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Mass Extinctions in the Marine Fossil Record

Abstract. *A new compilation of fossil data on invertebrate and vertebrate families indicates that four mass extinctions in the marine realm are statistically distinct from background extinction levels. These four occurred late in the Ordovician, Permian, Triassic, and Cretaceous periods. A fifth extinction event in the Devonian stands out from the background but is not statistically significant in these data. Background extinction rates appear to have declined since Cambrian time, which is consistent with the prediction that optimization of fitness should increase through evolutionary time.*

A number of mass extinctions have "reset" major parts of the evolutionary system during the Phanerozoic. However, the precise timing and magnitude of these events has been difficult to measure because data from the fossil record are fragmentary. Comprehensive and accurate data on extinct species have always been unobtainable, and therefore most workers have been forced to investigate extinctions at the level of genera, families, and orders, with family-level data generally preferred as the best compromise between sampling limitations and taxonomic uncertainty (1). Historically, the three best summaries of familial data from the fossil record have been those of Newell (2), Cutbill and Funnell (3), and Valentine (4). But even with these data sets, identification of specific mass extinctions has been difficult and often subjective because of taxonomic problems and especially stratigraphic imprecision. Many macroevolutionary phenomena including mass extinctions have characteristic time scales that are geologically rather short (less than several tens of millions years) and can become lost or grossly distorted when analyzed without adequate stratigraphic control.

We now present a new analysis of extinctions based on a more comprehensive and accurate data set for marine animal families. Marine vertebrates as well as invertebrates and protozoans are included, and the data benefit from compilation of taxonomic and stratigraphic investigations far beyond traditional sources (5). The compilation encompasses approximately 3300 fossil marine families, of which about 2400 are extinct. Times of extinction for 87 percent of the families have been resolved to the level of the stratigraphic stage (mean duration, 7.4×10^6 years), and most of the remaining data has been resolved to strati-

graphic series (mean duration, 20×10^6 years).

The rates of extinction calculated from the familial data plotted against geologic time are illustrated in Fig. 1. Each point was calculated as follows: the number of families that became extinct in each of the 76 post-Tommotian (early Lower Cambrian) stages (6) was divided by the estimated duration of the stage (7); these initial rates were then modified by adding extinction rates calculated from the lower resolution series-level data to the appropriate stages. Calculations were made separately for "shelly" taxa and for rarely preserved taxa (8). The effect of this segregation was negligible in most cases so that the data for rarely preserved animals are not included with most points in Fig. 1. For four stages, however, addition of rarely preserved families increased calculated extinction rates by more than 0.5 family per million

years. These are the stages that contain the four major Lagerstätten of the Phanerozoic marine record: Burgess Shale (Cambrian, Templetonian), Hunsrück Shale (Devonian, Siegenian), Mazon Creek concretions (Carboniferous, Moscovian), and Solnhofen Limestone (Jurassic, "Tithonian"). The combined rates for shelly and rarely preserved families for these four stages are indicated in Fig. 1 by X's with the rates for shelly families shown below. Only the Burgess Shale (Templetonian) stands out on the plot.

The distribution of the 76 points for shelly animals in Fig. 1 suggests that two rates of extinction have been operative through the Phanerozoic. (i) Normal, or background, extinction: the majority of points fall in a rather tight cluster at extinction rates less than 8.0 extinctions per million years. (ii) Mass extinction: several points stand out as being considerably higher than the background and show a maximum of 19.3 familial extinctions per million years.

