three arrows along the left-hand axis are the Late Permian extinctions of marine orders, families, and genera. The points on the abscissa where the arrows intersect the rarefaction curves are estimates of species extinctions in the Late Permian.

Given rarefaction curves for the standing diversity of a group (as in Fig. 1) the following logic can be used: If extinction at a high taxonomic level is known, the species extinction responsible for it can be determined graphically by finding the abscissa value corresponding to the known ordinate. In the case of echinoids, extinction of 52 percent of the families, for example, is equivalent to extinction of 96 percent of the species. This reasoning can be applied to the Permo-Triassic case only if there are reasonable estimates of the taxon size frequency distributions for Permian time. We have no way directly to observe the numbers of species within higher taxa on a worldwide basis for the Permian, and therefore proxy data must be used.

Rarefaction curves show variation in shape: some of this variation is caused by differences in taxonomic procedure and some by differences in evolutionary history. Hollow curve shape (and therefore rarefaction curve shape) evolves in a predictable fashion. Young groups tend to have many monotypic taxa and thus have rarefaction curves approaching the 45° limiting case; as groups evolve, taxa are filled in and the rarefaction curves become more convex. This progression

Table 1. Permian extinction data for well-skeletonized marine vertebrate and invertebrate animals (*3, 4*). Percent extinction for classes, orders, and families is based on the ratio between diversity at the Permo-Triassic boundary and that of the Leonardian stage.

| | Permian standing diversity | | | | | | |
|---|---|---|---|---|---|---|---|
| | Asselian | Sakmarian | Leonardian | Guadalupian | Dzhulfian | Permo-Triassic boundary | Percent extinction in Permian |
| Classes | 37 | 37 | 37 | 36 | 33 | 32 | 13.5 |
| Orders | 109 | 107 | 107 | 109 | 100 | 89 | 16.8 |
| Families | 378 | 378 | 377 | 340 | 248 | 181 | 52.0 |
| Genera* | | | | | | | 64.8 |

*Invertebrates only; see text.

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is not only a natural consequence of the evolutionary branching process (*8*) but also is a result of ecological species packing (*9*). The simplest index of this change is the overall ratio of species to genera. For groups of organisms living today, this ratio has a minimum of about 4. The living representatives of the paleontologically significant groups of marine organisms have ratios of species to genera averaging about 12 (*9*).

Valentine estimated that average ratios of species to genera increased from about 6 in the middle Cambrian to 10 in the late Cretaceous; his estimate closest to the Permian is for the Late Carboniferous: 8.2 species per genus (*9*). For my analysis, I have chosen to use data for living echinoids because this group has a species/genus ratio of 4.03 and thus is a conservative choice as a proxy for true species-level Permian data. The extinction data in Table 1 for genera, families, and orders have been entered in Fig. 1 in order to estimate species extinctions. Sepkoski's family and order data yield identical species extinction values: 96 percent. The generic data yield 88 percent.

These results support the conclusion of Valentine *et al.* (*2*) that the percentage of species going extinct was high. My analysis goes further, however, by suggesting a mass extinction of truly dramatic proportions, possibly approaching (though of course not reaching) complete extinction of marine life.

Species extinction of 88 or 96 percent is so high that a search for logical errors or biases in the analysis is necessary. One problem might be that estimates of species extinctions are exaggerated because some families and orders were small (near extinction) in the late Permian (*1*), but this is largely accounted for when rarefaction is used: it is assumed that most taxa are small. It could be argued that the Permo-Triassic extinctions are taxonomic artifacts caused by the reluctance of some taxonomists to continue taxa over a major era boundary, but if this were the case, the terrestrial fossil record would show a comparably severe mass extinction. It could even be argued that normal species turnover is so rapid that extinction of nearly 100 percent during the Permian is to be expected even without a mass extinction. But the concern here is not with normal turnover covering the span of the Permian but with extraordinary turnover in the late Permian (mass extinction). Finally, it could be argued that the extinctions were actually selective [in spite of some evidence to the contrary (*10*)], so that some higher taxa had relative immunity to extinction. If so, the estimates of species extinction would have to be lowered because the rarefaction method assumes nonselective extinction. In a worst case, if all species in half the higher taxa were immune to extinction, the family data (Table 1) would predict a 76 percent decrease in standing diversity. Thus, although the 88 and 96 percent estimates from Fig. 1 may be on the high side, we are still left with a bottleneck at least as narrow as that computed from Valentine's data.

The magnitude of the extinction has evolutionary implications. In the Permian, the standing species diversity was at least 45,000 (*2*) and at most 240,000 (*11*). If only 4 percent survived, the marine biosphere would have been left with between 1,800 and 9,600 species. Under the circumstances, chance sampling effects would have influenced the composition of the surviving biota through an evolutionary founder effect analogous to the phenomenon observed when oceanic islands are populated by small numbers of chance migrants. In such cases, the colonizing group is not typical of the source group because of accidents of dispersal as well as true differences in dispersal ability. The compositional changes that followed the Permo-Triassic extinction (*12*) may have resulted to some degree from founder effects. It would be predicted that some of these changes should make sense ecologically and others not. And this is indeed the case. The critical problem remaining is to measure the importance (or presence) of selectivity in species extinction in order better to evaluate the rarefaction results.

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### References and Notes

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# Estuarine Influences on a Continental Shelf Plankton Community

Abstract. *On the southeastern U.S. continental shelf, phytoplankton primary production and the densities of zooplankton, fish eggs, and fish larvae peak simultaneously in late summer and early fall. Some community response to irregular storm events is observed. However, the gross plankton community dynamics on this shelf are dominated by couplings with the local estuaries and shallow nearshore zone.*

Although man may have a great impact on estuarine ecology and an interest in maintaining the natural productivity of continental shelf communities, little is known of the ecological couplings between estuaries and coastal waters. Our purpose in this report is to describe some of these couplings for the plankton community of the South Carolina and Georgia continental shelf. Community metabolic processes in the local estuaries

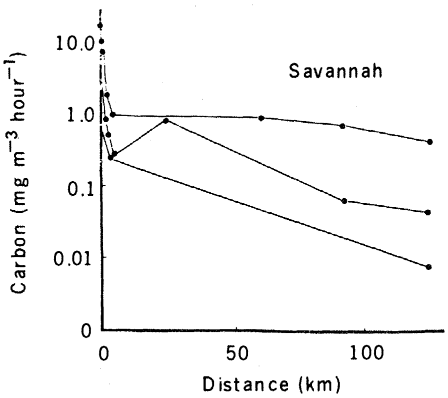

Fig. 1. An example of the seasonal changes in $P_{\max}$ along a transect at Savannah, Georgia (0 km is at the outermost sea buoy at the entrance to Wassaw Sound). From top to bottom the sampling months are November, August, and June. The rates vary up to 10 times between cruises and decrease going offshore. The pattern is similar for data collected along transects normal to the coast at Jacksonville, Florida; Sapelo Island, Georgia; and Charleston, South Carolina.