Selectivity of End-Cretaceous Marine Bivalve Extinctions

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Analyses of the end-Cretaceous or Cretaceous-Tertiary mass extinction show no selectivity of marine bivalve genera by life position (burrowing versus exposed), body size, bathymetric position on the continental shelf, or relative breadth of bathymetric range. Deposit-feeders as a group have significantly lower extinction intensities than suspension-feeders, but this pattern is due entirely to low extinction in two groups (Nuculoida and Lucinoidea), which suggests that survivorship was not simply linked to feeding mode. Geographically widespread genera have significantly lower extinction intensities than narrowly distributed genera. These results corroborate earlier work suggesting that some biotic factors that enhance survivorship during times of lesser extinction intensities are ineffectual during mass extinctions.

The major mass extinctions of the geologic past are becoming increasingly well documented, but patterns of selectivity remain poorly known. Selective survival, mediated by differences in environment, physiology, or life habits, might be a key to identifying the proximate causes of mass extinction and understanding the role of mass extinctions in large-scale evolutionary change (*1–3*). The Cretaceous-Tertiary (K-T) mass extinction, which caused a 70 to 80% reduction in marine biodiversity at the species level and a 50% reduction at the genus level (*4*), has received the most intensive study and thus affords the best opportunity to test for patterns of differential survival. In this report, we tested for patterns of selectivity related to life habits and distributional attributes, using a global database on K-T marine bivalves (*5*) and a subsidiary database on K-T marine bivalves and gastropods in the Gulf and Atlantic Coastal Plain (*1*, *6*).

Our global database consists of 3473 occurrences of 347 genera of bivalve mollusks from 105 Maastrichtian (uppermost Cretaceous) assemblages (*5*). The faunal lists were drawn for the most part from published sources but have been updated and revised on the basis of consultation with experts on subgroups or specific geographic areas and on examination of museum collections, to minimize taxonomic and stratigraphic inconsistencies. The subsidiary database (Gulf and Atlantic Coastal Plain of North America) contains perhaps the best preserved and most diverse Maastrichtian molluscan faunas in the world (*1*, *6*, *7*).

As in (*5*), we have not subdivided the Maastrichtian interval in this analysis, because samples rigorously confined to assemblages of latest Maastrichtian age would be too few and too scattered for meaningful statistical analysis. Thus, our results apply to extinction at the K-T boundary event only to the extent that genus-level bivalve extinctions were concentrated at the end of the Maastrichtian stage. Although dilution by extinction within the Maastrichtian is probably minor, some extinctions, such as that of inoceramids (*8*) and perhaps rudists (*9*), may have preceded the K-T event and thus may blur our results. However, in the well-studied faunas of the North American Coastal Plain and Northern Europe, bivalve diversity remains constant before and after the loss of inoceramids, which suggests that this enigmatic decline was not associated with a more general faunal turnover (*10*). The total extinction of the tropical platform-dwelling rudists contrasts so strongly with the milder extinction intensities of other tropical (and nontropical) bivalves (*5*) that they too appear to present an anomalous group. In order to minimize these artifacts, we excluded inoceramids and rudists from our analysis.

Table 1. Extinction intensities in K-T bivalves and one gastropod family, with 95% confidence limits given in parentheses (*32*). Rudists ($n = 50$ genera) were excluded from all analyses. The exclusion of seven inoceramid genera decreases epifaunal extinction intensities to 50% (40 to 60%) and reduces suspension-feeding extinction intensities to 60% (54 to 66%). Aporrhaid gastropod extinction data are from Roy (*29*). Poromyoidean bivalves, inferred to be carnivores by analogy to extant relatives, show an extinction intensity of 29% (0 to 64%) ($n = 7$ genera).