The problem of determining rigorously which points in Fig. 1 should be considered mass extinctions can be approached as a simple data analysis problem of identifying trends and outliers. As an initial step, we computed a linear regression (not shown) for all 76 extinction points as a function of geologic time and then searched for significant departures from this line. Four points (or 5 percent of the data) fell above the one-sided 99 percent confidence interval. These points, which are circled in Fig. 1, are (per million years) the Ashgillian (19.3 fm), Guadalupian (14.0 fm), Dzhulfian (15.7 fm), and Maestrichtian (16.3 fm). A fifth point, the Norian (10.8 fm), fell

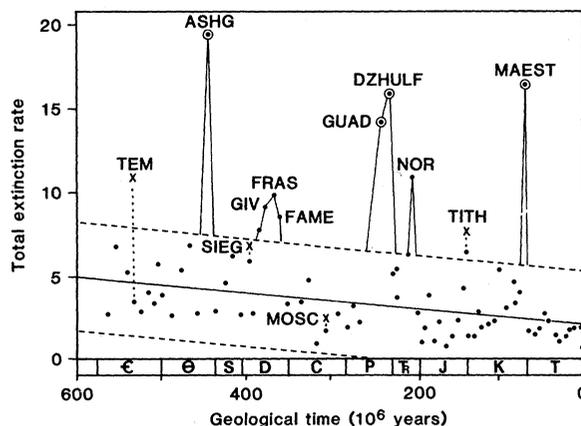


Fig. 1. Total extinction rate (extinctions per million years) through time for families of marine invertebrates and vertebrates. The plot shows statistically significant mass extinctions late in the Ordovician (ASHG), Permian (GUAD-DZHULF), Triassic (NOR), and Cretaceous (MAEST). An extinction event in the late Devonian (GIV-FRAS-FAME) is noticeable but not statistically significant. Circled points are those where the departure from the main cluster is highly significant ($P < .01$); X's indicate those cases where inclusion of rarely preserved animal groups substantially increases the calculated extinction rate (the point directly below the X is the rate calculated without the rarely preserved groups). The figure also shows a general decline in background extinction rate through time. The regression line is fit to the 67 points having extinction rates less than eight families per 10^6 years, and the dashed lines define the 95 percent confidence band for the regression. Abbreviations: TEM, Templetonian; ASHG, Ashgillian; SIEG, Siegenian; GIV, Givetian; FRAS, Frasnian; FAME, Famennian; MOSC, Moscovian; GUAD, Guadalupian; DZHULF, Dzhulfian; NOR, Norian; TITH, Tithonian; MAEST, Maestrichtian.

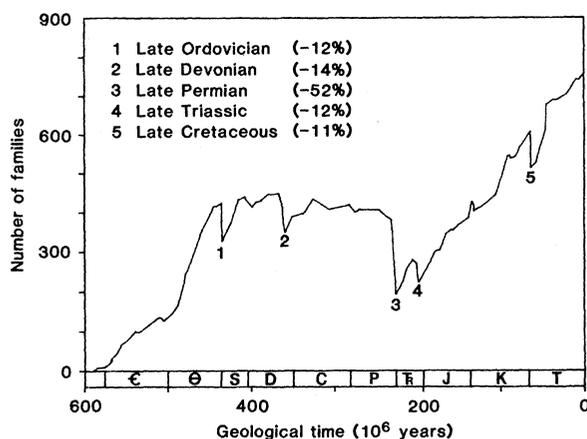


Fig. 2. Standing diversity through time for families of marine vertebrates and invertebrates. Rarely preserved groups are not included. Five mass extinctions, indicated by numerals, are recognizable by abrupt drops in the diversity curve. The relative magnitudes of these drops (measured from the stage before to the stage after the extinction event) are given in parentheses in the upper left. All mass extinctions but No. 2 (Devonian) are statistically significant in Fig. 1 and three (Nos. 1, 3, and 5) are highly significant ($P < .01$).

above the one-sided 95 percent confidence interval. Some or all of these mass extinctions have been recognized previously but without consistency and without statistical testing.

