23. G. Wallerstein and S. Elgar, *Science* 256, 1531 (1992).
24. We thank R. T. Guza for discussions and for reviewing the manuscript. S. A. Herndon rendered Fig. 2, and T. A. Tombrello facilitated our collaboration. The Office of Naval Research, Coastal Sciences [N00014-92-J-1095]; the Mellon Foundation; and the Division of Physics, Mathematics and Astronomy, California Institute of Technology, provided support.

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Geography of End-Cretaceous Marine Bivalve Extinctions

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Analysis of the end-Cretaceous mass extinction, based on 3514 occurrences of 340 genera of marine bivalves (Mollusca), suggests that extinction intensities were uniformly global; no latitudinal gradients or other geographic patterns are detected. Elevated extinction intensities in some tropical areas are entirely a result of the distribution of one extinct group of highly specialized bivalves, the rudists. When rudists are omitted, intensities at those localities are statistically indistinguishable from those of both the rudist-free tropics and extratropical localities.

The Cretaceous-Tertiary (K-T) mass extinction marked the end of the Cretaceous period and the Mesozoic era and caused a 60 to 80% reduction in global biodiversity at the species level (*1*). This extinction is far better documented than any other such event in the geologic past and thus provides the best opportunity to explore environmental or other stresses that can cause mass extinction. Comparison of victims and survivors with regard to their habitats, physiologies, and geographic distributions should aid understanding of the causes and nature of this extinction. Here, we explore geographic patterns in the K-T extinction using a global analysis of marine bivalves (Mollusca). We evaluate whether there were local "hot spots" (*2*) of extinction, whether one hemisphere was affected more or less severely, and whether there were regular latitudinal or other gradients.

The K-T extinction has often been portrayed as more severe in the tropics than in temperate or polar regions (*3*), although paleontologic data on this point have been sparse and taxonomically scattered. Our database contains 3514 occurrences of 340 genera of bivalve mollusks from 106 assemblages of Maastrichtian (uppermost Cretaceous) marine fossils (Fig. 1). We chose bivalves because they were an important component of Cretaceous marine bottom communities, their taxonomy is well known and reasonably stable, and their average extinction rate is well suited for statistical analysis (63% of Maastrichtian bivalve genera did not survive into the Tertiary period). Few other biologic groups have these qualifications. Furthermore, bivalve data have been used extensively to support the inferred latitudinal gradient in K-T extinctions (*3*).

Most of the 106 assemblages were drawn originally from published sources (*4*) but were subjected to an updating and evaluation procedure, including consultations with experts on subgroups or specific geographic areas and examination of museum collections (where possible), in order to minimize taxonomic and stratigraphic inconsistencies. Species in lists from the older literature were shifted according to modern genus definitions, and some local names were eliminated.

We did not attempt to subdivide the Maastrichtian interval in this analysis. Finer stratigraphic resolution would be valuable but is impossible on a global basis because of uncertainties in dating and correlation: a sample confined to assemblages of proven latest Maastrichtian age would be too small for meaningful geographic analysis. Thus, our results apply to extinction at the K-T boundary event only to the extent that Maastrichtian extinctions were concentrated at that event. Although dilution by extinction within the Maastrichtian is probably minor, the interval does encompass considerable environmental fluctuation (*5*), and some extinctions, such as that of inoceramids and rudists, may have preceded the K-T event and thus would blur our results.

The choice of an extinction metric for the analysis is critical. Ideally, Cretaceous assemblages should be compared with those in the immediately younger Tertiary deposits of the same area. However, there are so few truly continuous sequences across the K-T boundary, with comparable habitats and fossil preservation, that the usable sample is far too small to be robust. Therefore, extinction was quantified as the proportion of genera found in an assemblage, or local group of assemblages, that suffered global extinction in the final stage of the Cretaceous. This metric has the advantage of making use of the excellent compilations of global extinctions for the K-T boundary (*6*), but it has the disadvantage that genera may die out in one area, perhaps a hot spot, yet survive globally because they also lived outside the area. These genera would be labeled survivors; thus, the actual species kill in the local area would be underestimated. However, endemism in our database is sufficiently pronounced (22% in North

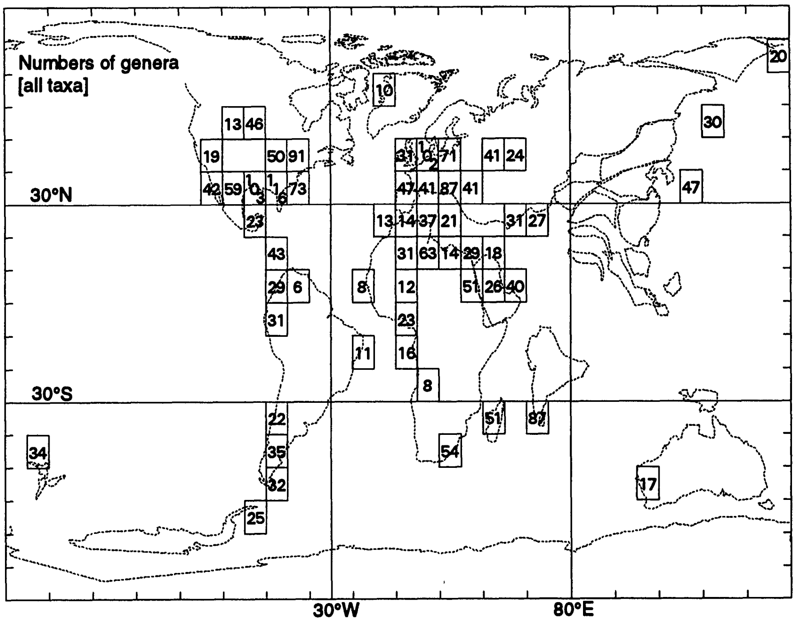

Fig. 1. Sample sizes in the 57 10° latitude-longitude blocks that contain one or more of the 106 bivalve assemblages (*20*), plotted on Maastrichtian geography. Rudists are included.

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America) that a hot spot is unlikely to be hidden by this effect.

Table 1 gives extinction levels for several large regions. The extinction rate for most individual regions or latitude-longitude belts was less than for the whole sample. This result is counterintuitive but is explained by the strongly negative relation between extinction and geographic range (*1, 7*): local endemics have a higher probability of going extinct than do more cosmopolitan genera. Each region contains a mixture of narrow- and wide-ranging genera, but the narrow-ranging genera are inevitably pooled in the global data, thus increasing the overall extinction percentage (*8*).

The raw extinction values suggest that extinction was highest in equatorial latitudes, as has been claimed, and west of 30°W paleolongitude. The region of highest extinction is thus in the New World tropics and includes the Chicxulub crater, currently considered to be the most probable site of the hypothesized impact at the K-T boundary (*9*). However, before this region can be considered to be an extinction hot spot, an important element of the late Cretaceous marine biota must be considered: the rudist bivalves, which reached peak diversity during the Maastrichtian or preceding Campanian stage (*10, 11*). These large, attached or recumbent filter-feeders dominated tropical carbonate platforms but were rare at higher latitudes; some researchers have argued that rudists suffered precipitous decline and were virtually extinct 1 to 2 million years before the K-T boundary event (*7, 11*). Inoceramid bivalves may also have become extinct before the K-T boundary event (*12*), but these comprise only about 1% of our database and do not affect the analysis significantly.

If all 46 rudist genera are ignored, the high extinction value in the region that contains the Chicxulub crater disappears (Table 1) and a latitudinal plot (Fig. 2) shows no north-south gradient. The mean extinction value (52.2%, indicated by the horizontal line in Fig. 2) is virtually identical to the median (53.5%); this suggests that the dispersion could be a result of sampling error alone. Some of the error bars do not intersect the mean extinction line but are no more than would be expected from random sampling.

We conclude that the appearance of a latitudinal gradient in the K-T mass extinction was caused, among bivalves, entirely by the rudists; when rudists are excluded, extinction intensities in tropical bivalves are indistinguishable from extratropical values (Fig. 3). Although a larger database might show meaningful structure, our analysis indicates that there is no pattern beyond what is expected from chance clumping of randomly assorted data (*13*).

If rudist diversity did collapse well before the K-T event, then it is appropriate to exclude rudists from the analysis. Even if the collapse occurred at the K-T boundary, our data also show unexceptional extinction intensities in most low-latitude localities outside the rudist-bearing habitats, and this result, along with the data on the nonrudist faunal component, further undermines any general latitudinal trend. We cannot distinguish whether preferential extinction of rudists was taxon- or habitat-based. Zooxanthellate corals suffered far greater K-T losses than corals apparently

Table 1. Extinction levels (percent) and samples sizes (numbers in parentheses) for Maastrichtian genera in arbitrarily defined regions (Fig. 1). Extinction percentages are given only for regions containing at least 25 genera (*18*). Uncertainties are equivalent to ±1 standard error (*19*). ND, no data.