Strategy and taxa	*n*	Extinction intensities (%) (95% confidence limit)
Living position		
Infaunal	198	58 (51 to 67%)
Epifaunal	99	54 (44 to 64%)
Feeding strategy		
Suspension	250	61 (55 to 67%)
Deposit	40	30 (16 to 45%)
Deposit-feeding taxa		
Nuculoida	13	15 (0 to 37%)
Lucinoidea	15	20 (1 to 42%)
Tellinidae	12	58 (30 to 86%)
Aporrhaidae	25	76 (58 to 92%)

The analysis was also run with and without a possible relict fauna of Cretaceous mollusks in earliest Tertiary strata of northern Alaska (*11*). Inclusion of this fauna converts only four genera from victim to survivor status and does not affect the statistical results. In this report, we treated the four genera as survivors.

Several investigators have recorded differences in extinction rates between infaunal organisms (for example, burrowing bivalves such as quahogs and cherrystones) and those that live epifaunally (for example, surface-dwelling bivalves such as scallops and oysters) (*12–14*). When rudists are excluded, K-T extinction intensities do not differ significantly between infauna and epifauna (Table 1).

Several studies have concluded on theoretical or empirical grounds that large-bodied forms are more vulnerable to extinction than small-bodied forms (*15*, *16*). For K-T bivalve genera, however, victims and survivors do not differ significantly in their frequency distribution of sizes (Fig. 1). Significant differences in survivorship are absent even for the smallest size class (with shells <1 cm); the smallest bivalves

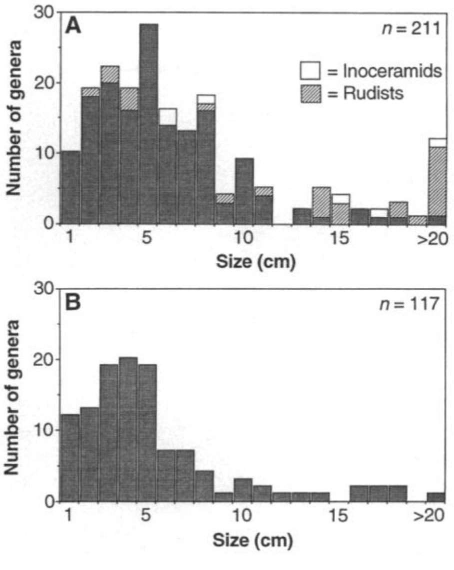

Fig. 1. Body size of victims (**A**) and survivors (**B**) of K-T mass extinction. The size for each genus was calculated as the geometric mean of length times height [following Stanley (*13*)] for the largest Maastrichtian specimen in the literature or collections of the U.S. Geological Survey and the Natural History Museum, London. Some genera are omitted because of a lack of reliable size data. When rudists (hatched boxes) are excluded, the two distributions are not significantly different, with or without inoceramids (open boxes), on the basis of a Kolmogorov-Smirnov test.

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are most likely to have annual life cycles and thus to be vulnerable to short-term excursions in ocean and atmospheric composition.

For the Gulf and Atlantic Coastal Plain, where the distributions of taxa among environments are known in the greatest detail, extinction intensities are statistically indistinguishable across the continental shelf (*17*). Bivalve and gastropod genera that extend into the shallowest waters do no better, as a group, than those that penetrate outer shelf habitats or those that are restricted to intermediate depth zones (Fig. 2A). Extinction intensities do not differ significantly for genera found in a single depth zone versus those occurring in two, three, or four zones across the shelf (Fig. 2B). Sepkoski (*18*) also found no bathymetric pattern for the Paleozoic mass extinctions. However, Erwin (*19*) found that gastropod genera with broad environmental distributions (encompassing both basinal and platform settings) had lower end-Permian extinction intensities than those with narrow distributions. Several researchers have reported higher extinction intensities in shallow-water benthos during the late Devonian mass extinction (*20, 21*), but that result is complicated both by the inclusion of tropical reef habitats and by the grouping of all shelf habitats into a single depth category that is then compared to deep-basinal settings absent from our Coastal Plain database.