The outlying points identified above also can be recognized as major perturbations in marine diversity. The Phanerozoic diversity curve compiled from the familial data is shown in Fig. 2. Five extinction events are seen as sharp drops in standing diversity. Four of these (counting the Guadalupian and Dzhulfian as a single event) match the statistically significant outliers in Fig. 1. The fifth, labeled "2" in Fig. 2, is a late Devonian extinction that has been recognized by previous workers. This extinction does not appear as a statistically significant event in Fig. 1 because the family extinctions are distributed over two stages, the Frasnian and the preceding Givetian, which have a combined duration of about 15 million years (9). This smearing of extinctions may represent sampling error in that failure to identify the actual time of extinction will almost always push apparent extinctions backward in time. Alternatively, the smearing may reflect a real phenomenon—an extinction "event" that took place over millions of years. The continuation of high extinction rates into the Famennian is consistent with this hypothesis. However, it should be noted that, on the basis of other information, McLaren (10) suggested a meteorite impact as one possible explanation for the Frasnian extinctions.

In summary, five mass extinctions are clearly defined in the familial data. These extinctions occurred in the Late Ordovician (Ashgillian), Late Devonian (Givetian-Frasnian), Late Permian (Guadalupian-Dzhulfian), Late Triassic (Norian), and Late Cretaceous (Maestrichtian). The occurrence of these major extinctions near the ends of geologic periods simply reflects the fact that the strati-

graphers who established the geologic time scale in the first half of the 19th century chose major faunal breaks as boundaries for the principal subdivisions.

With the major Phanerozoic events isolated in Fig. 1, a more accurate assessment of the nature of background extinction can be made. Although some smaller but well-known extinction events may remain hidden in Fig. 1 (11), the residual cluster of points suggests that background rates have been declining since the early Paleozoic. The solid line in Fig. 1 is a linear regression fitted to the 67 extinction rates for shelly animals after removal of the major extinction events; the dashed lines, which envelop nearly all these points, represent the 95 percent confidence band for the regression. The correlation coefficient for the regression is .47, which can be considered statistically significant if problems of time series and data selection are ignored. The slope of the regression line is nontrivial and indicates that the total rate of background extinction has decreased from about 4.6 to 2.0 fm per million years since the Early Cambrian. This is surprising in view of the fact that the rates are not normalized for standing diversity, which has increased substantially since the Cambrian (Fig. 2). The decline in extinction rates could be just an artifact of the "pull of the Recent" (12). In contrast, a decrease in extinction rate is predictable from first principles if one argues that general optimization of fitness through evolutionary time should lead to prolonged survival. This is speculative but it is worthy of further consideration because broad predictions of progressive change in evolutionary dynamics are so rarely realized when tested with data.

The decline in background extinction rate from the Early Cambrian to the Recent means that approximately 710 family extinctions did not occur that

would have if the Cambrian rate had been sustained. This number is essentially identical to the amount by which familial diversity increased over that interval (680 families) (Fig. 2). This suggests that the net increase in standing diversity through the Phanerozoic may have been more an effect of decrease in extinction than increase in origination.

In conclusion, our analysis shows that major mass extinctions are far more distinct from background extinction than has been indicated by previous analyses of other data sets. Four mass extinctions are statistically significant events and are likely to represent phenomena qualitatively different from the background. The data do not tell us, of course, what stresses caused the mass extinctions. The extinctions were short-lived events in geological time, but the data do not have the resolving power to show whether the events were also short-lived in human or ecological time.