Region	180°W to 30°W	30°W to 80°E	80°E to 180°E	All longitudes
		All taxa		
North of 30°N	55 ± 4 (166)	53 ± 4 (175)	51 ± 6 (63)	59 ± 3 (266)
30°N to 30°S	67 ± 5 (87)	59 ± 4 (151)	ND	62 ± 4 (184)
South of 30°S	53 ± 6 (81)	53 ± 5 (116)	(17)	56 ± 4 (157)
All latitudes	63 ± 3 (233)	56 ± 3 (237)	53 ± 6 (74)	63 ± 3 (340)
		All taxa minus 46 rudist genera		
North of 30°N	53 ± 4 (160)	47 ± 4 (154)	51 ± 6 (63)	55 ± 3 (240)
30°N to 30°S	52 ± 5 (61)	48 ± 4 (120)	ND	50 ± 4 (140)
South of 30°S	53 ± 6 (81)	52 ± 5 (114)	(17)	55 ± 4 (155)
All latitudes	58 ± 3 (206)	49 ± 3 (204)	53 ± 6 (74)	57 ± 3 (294)

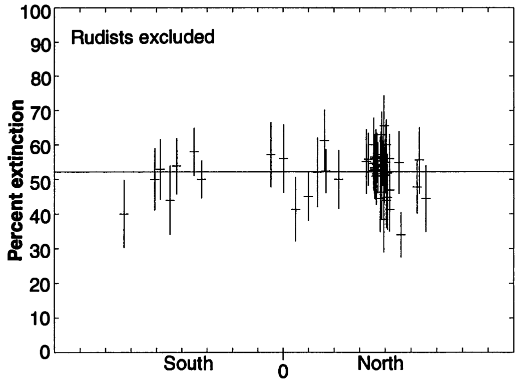

Fig. 2. Extinction intensity and latitude for the 60 fossil assemblages containing at least 25 nonrudist genera (*18, 19*). The horizontal line marks the mean (52.2% extinction). No significant trends or gradients are detectable.

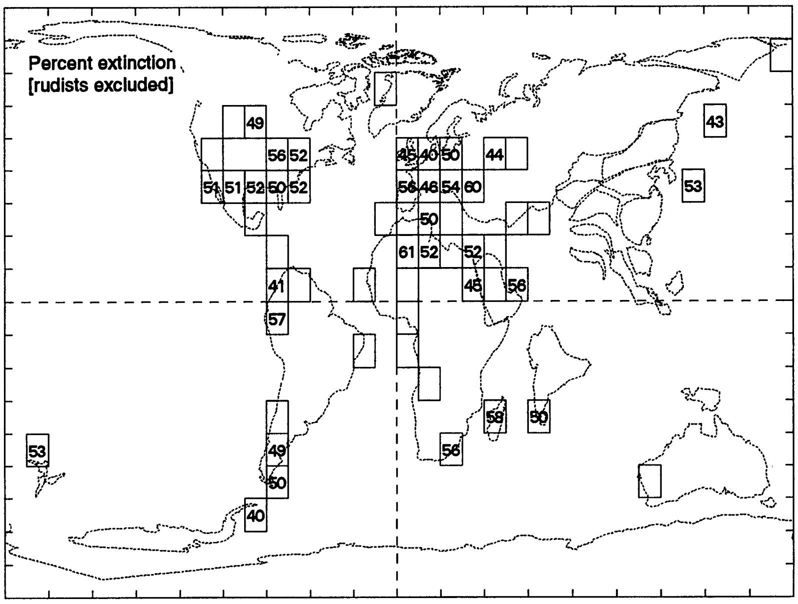

Fig. 3. Extinction intensity in the 33 10° latitude-longitude blocks that contain at least 25 nonrudist genera. Although the distribution is somewhat patchy, as expected from sampling error, there are no recognizable hot spots or gradients. The mean of the 33 values is 50.7%, and the median is 51.

lacking symbionts (*14*), and more genera of carbonate platform gastropods became extinct than did those from other regions and environments, even within the tropics (*15*). These data argue for habitat selectivity, but only for carbonate platforms and associated lagoons in the tropics. Certain microplankton groups also suffered greater extinction in the tropics than in polar regions (*16*), but here too the pattern may reflect disruption of particular habitats rather than a true latitudinal gradient (*17*).

