

Assessing the role of abundance in marine bivalve extinction over the post-Paleozoic

Carl Simpson and Paul G. Harnik

Abstract.—Abundance is one of the primary factors believed to influence extinction yet little is known about its relationship to extinction rates over geologic time. Using data from the Paleobiology Database we show that abundance was an important factor in the extinction dynamics of marine bivalve genera over the post-Paleozoic. Contrary to expectations, our analyses reveal a nonlinear relationship between abundance and extinction rates, with rare and abundant genera exhibiting rates elevated over those of genera of moderate abundance. This U-shaped pattern is a persistent feature of the post-Paleozoic history of marine bivalves and provides one possible explanation for why we find strong support for heterogeneous extinction rates among genera grouped by similarity in abundance yet effectively no net relationship among these rates when using models of directional selection on abundance.

Carl Simpson. Museum für Naturkunde - Leibniz Institute for Research on Evolution and Biodiversity at the Humboldt University Berlin, Invalidenstrasse 43, D-10115 Berlin, Germany. E-mail: Carl.Simpson@mfn-berlin.de

Paul G. Harnik. Committee on Evolutionary Biology, University of Chicago, Chicago, Illinois 60637. E-mail: pharnik@uchicago.edu

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Introduction

Abundance is widely believed to be a primary determinant of extinction (Diamond 1984; Stanley 1986; Pimm et al. 1988; Stanley et al. 1988; Lande 1993; