

# Abundance not linked to survival across the end-Cretaceous mass extinction: Patterns in North American bivalves

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Edited by James W. Valentine, University of California, Berkeley, CA, and approved January 9, 2003 (received for review August 23, 2002)

**Ecological studies suggest that rare taxa are more likely to go extinct than abundant ones, but the influence of abundance on survivorship in the fossil record has received little attention. An analysis of Late Maastrichtian bivalve subgenera from the North American Coastal Plain found no evidence that survivorship is tied to abundance across the end-Cretaceous mass extinction (65 million years ago), regardless of abundance metric or spatial scale examined. The fact that abundance does not promote survivorship in end-Cretaceous bivalves suggests that the factors influencing survivorship during mass extinctions in the fossil record may differ from those operating during intervals of background extinction.**

Paleontologists have long debated the role that ecological, biogeographic, life history, reproductive, and developmental traits play in taxon survivorship across extinction events in the fossil record (see review in ref. 1). Ecological studies of living taxa suggest that abundant species are less likely to go extinct than rare ones (2). The idea that small population size increases extinction risk has received considerable support in ecology and conservation biology and forms the foundation of modern extinction theory (3).

The effect of abundance on survivorship at paleontological time scales has not been examined in detail. Increasing evidence indicates that fossil data provide a robust proxy of living abundance for marine benthic taxa with mineralized skeletons (4–7). A particularly strong case has been provided for molluscan assemblages by Kidwell's (8) recent metaanalysis of live-dead studies. These studies document a strong correlation between living and fossil abundance data in benthic mollusks, making it possible to examine the influence of abundance on survivorship of these taxa across extinction events in the fossil record. Here I test whether the link between abundance and survivorship observed in living taxa can be traced across mass extinctions in the fossil record, by using data for bivalve subgenera from the Late Maastrichtian of the North American Coastal Plain.

## Data and Methods

Abundance data for marine bivalve species were compiled from Sohl and Koch's (9–11) extensive faunal inventory of the *Haus-tator bilira* zone of the Coastal Plain, the most complete and thoroughly sampled macrofossil record available for the two million years preceding the end-Cretaceous (K/T) mass extinction. The Sohl and Koch data set is particularly useful for the current study because (i) it includes broad taxonomic (over 50 families) and geographic (5,000 km) coverage, (ii) it is particularly well-sampled (based on bulk samples and other collections made by U.S. Geological Survey personnel from 1890 to 1979) and sample sizes are substantial (>110,000 macroinvertebrate specimens), (iii) all identifications were made by one individual (N. F. Sohl), which greatly increases taxonomic consistency, and (iv) sampling and preservational effects on these data are well documented (12). For this analysis, data were compiled from 256 localities spanning 10 stratigraphic formations and containing raw abundance data for 293 bivalve species representing 121

subgenera. Only localities sampling >100 mollusk specimens were included. Sixteen taxa originally included in the Sohl and Koch database (9–11) were not used in these analyses because not enough information was available to place them subgenerically (see Table 2, which is published as supporting information on the PNAS web site, [www.pnas.org](http://www.pnas.org)).