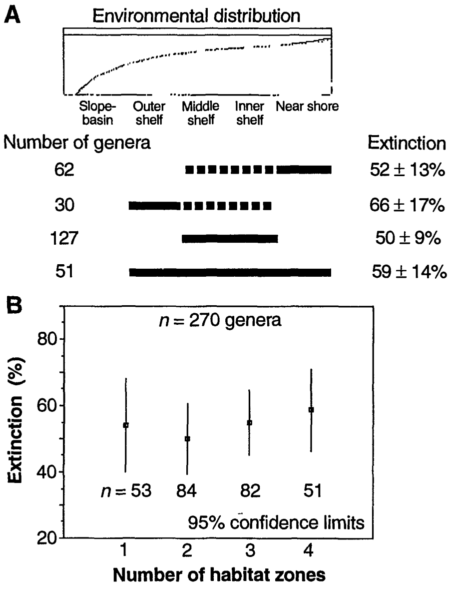

Fig. 2. Extinction intensity relative to bathymetric distribution for K-T bivalve and gastropod genera of the Gulf and Atlantic Coastal Plain. Habitat zones reflect environmental energy rather than absolute depth and are inferred according to sedimentary and stratigraphic criteria given by Bottjer and Jablonski (*17*). (**A**) There are no significant differences in extinction intensities [±95% confidence limits (*32*)] according to position on the continental shelf. From top to bottom, data are for: genera that reach the shallowest depths but do not encompass the entire shelf; genera that reach the outer shelf but do not encompass the entire shelf; genera at intermediate depths only; and genera that range over the entire shelf. (**B**) There are no significant differences in extinction intensities according to the breadth of distribution [number of habitat zones and shown in (A)] on the continental shelf.

K-T survivorship was not, however, completely random. Extinction intensities were highest for bivalve genera that occupied fewer biogeographic provinces (*22*) (Fig. 3). When taxa are divided into two geographic range classes, the widespread taxa have significantly fewer extinctions than the more narrowly distributed genera, regardless of the exact cutoff used to distinguish broad from restricted ranges (*23*). Such biogeographic controls on survivorship, which have been noted for other mass extinction events (*1, 2, 24*), may help to explain apparent latitudinal patterns in K-T planktonic foraminifera, whose polar assemblages tend to be dominated by extinction-resistant cosmopolitan taxa (*25*). Bivalve polar assemblages are not dominated by cosmopolitans, however, which may help to explain the lack of a significant latitudinal gradient in their extinction intensities (*5*).

K-T survivorship also varied among feeding types, but in a more complex fashion than previously suggested. Suspension-feeders, which collect plankton from the water column, suffered significantly greater losses than deposit-feeders, which feed on detritus and its microbial populations (Table 1). Similar selectivity has been suggested for K-T nonmarine communities and for other extinction events (*26*). In our data, however, these differences become clouded when marine deposit-feeders are subdivided by evolutionary lineage (Table 1). The Nuculoida, classic deposit-feeders in muddy sediments, show low extinction values, as do the Lucinoidea, many of which have chemosymbionts that contribute to nutrition and perhaps justify a different nutritional category altogether (*27*). Significantly higher losses occurred in the Tellinidae, whose members do not fit so neatly into trophic categories: Some are suspension-feeders, whereas others mainly deposit-feed but can switch to suspension-feeding depending on microhabitat, hydrodynamics, or even concentration of suspended food (*28*); it is surprising that this flexibility was accompanied by greater extinction intensities. Roy (*29*) found similarly high losses in a group of detritus-feeding gastropods, the Aporrhaidae, at the K-T boundary.

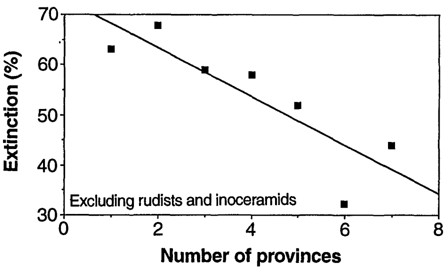

Fig. 3. Statistically significant inverse relation between extinction intensity and the number of biogeographic provinces occupied (*22*) for all range classes with >10 genera (Kendall's rank test, $P < 0.05$). This plot conveys the structure of the data (the line is a simple least squares best fit) but is inappropriate for regression analysis because error terms increase with the number of provinces (more genera are restricted than widespread).