Taken together, our analyses indicate that the end-Cretaceous mass extinction was a globally uniform event. Although this result does not verify bolide impact or any other proposed cause of the extinction, it does rule out mechanisms having purely regional or latitudinal effects.

REFERENCES AND NOTES

1. D. Jablonski, *Science* **253**, 754 (1991).
2. The term is from N. Myers [*The Environmentalist* **10**, 243 (1990)].
3. S. M. Stanley, in *Extinctions*, M. H. Nitecki, Ed. (Univ. of Chicago Press, Chicago, 1984), pp. 69–117; *Am. J. Sci.* **288**, 334 (1988); D. Jablonski, in *Dynamics of Extinction*, D. K. Elliott, Ed. (Wiley, New York, 1986), pp. 183–229; W. J. Zinsmeister, R. M. Feldmann, M. O. Woodburne, D. H. Elliott, *J. Paleontol.* **63**, 731 (1989).
4. A full bibliography of sources is available from the authors.
5. P. D. Ward, *Geol. Soc. Am. Spec. Pap.* **247**, 425 (1990); E. G. Kauffman, in *Global Bio-Events*, O. H. Walliser, Ed. (Springer-Verlag, Berlin, 1986), pp. 279–335.
6. J. J. Sepkoski, Jr., *J. Geol. Soc. London* **146**, 7 (1989); *Geol. Soc. Am. Spec. Pap.* **247**, 33 (1990).
7. D. Jablonski, *Science* **231**, 129 (1986); *Philos. Trans. R. Soc. London Ser. B* **325**, 357 (1989); S. R. Westrop, *Paleobiology* **15**, 46 (1989); D. H. Erwin, *Palaios* **4**, 424 (1989).
8. Consider an extreme, hypothetical case of seven genera: one nonsurviving genus confined to each of the six regions in Fig. 1 and one surviving genus that is cosmopolitan, occurring in all regions. Each region shows 50% extinction (one out of two), whereas the global sample shows 86% extinction (six out of seven).
9. V. L. Sharpton *et al.*, *Nature* **359**, 819 (1992).
10. E. G. Kauffman and C. C. Johnson, *Palaios* **3**, 194 (1988).
11. J.-P. Masse and J. Philip, *Bull. Cent. Rech. Explor.-Prod. Elf-Aquitaine* **10**, 437 (1986); C. C. Johnson and E. G. Kauffman, in *Extinction Events in Earth History*, E. G. Kauffman and O. H. Walliser, Eds. (Springer-Verlag, Berlin, 1990), pp. 305–324.
12. K. G. MacLeod and P. D. Ward, *Geol. Soc. Am. Spec. Pap.* **247**, 509 (1990).
13. High-latitude extinction intensities might decrease slightly with inclusion of the Ocean Point fauna from North Slope, Alaska, which is mostly undescribed and may be either latest Cretaceous or earliest Tertiary in age [L. Marincovich, Jr., *et al.*, *Geology* **13**, 770 (1985); T. R. Waller and L. Marincovich, Jr., *J. Paleontol.* **66**, 215 (1992)]. The effect of this fauna on our analyses will depend on its geologic age: if Tertiary, it includes survivors with various biogeographic affinities; if Maastrichtian, it contains several high-latitude precursors of typically Cenozoic taxa.
14. B. R. Rosen and D. Turnsek, *Mem. Assoc. Australas. Paleontol.* **8**, 355 (1989).
15. N. F. Sohl, *J. Paleontol.* **61**, 1085 (1987).
16. K. Perch-Nielsen *et al.*, *Geol. Soc. Am. Spec. Pap.* **190**, 353 (1982); G. Keller, *Geol. Soc. Am. Bull.* **101**, 1408 (1989).
17. J. H. Lipps, in *Dynamics of Extinction*, D. K. Elliott, Ed. (Wiley, New York, 1986), pp. 87–104; J. C. Zachos and M. A. Arthur, *Paleoceanography* **1**, 5 (1986).
18. With less than 25 rudist genera ($n < 25$), scatter due to sampling error becomes extreme. For example, with $n = 10$, a true extinction of 50%, and random sampling, the 68% confidence limits are 33.9 and 66.1%, and the 95% confidence limits are 18.2 and 81.8%. Given that the total number of samples being considered is relatively small, extinction values based on the smaller samples are virtually meaningless.
19. We calculated standard errors explicitly by summing binomial probabilities using a program given by D. M. Raup, in *Analytical Paleobiology*, N. L. Gilinsky and P. W. Signor, Eds. (Paleontological Society, Knoxville, TN, 1991), pp. 207–216. For the range of sample sizes we used, the results are virtually identical to standard errors estimated from conventional approximation formulas.
20. The surface area contained in a 10° latitude-longitude block naturally decreases with distance from the equator. Therefore, Fig. 1 should not be used to assess biologic diversity (genera per unit area). However, the latitude effect does not influence the comparisons of extinction intensities (percentages) considered in this report.
21. We thank R. J. Cleevely, A. V. Dhondt, C. Heinberg, C. C. Johnson, E. G. Kauffman, G. L. Kennedy, N. Malchus, M. Machalski, N. J. Morris, L. R. Saul, J. J. Sepkoski, Jr., N. F. Sohl, T. R. Waller, and L. R. Wingard for advice and access to collections or information. We thank D. B. Rowley (Paleogeographic Atlas Project, University of Chicago) for the Maastrichtian latitude-longitude conversions for bivalve sample sites. Special thanks go to A. Koziol, D. McShea, and J. Schneider for undertaking the initial literature search and data compilation that served as the skeleton for development of the full database. Supported by National Aeronautics and Space Administration grants NAGW-1508 and 1527 (D.M.R.) and NSF grants EAR90-05744 and INT86-2045 (D.J.).