Survivorship of subgenera across the K/T boundary was determined by using J. J. Sepkoski's unpublished generic compendium and the data of Jablonski and Raup (13). Approximately 65% of Coastal Plain bivalve subgenera went extinct at the K/T boundary. Bivalve sizes, measured as the geometric mean of shell length (anterior-posteriorly) and height (dorsal-ventrally) in millimeters (following ref. 14), were obtained from the data of Jablonski (15). Subgenera were scored according to feeding ecology and life habit following Skelton *et al.* (16). Subgenera were divided into three trophic categories: deposit-feeding, suspension-feeding, and predatory. Life habit of each subgenus was scored as either epifaunal or infaunal. Shell mineralogy data were compiled for all subgenera based on Taylor and colleagues (17, 18) and Carter (19) for both fossil bivalves and their modern relatives. Subgenera were divided into two categories based on the presence or absence of calcite in the shell. Wholly calcitic taxa (e.g., ostreids) and bimineralic taxa (calcitic and aragonitic; e.g., some mytilids, pectinids, spondylids, bakevellids, pteriids, inoceramids, etc.), were grouped together as calcite-bearing taxa. I considered these two groups as a single unit because the outer shell layer and extra-pallial shell interiors in the latter are composed of calcite and thus have higher preservation potential than purely aragonitic shells. Aragonitic bivalves included all taxa with calcite-free shells. Data on the organic content of shells were obtained by S. M. Kidwell (personal communication, see also table 11.2 in ref. 33) from the literature. Subgenera were divided into three categories: (i) high-organic taxa, which contain nacreous aragonite, simple prismatic aragonite, simple prismatic calcite, and/or composite prismatic aragonite; (ii) low-organic taxa, which contain foliated calcite, cross-lamellar aragonite, and/or complex cross-lamellar aragonite; and (iii) mixed-organic taxa, which possess both high- and low-organic layers.

Three metrics were used to measure abundance (raw, rank, and proportional abundance) and differences in abundance between K/T victims and survivors were assessed. Raw abundance was assessed by Sohl and Koch (9–11) as the number of valves for each subgenus sampled at a given locality and ranged from 1 to 4,194 in this study. Rank abundance is the rank-order of subgenera present at a given locality according to their raw abundance relative to one another (i.e., the most abundant subgenus has a rank of 1). Proportional abundance is the raw abundance of each subgenus relative to the total raw abundance

This paper was submitted directly (Track II) to the PNAS office.

Abbreviation: K/T, end-Cretaceous.

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across all subgenera at a given locality (percentage abundance). Use of the three metrics yielded similar results. The abundance data are not normally distributed; hence, I used both nonparametric tests (Mann–Whitney *U* and Kolmogorov–Smirnov) and parametric tests with data transformation (*t* test with Box–Cox transformation) to test for differences in abundance between K/T victims and survivors. Nonparametric and parametric tests yielded similar results. All statistical transformations and tests were performed by using STATISTICA 5.0 for Windows 95.

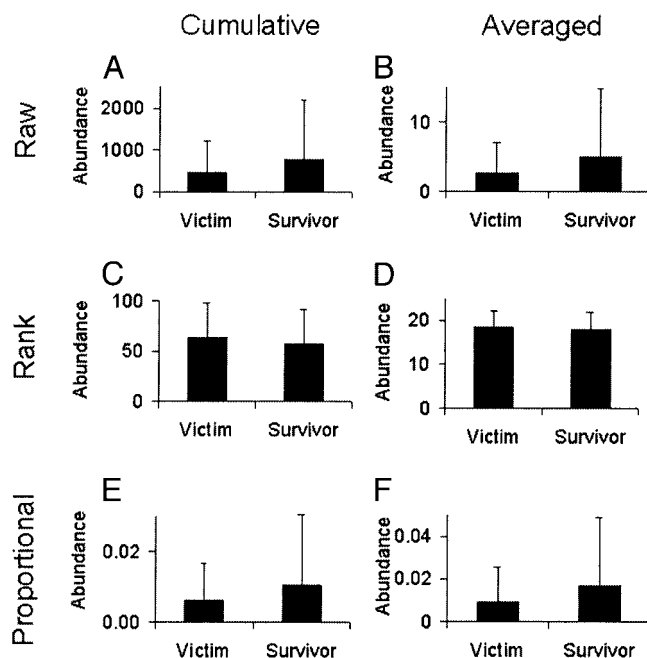
The absence of a particular taxon at a locality can represent legitimate absence from the locality, taphonomy, or incomplete sampling, and so I designated a taphonomic control group (following ref. 20) for each taxon on the basis of shell mineralogy and size. Size for each subgenus was determined by calculating the average size of the species within each subgenus. Next, subgenera were divided into three categories based on the mean and standard deviation (SD) of size across all subgenera as follows: (category 1) 0 to [mean – SD], (category 2) [mean – SD] to [mean + SD], and (category 3) [mean + SD] to maximum. Taphonomic codes were defined as follows: (i) calcite present, size category 1; (ii) calcite present, size category 2; (iii) calcite present, size category 3; (iv) calcite absent, size category 1; (v) calcite absent, size category 2; and (vi) calcite absent, size category 3. I considered the absence of a taxon at a particular locality legitimate if a member of its taphonomic control group was present at that locality. Species information on subgeneric placement, K/T survivorship of subgenera within which the species is placed, shell mineralogy, shell organic content level, life habit, feeding mode, size, and taphonomic code are available Table 2.