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5. The data were compiled from R. C. Moore et al., Eds. *Treatise on Invertebrate Paleontology* (Geological Society of America and Univ. of Kansas Press, Lawrence, 1953-1979); W. B. Harland et al., Eds., *The Fossil Record* (Geological Society of London, London, 1967); A. S. Romer, *Vertebrate Paleontology* (Univ. of Chicago Press, Chicago, 1966); also, 380 additional papers and monographs. A complete listing of these data is scheduled to appear in J. J. Sepkoski, Jr., *Milwaukee Pub. Mus. Contrib. Biol. Geol.*, in press.
6. Vendian and Tommotian points were excluded from the analysis because these intervals have exceptionally low diversities and therefore exceptionally low extinction rates.
7. The geologic time scale used is a composite based on a number of recently published stage-level time scales and differs only slightly from that used by J. J. Sepkoski, Jr., *Paleobiology* **5**, 222 (1979).
8. Four general kinds of animals were considered to have low fossilization potential: (i) soft-bodied animals without mineralized skeletons (for example: Nemertina, Priapulida, and Sipunculida as well as many Hydrozoa, Scyphozoa, and Polychaeta); (ii) animals with lightly sclerotized skeletons (such as many Crustacea); (iii) rarely reported fossil animals with multielement skeletons that dissociate rapidly after death (such as Octocorallia and Holothuroidea as well as some Asterozoa and Osteichthyes); and (iv) deep-sea animals with extremely poor fossil records (such as some Crinoidea, Chondrichthyes, and Osteichthyes).
9. The Frasnian might still be considered statistically distinct in Fig. 1. If each point in that figure is considered an independent event, then the probability that three of the nine highest points would be clustered about the Frasnian point is quite low ($P = .002$).
10. D. J. McLaren, *J. Paleontol.* **44**, 801 (1970).
11. "Minor" mass extinctions, which do not appear as noticeable perturbations in Figs. 1 and 2,

include at least three to five events in the Cambrian [A. R. Palmer, *J. Paleontol.* 39, 149 (1965); M. E. Taylor, *ibid.* 42, 1319 (1968); J. H. Stitt, *ibid.* 45, 178 (1971)], an Early Jurassic (Toarcian) event [A. Hallam, *Paleobiology* 3, 58 (1977)], a terminal Eocene event [H. Tappan and A. R. Loeblich, *Geol. Soc. Am. Spec. Pap.* 127, 247 (1971); A. G. Fischer and M. A. Arthur, *Soc. Econ. Paleontol. Mineral* 25, 19 (1977)],

and possible events in the latest Jurassic (Tithonian) and early Late Cretaceous (Cenomanian) (see A. G. Fisher and M. A. Arthur, above).
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Lumber Spill in Central California Waters: Implications for Oil Spills and Sea Otters

Abstract. A large quantity of lumber was spilled in the ocean off central California during the winter of 1978, and it spread through most of the range of the threatened California sea otter population within 4 weeks. The movement rates of lumber were similar to those of oil slicks observed elsewhere. These observations indicate that a major oil spill could expose significant numbers of California sea otters to oil contamination.

The California population of the sea otter [*Enhydra lutris nereis* (Merriam)] was listed as "threatened" in 1977 (1) pursuant to the Endangered Species Act of 1973 (2). The listing was based on the possibility that a major oil spill could occur within the sea otter range and could kill a significant portion of the population, placing it in danger of extinction. This concern arises from the known sensitivity of the species to oil contamination (3). A spill of gasoline and diesel oil nearshore in the Kurile Islands, U.S.S.R., spread through 40 km of coastline and killed over 100 sea otters (4). Concern for the status of the California sea otter is heightened by the lack of evidence of significant population growth since 1973 (5).

It is difficult to project the critical day-to-day movements of floating oil near the sea otter range on the basis of existing oceanographic data. Surface current patterns off central California (San Francisco to Point Conception) have been examined with several techniques (6-9). The principal result is the description of mean flow patterns on a seasonal scale. However, studies of drogues and remote imagery have shown that short-term departures from mean seasonal drift may be frequent in the California current system (6, 7, 10, 11). Such departures involve tidal oscillations and mesoscale meanders and eddies (6, 7, 10, 11). The prediction of the direction of drift of floating oil is further complicated by the dominant role of wind stress at the air-sea interface (12). As far as we know, there are no records of major oil spills off central California on which to base predictions of oil drift. We know of no published studies of day-to-day movements of other floating materials off central California over an appropriately small time scale.

In this report we describe the movements and beaching of a large volume of lumber spilled off central California in the winter of 1978. Floating materials such as drift cards and plastic sheets have been used successfully by others in

modeling the movements of oil on the sea surface (13). Our data provide a first approximation of the disposition of the floating component of a large oil spill occurring under similar conditions of weather and sea. Information of this kind is needed if we are to understand the potential impacts of oil spills on the California sea otter population and to develop management plans for improving the status of the population, now numbering about 1800 animals (5).