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Interaction of the San Jacinto and San Andreas Fault Zones, Southern California: Triggered Earthquake Migration and Coupled Recurrence Intervals

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Two lines of evidence suggest that large earthquakes that occur on either the San Jacinto fault zone (SJFZ) or the San Andreas fault zone (SAFZ) may be triggered by large earthquakes that occur on the other. First, the great 1857 Fort Tejon earthquake in the SAFZ seems to have triggered a progressive sequence of earthquakes in the SJFZ. These earthquakes occurred at times and locations that are consistent with triggering by a strain pulse that propagated southeastward at a rate of 1.7 kilometers per year along the SJFZ after the 1857 earthquake. Second, the similarity in average recurrence intervals in the SJFZ (about 150 years) and in the Mojave segment of the SAFZ (132 years) suggests that large earthquakes in the northern SJFZ may stimulate the relatively frequent major earthquakes on the Mojave segment. Analysis of historic earthquake occurrence in the SJFZ suggests little likelihood of extended quiescence between earthquake sequences.

Historically, large earthquakes have occurred in the SJFZ in 1899, 1918, 1923, 1937, 1954, 1968, 1969, and 1987 (see Table 1 for source parameters and references). These earthquakes were preceded by the moment magnitude (**M**) 8 Fort Tejon earthquake of 1857 that ruptured $\sim$360 km of the SAFZ from near Cholame to Cajon Pass with 3 to 9 m of right slip (*1*) (Fig. 1). At its southeastern end, the 1857 rupture probably terminated in the Cajon Pass area (*1*, *2*). The SJFZ branches from the SAFZ in the Cajon Pass area (Fig. 1); northwest of the pass the SAFZ accommodates right slip of $\sim$3.5 cm year^{-1} (*3*), whereas southeast of the pass it accommodates $\sim$2.5 cm year^{-1} (*4*, *5*), with $\sim$1 cm year^{-1} (*6–8*) accommodated by the SJFZ.

Although attention previously has focused primarily on the SJFZ and SAFZ as separate mechanical entities, structural and geodetic evidence clearly shows that the fault zones are closely linked. For instance, the 1857 rupture terminated to the southeast near the area where the SJFZ branches from the SAFZ; this coincidence has been appreciated in notions of fault zone segmentation (*9–11*). In this report, I investigate the triggering of large earthquakes in either fault zone by large earthquakes in the other.

The primary data for this analysis are the recorded dates of occurrence, the epicenters and rupture lengths, the seismic moments, and the down-dip rupture widths of large earthquakes in the SJFZ (Table 1). The dates and times of occurrence and the epicenters of the large earthquakes in the SJFZ were obtained from compilations of historical accounts of major ground shaking (*12–14*) and from the catalog of instrumentally determined earthquake locations assembled by the California Institute of Technology and the U.S. Geological Survey. In some cases, the epicenters used are from relocation studies (*15*, *16*). The rupture

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