Data were analyzed at four different spatial scales: (i) locality, (ii) stratigraphic formation, (iii) region, and (iv) overall study area. I divided the Coastal Plain into three main regions (following refs. 9–11): the West Gulf region, including Texas and Arkansas; the East Gulf region, including Missouri, Tennessee, Mississippi, Alabama, and Georgia; and the Atlantic region, including South Carolina, North Carolina, Maryland, and New Jersey. At larger spatial scales (i.e., formation, region, overall), abundance data were treated in two ways: (i) cumulatively (all data were summed across localities, and abundance metrics were recalculated) and (ii) averaged (data were averaged across localities). It should be noted that, because the nonparametric tests involve ranking of the data, they do not differentiate between the three abundance metrics when the data are treated cumulatively. Use of the four spatial scales yielded similar results.

### Abundance and Survivorship: Results

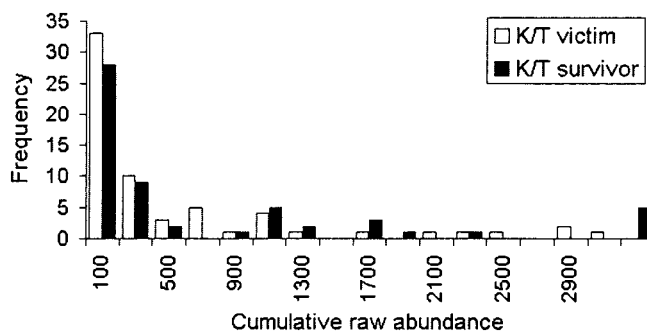
Abundance did not promote survival in Coastal Plain bivalves across the K/T mass extinction. Abundant subgenera were just as likely to go extinct as their rare counterparts (Fig. 1). A comparison of frequency distributions of abundance in victims versus survivors emphasizes the fact that the two groups differ little in abundance (Fig. 2). The relationship between abundance and survivorship did not vary according to spatial scale (Table 3, which is published as supporting information on the PNAS web site) after Bonferroni adjustment. Although the analyses involved in this study do not strictly represent a correlation table, they do address a single null hypothesis, which requires some form of adjustment for multiple comparisons (21). Sequential Bonferroni adjustment was applied to each independent pool of statistical analyses, defined as a group of analyses at the same spatial scale that use the same abundance data and statistical techniques. Sequential Bonferroni represents a more powerful approach than standard Bonferroni adjustment and is more likely to retain significant differences between populations (22).

It is worth considering whether bivalve size, ecology, or preservation affect the relationship between abundance and