A cargo of 2×10^6 board feet of finished lumber (volume equivalent to 2.9×10^4 barrels of oil) spilled from a barge under tow in heavy weather 40 km west of Point Sur on 12 February 1978 (14). The spilled lumber was hazardous to navigation (15) and was therefore monitored by aircraft and merchant vessels in subsequent weeks (16). We compiled a record of observations of the floating lumber at sea along with sightings of lumber washed ashore after the spill.

Much of the spilled lumber remained in a single large patch that moved first toward the coast and then southeastward, parallel to the shoreline, during the first 10 days after the spill (Fig. 1). By 24 February the major patch was within 7 km of shore near Point Estero and remained relatively close to shore for the balance of the observation period (through March). Other patches of floating lumber were seen off Monterey, Point Lobos, Cape San Martin, and Point Arguello during the survey period. Beached lumber was found throughout two sections of coastline within the sea otter range, a northern section of about

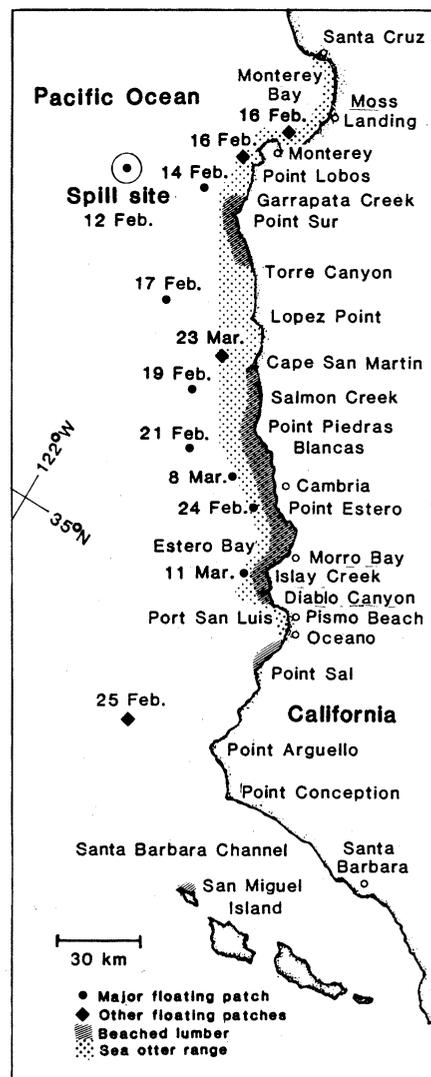


Fig. 1. Sightings of the major patch and smaller patches of floating lumber and areas of significant lumber beaching in and near the range of the sea otter population in California. Observations were made after the spillage of 2×10^6 board feet of lumber off Point Sur on 12 February 1978. All sightings of beached lumber were recorded between 12 February and 31 March 1978. The times and the positions corresponding to each sighting of the major patch of floating lumber are as follows: 12 February, 0650 GMT, 36°15'N, 122°25'W (spill site); 14 February, 1930 GMT, 36°19'N, 122°07'W; 17 February, 0130 GMT, 35°55'N, 121°51'W; 19 February, 2030 GMT, 35°40'N, 121°37'W; 21 February, 0136 GMT, 35°29'N, 121°29'W; 24 February, 2100 GMT, 35°27'N, 121°05'W; 8 March, 1816 GMT, 35°30'N, 121°16'W; 11 March, 2006 GMT, 35°18'N, 120°58'W. Mean wind speed (meters per second) and the direction (relative to true north) between sightings of the major floating patch, during the period when the patch was closest to shore, were as follows: 21 to 24 February, 3.57, 317°; 24 February to 8 March, 0.90, 154°; 8 to 11 March, 4.30, 308° [wind data are from the shore station at Point Piedras Blancas (18, 19)].