There are several alternative explanations for the variation in extinction intensities among K-T deposit-feeders. The Nuculoida are probably taxonomically undersplit relative to the Tellinidae and Aporrhaidae—there are clearly a greater number of discrete evolutionary units in the Cretaceous nuculoids than is reflected in their present taxonomy. The groups also differ in how they exploit their detrital food resources, so that their respective resource pools might be buffered to different extents (*30*). However, deposit-feeders are more tightly coupled to pelagic input than generally recognized; both in shallow water and in the deep sea, metabolic rates, biomass, population dynamics, and even taxonomic diversity of deposit-feeders appear to track the flux of phytoplankton and other organic detritus to the sea floor (*31*). This suggests that the observed selectivity may not be related to feeding strategies at all. The greater extinction resistance of nuculoids and lucinoids cannot, however, be linked to broader geographic ranges: These two groups collectively average the same number of provinces (3.9 per genus) as do the suspension-feeders plus tellinids.

The selectivity patterns—and lack of patterns—documented here are largely neutral regarding specific extinction mechanisms. The effect of broad geographic range attests to the global scale of the event, also demonstrated in our earlier analysis (*5*). Further, our results do not obscure patterns at smaller scales: Analyses for each province containing >30 genera are statistically indistinguishable from our global outcome. The effect of deposit-feeding may relate to a plankton crisis that involved not only taxon extinction but extreme biomass decline, but the differential extinction among deposit-feeders calls for further analysis.

Our analyses corroborate earlier work suggesting that some biotic factors that enhance survival during times of low extinction rates are ineffectual during mass extinctions (*1*). Mass extinctions will therefore tend to disrupt rather than reinforce evolutionary patterns seen during times of lesser extinction intensities.

REFERENCES AND NOTES

1. D. Jablonski, *Science* **231**, 129 (1986); *ibid.* **253**, 754 (1991).
2. D. H. Erwin, *The Great Paleozoic Crisis: Life and Death in the Permian* (Columbia Univ. Press, New York, 1993); *Nature* **367**, 231 (1994).
3. L. M. Van Valen, in *Mass Extinction Debates*, W. Glen, Ed. (Stanford Univ. Press, Stanford, CA, 1994), pp. 200–216.
4. D. Jablonski, *Philos. Trans. R. Soc. London Ser. B* **344**, 11 (1994).
5. Updated from D. M. Raup and D. Jablonski, *Science* **260**, 971 (1993). A full bibliography of sources is available from the authors.
6. D. Jablonski, *Bull. Mar. Sci.* **39**, 565 (1986).
7. G. L. Wingard and N. F. Sohl, *U.S. Geol. Surv. Bull.* **1881**, D1 (1990); G. L. Wingard, *U.S. Geol. Surv. Prof. Pap.* **1535**, 1 (1994).
8. K. G. MacLeod and P. D. Ward, *Geol. Soc. Am. Spec. Pap.* **247**, 509 (1990); K. G. MacLeod, *Geology* **22**, 139 (1994); *J. Paleontol.* **68**, 1048 (1994).
9. E. G. Kauffman, in *Global Bio-Events*, O. H. Walliser, Ed. (Springer-Verlag, Berlin, 1986), pp. 279–335; 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. 305–331.
10. P. D. Ward, W. J. Kennedy, K. MacLeod, J. Mount, *Geology* **19**, 1181 (1991). Our own data suggest that other bivalves lack any decline parallel to that of the inoceramids, both in the Gulf and Atlantic Coastal Plain [D. Jablonski, in *Dynamics of Extinction*, D. K. Elliot, Ed. (Wiley, New York, 1986), pp. 183–229] and in the classic Denmark sections.
11. L. Marincovich Jr., *Paleontol. Soc. Mem.* **35** (*J. Paleontol.* **67**, suppl. to no. 5), 1 (1993).
12. E. G. Kauffman, *Philos. Trans. R. Soc. London Ser. B* **284**, 277 (1978).
13. S. M. Stanley, *Paleobiology* **12**, 89 (1986).
14. Life habits were inferred by analogy with living relatives of similar morphology and were based on widely used criteria available in the functional morphology literature. See S. M. Stanley, in *The Mollusca*, vol. 11, *Form and Function*, E. R. Trueman and M. R. Clarke, Eds. (Academic Press, San Diego, CA, 1988), pp. 105–141.
15. R. H. Peters, *The Ecological Implications of Body Size* (Cambridge Univ. Press, Cambridge, 1983); W. A. Calder, *Size, Function, and Life History* (Harvard Univ. Press, Cambridge, MA, 1984).
16. S. L. Pimm, H. L. Jones, J. Diamond, *Am. Nat.* **132**, 757 (1988); M. K. McKinney, in *Evolutionary Trends*, K. J. McNamara, Ed. (Univ. of Arizona Press, Tucson, 1990), pp. 75–118; J. H. Brown, P. A. Marquet, M. L. Taper, *Am. Nat.* **142**, 573 (1993); but see R. A. Martin, *Historical Biology* **6**, 73 (1992).
17. D. J. Bottjer and D. Jablonski, *Palaios* **3**, 540 (1988).
18. J. J. Sepkoski Jr., *Science* **235**, 64 (1987).
19. D. H. Erwin, *Palaios* **4**, 424 (1989); see also S. R. Westrop, *Paleobiology* **15**, 46 (1989).
20. J. E. Sorauf and A. E. H. Pedder, *Can. J. Earth Sci.* **23**, 1265 (1986).
21. G. R. McGhee, in *Mass Extinctions*, S. K. Donovan, Ed. (Columbia Univ. Press, New York, 1989), pp. 133–151.
22. We divided the world into the 16 Late Cretaceous provinces recognized by E. G. Kauffman, in *Atlas of Palaeobiogeography*, A. Hallam, Ed. (Elsevier, Amsterdam, 1973), pp. 353–383.
23. The maximum difference between extinction intensities occurs when restricted taxa are defined as less than two or three provinces, suggesting a threshold effect. For example, for nonrudist taxa restricted to ≤ 2 provinces, the extinction rate is 64 ± 7% [see (*32*)], whereas taxa in ≥ 3 provinces have an extinction rate of 48 ± 8%. If the cutoff is set between three and four provinces, extinction intensities are 62 ± 7% and 46 ± 9%, respectively. If inoceramids are omitted, the differential between widespread and restricted taxa increases slightly.
24. Reviewed by D. Jablonski, in *Extinction Rates*, J. H. Lawton and R. M. May, Eds. (Oxford Univ. Press, Oxford, 1995), pp. 25–44; *Geol. Soc. Am. Spec. Pap.*, in press.
25. G. Keller, *Mar. Micropaleontol.* **21**, 1 (1993); ———, E. Barrera, B. Schmitz, E. Mattson, *Geol. Soc. Am. Bull.* **105**, 979 (1993); but see B. T. Huber *et al.* *Mar. Micropaleontol.* **24**, 91 (1994).
26. For nonmarine communities, see P. M. Sheehan and T. A. Hansen, *Geology* **14**, 868 (1986); P. M. Sheehan and D. E. Fastovsky, *ibid.* **20**, 556 (1992). For marine communities, see G. R. McGhee (*21*); M. C. Rhodes and C. W. Thayer, *Geology* **19**, 877 (1991); C. R. C. Paul and S. F. Mitchell, *ibid.* **22**, 679 (1994).
27. R. G. Reid and D. G. Brand, *Veliger* **29**, 3 (1986); C. S. Hickman, *ibid.* **37**, 43 (1994); P. R. Dando *et al.*, *Mar. Ecol. Prog. Ser.* **107**, 169 (1994).
28. R. Pohlo, *Proc. Malacol. Soc. London* **38**, 361 (1969); J. S. Levinton, *Mar. Biol.* **110**, 375 (1991); P. Kamermans, *Mar. Ecol. Prog. Ser.* **104**, 63 (1994); J. Lin and A. H. Hines, *Oikos* **69**, 28 (1994).
29. K. Roy, *Paleobiology* **20**, 274 (1994).
30. P. A. Jumars *et al.* [*Philos. Trans. R. Soc. London Ser. A* **331**, 85 (1990)] distinguish among surface deposit-feeders such as the tellinids, subsurface deposit-feeders such as the nuculoids, and chemautotrophic deposit-feeders such as the lucinoideans.
31. P. A. Tyler, *Oceanogr. Mar. Biol. Annu. Rev.* **26**, 227 (1988); A. J. Gooday and C. M. Turley, *Philos. Trans. R. Soc. London Ser. A* **331**, 119 (1990); P. J. D. Lambshead and A. J. Gooday, *Deep-Sea Res.* **37**, 1263 (1990); M. A. Rex *et al.*, *Nature* **365**, 636 (1993); L. S. Campos-Creasey *et al.*, *Deep-Sea Res.* **41**, 369 (1994); M. Nakaoka, *Mar. Ecol. Prog. Ser.* **88**, 215 (1992).
32. We calculated the 95% confidence limits 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.
33. We thank S. Calzada, R. J. Cleevely, A. V. Dhondt, C. Heinberg, E. G. Kauffman, G. L. Kennedy, M. Machalski, N. Malchus, L. Marincovich Jr., 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 for the Maastrichtian latitude-longitude conversions for bivalve sample sites and G. E. Boyajian, S. M. Kidwell, J. S. Levinton, A. I. Miller, and J. J. Sepkoski Jr. for discussions and reviews. We are especially grateful to A. Koziol, D. McShea, and J. Schneider for undertaking the initial literature search and data compilation. Supported by NSF grants EAR93-17114 and INT86-2045 (D.J.) and National Aeronautics and Space Administration grants NAGW-1508 and 1527 (D.M.R.). D.J. did much of this work as a research associate of the Natural History Museum, London.