**Fig. 1.** Mean ( $\pm$ SD) abundance for K/T victims and survivors across all localities at the subgeneric rank. No significant differences in abundance between victims and survivors were recorded, regardless of the abundance metric (raw, rank, or proportional) or statistical test (Mann–Whitney, Kolmogorov–Smirnov, or *t* test with data transformation) used and regardless of whether the data were treated cumulatively or averaged. It should be noted that, because the nonparametric tests involve ranking of the data, they do not differentiate among the three abundance metrics when the data are treated cumulatively. (A) Raw abundance data with cumulative data treatment ( $U_{64,57} = 1617$ ,  $P = 0.28$ ;  $D_{64,57} = 0.15$ ,  $P > 0.10$ ;  $t_{1,119} = -1.19$ ,  $P = 0.24$ ). (B) Raw abundance data with average data treatment ( $U_{64,57} = 1586$ ,  $P = 0.22$ ;  $D_{64,57} = 0.17$ ,  $P > 0.10$ ;  $t_{1,119} = -1.39$ ,  $P = 0.17$ ). (C) Rank abundance data with cumulative data treatment ( $t_{1,119} = 1.12$ ,  $P = 0.26$ ). (D) Rank abundance data with average data treatment ( $U_{64,57} = 1683$ ,  $P = 0.46$ ;  $D_{64,57} = 0.15$ ,  $P > 0.10$ ;  $t_{1,119} = 0.71$ ,  $P = 0.48$ ). (E) Proportional abundance data with cumulative data treatment ( $t_{1,119} = -1.19$ ,  $P = 0.24$ ). (F) Proportional abundance data with average data treatment ( $U_{64,57} = 1,609$ ,  $P = 0.26$ ;  $D_{64,57} = 0.16$ ,  $P > 0.10$ ;  $t_{1,119} = -1.35$ ,  $P = 0.18$ ).

survivorship. If size and abundance are not independent, but each influences survivorship independently of the other, then a correlation between abundance and survivorship may be obscured. To control for size, geometric mean of shell length and height was used as a covariate in an analysis of covariance with Box–Cox transformation, which compared subgeneric abun-



**Fig. 2.** Frequency distributions of abundance (raw abundance with cumulative data treatment) for victims versus survivors across all localities at the subgeneric level. K/T victims and survivors do not differ significantly according to abundance.

dance of victims and survivors across all localities. No significant difference was recorded between victims and survivors (Table 4, which is published as supporting information on the PNAS web site) even after size was removed from the analysis.

The effect of abundance on survivorship may also differ according to bivalve ecology. For example, suspension-feeding bivalves as a group tend to include more opportunists and tend to have higher local abundance than deposit-feeding bivalves (23). I controlled for ecology by comparing the subgeneric abundance of victims versus survivors within each ecological category. The abundance of victims was not significantly different from survivors within the two feeding modes tested: suspension versus deposit (Table 5, which is published as supporting information on the PNAS web site).

It should be noted that the characterization of the tellinaceans and lucinaceans as deposit-feeders in this analysis is an oversimplification. Many tellinacean species are capable of both deposit- and suspension-feeding, whereas many lucinaceans harbor chemosymbionts that contribute to nutrition, distinguishing both groups from the majority of bivalves. Unfortunately, when lucinaceans and tellinaceans were removed from this analysis, the number of deposit-feeders was too small ( $n$  of victims = 0) to compare the abundance of victims and survivors. Similarly, the sample sizes of both tellinaceans ( $n$  of survivors = 1) and lucinaceans ( $n$  of victims = 1) were too small to test for a relationship between abundance and survivorship within facultative deposit-feeders or chemosymbionts, respectively.

Turning to life habit, no significant difference in abundance was recorded in infaunal victims versus survivors. A significant positive relationship between abundance and survivorship was found for epifaunal taxa, but this result was not robust to changes in abundance metric or statistical test (Table 5).

Taxa with calcitic shells are more robust to diagenetic processes than aragonitic taxa (24) and may provide a more accurate representation of the relationship between abundance and survivorship. The possibility that this relationship differs according to shell mineralogy was assessed by comparing the difference in abundance between victims and survivors within each shell mineralogical category (calcitic versus noncalcitic). No significant difference in the abundance of victims versus survivors was recorded in taxa with noncalcitic shells (Table 1). Calcite-bearing taxa do show a significant positive relationship between abundance and survivorship, although this relationship is not robust to changes in abundance metric or statistical test and the difference in abundance between victims and survivors is not significant when the analysis is based on rank abundance, often considered the most reliable fossil proxy of living abundance (8). When I subdivided calcitic taxa in this study into wholly calcitic and bimineralic taxa, the latter show a significant correlation between abundance and survivorship (depending on the abundance metric and statistical test used), but not the former. If wholly calcitic taxa have a higher preservation potential than bimineralic taxa and abundance is correlated with survivorship at this event, then a stronger relationship between abundance and survivorship should be recorded in calcite-bearing taxa. This observation undermines preservability as a possible explanation for these results, but the limited sample size of calcite-bearing taxa in this study ( $n = 8$ ) requires caution. The results obtained for shell organic content also argue against the possibility that preservation is obscuring a link between abundance and survivorship. If preservation potential is exerting an effect on the relationship between abundance and survivorship, then one would expect other factors involved in preservation, including level of shell organic content, to yield similar results. When I controlled for level of shell organic content in these analyses, I found no significant difference in abundance between victims and survivors (Table 1). In fact, taxa with low shell organic content (i.e., high preservability) showed a slightly negative

(though nonsignificant) relationship between abundance and survivorship. Although further investigation is needed, these results suggest that preservation is not substantially biasing the results of this study.

### Abundance and Survivorship: Implications

Modern ecological analyses suggest that abundance is positively correlated with survivorship in living species. Fossil bivalve data for the two million years preceding the K/T extinction in North America show no link between abundance and survivorship. Several possible explanations for this discordance deserve consideration.

First, sampling bias may affect the fossil abundance data. If abundant victims and rare survivors were preferentially collected, a positive relationship between abundance and survivorship could be obscured. Given the bulk sampling protocol used by Sohl and Koch (9–11) to collect the majority of these data, this sort of systematic sampling bias is extremely unlikely.

Next, inappropriate scaling, whether spatial or temporal, may bias the relationship between fossil abundance and survivorship. I found no evidence to suggest that spatial scaling affected the correlation between abundance and survivorship. Temporal scaling may affect these results if, for example, abundance distributions shifted substantially during the time interval sampled. Unfortunately, finer temporal resolution of these data are not feasible given the time-averaged data and stratigraphic correlations available for the Coastal Plain during this interval.

Third, preservational factors may bias the results if, for example, abundance information is more likely to be preserved faithfully for some taxa than others (25). I investigated this possibility by assessing abundance and survivorship within shell mineralogical and organic content categories and have obtained mixed results, though the evidence seems to suggest that preservation is not significantly biasing these data.

Fourth, phylogenetic effects might influence these data if, for example, factors such as mineralogy or life habit covary phylogenetically, so that differential clade survivorship on other grounds might mask a weak correlation between fossil abundance and survivorship. Addressing this bias may be possible if the relationship between abundance and survivorship is reexamined for a subsample of these data within a phylogenetic framework. Unfortunately, the feasibility of this approach is severely limited by the paucity of phylogenetic analyses available for Cretaceous bivalves.

The most plausible explanation for these results is that abundance exerts little influence on survivorship during the K/T mass extinction event. On the basis of K/T molluscan survivorship patterns, Jablonski (26) proposed an alternation of extinction regimes between background and mass extinction events, a result corroborated by subsequent analyses of attributes such as species richness, life habit, body size, and habitat type across a range of extinction events (refs. 13 and 27; see review in refs. 28 and 29). Attributes thought to promote survival during background extinction do not necessarily promote survivorship during mass extinctions. Abundance may be yet another example of a trait that influences survivorship during background extinction intervals but not during large-scale events. It is unclear whether the patterns documented in this study are generalizable across all mass extinctions or even to abundance at the K/T boundary for other clades or geographic regions. Although the interaction between abundance and survivorship has been assessed at ecological time scales, the effect of abundance on survivorship during background intervals in the fossil record is poorly understood. All evidence does suggest, however, that mollusk selectivity at the K/T represented an exceptional departure from the status quo.