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Seismic Images of Active Magma Systems Beneath the East Pacific Rise Between 17°05′ and 17°35′S

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Seismic reflection data from the East Pacific Rise between 17°05′ and 17°35′S image a magma lens that varies regularly in depth and width as ridge morphology changes, confirming the notion that axial morphology can be used to infer ridge magmatic state. However, at 17°26′S, where the ridge is locally shallow and broad, the magma lens is markedly shallower and wider than predicted from regional trends. In this area, submersible dives reveal recent volcanic eruptions. These observations indicate that it is where the width and depth of the magma chamber differ from regional trends, indicating an enhanced magmatic budget, that is diagnostic of current magmatism.

On fast-spreading ridges, such as the East Pacific Rise (EPR) south of the Garrett fracture zone, axis morphology is characterized by a prominent bathymetric high with smooth flanks and a relatively flat summit about 2 km wide, standing ~400 m above the regional sea floor (*1*). The depth of the axis and the cross-sectional area of the axial high change along the axis in a sympathetic manner, the shallowest regions generally having the broadest cross sections (*2*, *3*). These "inflated" regions are thought to overlie centers of magma upwelling (*1*, *2*, *4*–*6*), the enlarged shape being an expression of volcanic tumescence. The summit region of the axial high often includes a small, narrow depression, now commonly referred to as the axial summit caldera (ASC) (*7*), believed to be the product of magma withdrawal and subsequent collapse. In some inflated regions, the ASC is absent, perhaps because of a recent filling of the depression with lava (*8*). These variations in axial morphology have been interpreted as reflecting variable magma supply along the ridge axis (*2*, *5*, *6*).

Seismic reflection imaging provides another indicator of variable magmatic activity. The horizon marking the top of the axial magma chamber (AMC) is typically observed beneath broad, shallow regions of the ridge and is absent or less commonly observed beneath narrow, deep regions (*8*, *9*). In a few areas of the EPR, near-bottom observations of recent volcanic activity (*10*) provide further support for the conjecture that a broadened ridge profile, shallow axial

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