The predictive relationship between abundance and survivorship observed in modern ecosystems appears to break down

**Table 1. Results of testing for abundance differences between victims and survivors, controlling for shell mineralogy and organic content across all localities at the subgeneric level**

Preservation potential	Data treatment	Test	Abundance metric		
			Raw	Rank	Proportional
Noncalclitic	Cumulative	MW	$U_{38,38} = 710, P = 0.90$		
		KS	$D_{38,38} = 0.13, P > 0.10$		
		t test	$t_{1,74} = 0.09, P = 0.93$	$t_{1,74} = -0.04, P = 0.97$	$t_{1,74} = 0.09, P = 0.93$
	Average	MW	$U_{38,38} = 710, P = 0.90$	$U_{38,38} = 696, P = 0.79$	$U_{38,38} = 689, P = 0.73$
		KS	$D_{38,38} = 0.16, P > 0.10$	$D_{38,38} = 0.13, P > 0.10$	$D_{38,38} = 0.18, P > 0.10$
		t test	$t_{1,74} = 0.05, P = 0.96$	$t_{1,74} = -0.07, P = 0.94$	$t_{1,74} = 0.18, P = 0.86$
Calcite-bearing	Cumulative	MW	$U_{26,19} = 166, P = 0.06$		
		KS	$D_{26,19} = 0.38, P > 0.05$		
		t test	$t_{1,43} = -2.03, P = 0.05$	$t_{1,43} = 1.86, P = 0.07$	$t_{1,43} = -2.03, P = 0.05$
	Average	MW	$U_{26,19} = 161, P = 0.05$	$U_{26,19} = 183, P = 0.14$	$U_{26,19} = 150, P = 0.03$
		KS	$D_{26,19} = 0.38, P > 0.05$	$D_{26,19} = 0.30, P > 0.10$	$D_{26,19} = 0.42, P < 0.05$
		t test	$t_{1,43} = -2.15, P = 0.05$	$t_{1,43} = 1.16, P = 0.25$	$t_{1,43} = -2.32, P = 0.03$
High shell organic content	Cumulative	MW	$U_{16,16} = 99, P = 0.27$		
		KS	$D_{16,16} = 0.31, P > 0.10$		
		t test	$t_{1,30} = -1.24, P = 0.22$	$t_{1,30} = 1.18, P = 0.25$	$t_{1,30} = -1.25, P = 0.22$
	Average	MW	$U_{16,16} = 95, P = 0.21$	$U_{16,16} = 110, P = 0.50$	$U_{16,16} = 90, P = 0.15$
		KS	$D_{16,16} = 0.31, P > 0.10$	$D_{16,16} = 0.25, P > 0.10$	$D_{16,16} = 0.38, P > 0.10$
		t test	$t_{1,30} = -1.39, P = 0.17$	$t_{1,30} = 0.77, P = 0.45$	$t_{1,30} = -1.58, P = 0.12$
Low shell organic content	Cumulative	MW	$U_{38,29} = 471, P = 0.31$		
		KS	$D_{38,29} = 0.20, P > 0.10$		
		t test	$t_{1,65} = -0.97, P = 0.34$	$t_{1,65} = 1.04, P = 0.30$	$t_{1,65} = -0.97, P = 0.33$
	Average	MW	$U_{38,29} = 464, P = 0.27$	$U_{38,29} = 507, P = 0.57$	$U_{38,29} = 463, P = 0.27$
		KS	$D_{38,29} = 0.26, P > 0.10$	$D_{38,29} = 0.19, P > 0.10$	$D_{38,29} = 0.24, P > 0.10$
		t test	$t_{1,65} = -1.11, P = 0.27$	$t_{1,65} = 0.77, P = 0.45$	$t_{1,65} = -1.04, P = 0.30$
Mixed shell organic content	Cumulative	MW	$U_{10,10} = 44, P = 0.62$		
		KS	$D_{10,10} = 0.20, P > 0.10$		
		t test	$t_{1,18} = -0.49, P = 0.63$	$t_{1,18} = 0.38, P = 0.71$	$t_{1,18} = -0.49, P = 0.63$
	Average	MW	$U_{10,10} = 47, P = 0.82$	$U_{10,10} = 50, P = 0.99$	$U_{10,10} = 46, P = 0.76$
		KS	$D_{10,10} = 0.20, P > 0.10$	$D_{10,10} = 0.20, P > 0.10$	$D_{10,10} = 0.30, P > 0.10$
		t test	$t_{1,18} = -0.55, P = 0.59$	$t_{1,18} = 0.13, P = 0.90$	$t_{1,18} = -0.31, P = 0.76$

Differences were assessed within shell mineralogical categories and organic content categories independently. Three abundance metrics (raw, rank, and proportional), two data treatments (cumulative and averaged), and three statistical tests [Mann–Whitney (MW), Kolmogorov–Smirnov (KS), and t test with data transformation] were used. Calcite-bearing victims were significantly less abundant than survivors, but this result was not robust to changes in abundance metric or statistical test. No significant relationship between abundance and survivorship was found within noncalclitic taxa or taxa in any of the shell organic categories. It should be noted that the nonparametric tests do not differentiate among the three abundance metrics when the data are treated cumulatively. Boldface indicates statistical significance.

during mass extinction events. It is worth considering whether rarity, as typified here, can be equated with rarity in modern ecosystems. To enter the fossil record, a taxon must be abundant to some extent, and it is possible that paleontological studies do not always capture a sufficiently broad range of living abundance to accurately record a relationship between abundance and survivorship. The taxa sampled in this study may not include the rarest species that constitute the tail of typical abundance distributions in modern ecosystems (30), thereby weakening any relationship that might exist between survivorship and abundance.

Even in modern studies, the causal link between abundance and survivorship is not straightforward. The two systems most commonly cited as evidence for this link are island populations of British birds and Bahamian orb spiders (31, 32), but these studies are limited by the fact that the taxa studied are extremely mobile, sample sizes are small, and extrapolations from island to continental spatial scales and from decadal to millennial time scales are difficult to justify. The local extinctions documented in these studies differ in several key respects from mass extinctions in the fossil record. For example, it is unclear whether the results obtained in these studies can be extrapolated beyond the scope of islands and whether the disappearance of a population can be equated with the dis-

appearance of a species. Perhaps more importantly, these modern populations are studied under relatively stable environmental conditions. These patterns may not be applicable to times of rapid worldwide ecological devastation, such as that seen during the K/T mass extinction.

In conclusion, fossil abundance data for Late Maastrichtian bivalves from North America indicates that abundant taxa are no more likely to survive mass extinctions than rare ones. The relationship between abundance and survivorship observed at ecological time scales cannot be readily translated into paleontological time scales, suggesting that the factors influencing survivorship during mass extinctions in the fossil record may differ from those operating during background extinction intervals.

I thank C. F. Koch and L. Brewster-Wingard for providing access to these data; S. M. Kidwell for providing data on bivalve mineralogy and access to unpublished manuscripts; D. Jablonski for providing data on bivalve sizes; and J. J. Sepkoski for providing data on generic stratigraphic ranges. This manuscript has greatly benefited from the comments of D. Jablonski, S. M. Kidwell, M. Foote, M. LaBarbera, C. F. Koch, M. Kosnik, S. Peters, G. Hunt, and J. Swaddle. This work was supported in part by Sigma Xi, the Paleontological Research Institution, the Lerner-Gray Fund for Marine Research, and the Paleontological Society, as well as National Science Foundation Grant EAR 93-17114 (to D. Jablonski).

1. McKinney, M. L. (1997) *Annu. Rev. Ecol. Syst.* **28**, 495–516.
2. Gilpin, M. E. & Soulé, M. E. (1986) in *Conservation Biology: The Science of Scarcity and Diversity*, ed. Soulé, M. E. (Sinauer, Sunderland, MA), pp. 13–34.
3. Gaston, K. J., Blackburn, T. M., Greenwood, J. J. D., Gregory, R. D., Quinn, R. M. & Lawton, J. H. (2000) *J. Appl. Ecol.* **37** (Suppl. 1), 39–59.
4. Valentine, J. W. (1961) *Univ. Calif. Publ. Geol. Sci.* **34**, 309–442.
5. Kidwell, S. M. & Flessa, K. W. (1995) *Annu. Rev. Ecol. Syst.* **26**, 269–300.
6. McKinney, M. L. (1996) *Rev. Esp. Paleo.* **11**, 125–133.
7. McKinney, M. L. (1997) in *The Biology of Rarity*, eds. Kunin, W. E. & Gaston, K. J. (Chapman & Hall, London), pp. 110–129.
8. Kidwell, S. M. (2001) *Science* **294**, 1091–1094.
9. Sohl, N. F. & Koch, C. F. (1983) *U.S. Geol. Surv. Open File Rep.* 83–451.
10. Sohl, N. F. & Koch, C. F. (1984) *U.S. Geol. Surv. Open File Rep.* 84–687.
11. Sohl, N. F. & Koch, C. F. (1987) *U.S. Geol. Surv. Open File Rep.* 87–194.
12. Koch, C. F. (1987) *Paleobiology* **13**, 100–107.
13. Jablonski, D. & Raup, D. M. (1995) *Science* **268**, 389–391.
14. Stanley, S. M. (1986) *Paleobiology* **12**, 89–110.
15. Jablonski, D. (1997) *Nature* **385**, 250–252.
16. Skelton, P. W., Crame, J. A., Morris, N. J. & Harper, E. M. (1990) in *Major Evolutionary Radiations*, eds. Taylor, P. D. & Larwood, G. P. (Clarendon, Oxford), pp. 91–117.
17. Taylor, J. D., Kennedy, W. J. & Hall, A. (1969) *Bull. Br. Mus. Nat. Hist.* (Suppl. 3), 1–125.
18. Taylor, J. D., Kennedy, W. J. & Hall, A. (1973) *Bull. Br. Mus. Nat. Hist.* **22**, 253–294.
19. Carter, J. G. (1990) in *Skeletal Biomineralization: Patterns, Processes, and Evolutionary Trends*, ed. Carter, J. G. (Van Nostrand Reinhold, New York), pp. 297–411.
20. Bottjer, D. J. & Jablonski, D. (1988) *Palaios* **3**, 540–560.
21. Rice, W. M. (1989) *Evolution (Lawrence, Kans.)* **43**, 223–225.
22. Sokal, R. R. & Rohlf, F. J. (1995) *Biometry* (Freeman, New York).
23. Levinton, J. S. (1974) *Palaeontology* **17**, 579–585.
24. Kidwell, S. M. & Bosence, D. W. J. (1991) in *Taphonomy: Releasing the Data Locked in the Fossil Record*, eds. Allison, P. A. & Briggs, D. E. G. (Plenum, New York), pp. 115–209.
25. Koch, C. F. & Sohl, N. F. (1983) *Paleobiology* **9**, 26–34.
26. Jablonski, D. (1986) *Science* **231**, 129–133.
27. Raup, D. M. & Jablonski, D. (1993) *Science* **260**, 971–973.
28. Jablonski, D. (1986) in *Patterns and Processes in the History of Life*, eds. Raup, D. M. & Jablonski, D. (Springer, Berlin), pp. 313–329.
29. Jablonski, D. (1996) in *The Cretaceous-Tertiary Event and Other Catastrophes in Earth History*, eds. Ryder, G., Fastovsky, D. & Gartner, S. (Geological Society of America, Boulder, CO), Special Paper, Vol. 307, pp. 1–9.
30. Rabinowitz, D. (1981) in *The Biological Aspects of Rare Plant Conservation*, ed. Synge, J. (Wiley, Chichester, U.K.), pp. 205–217.
31. Tracy, C. R. & George, T. L. (1992) *Am. Nat.* **139**, 102–122.
32. Rosenzweig, M. L. & Clark, C. W. (1994) *Conserv. Biol.* **8**, 491–494.
33. Kidwell, S. M. & Brenchley, P. J. (1996) in *Evolutionary Paleobiology*, eds. Jablonski, D., Erwin, D. H. & Lipps, J. H. (Univ. of Chicago Press, Chicago), pp. 290–336.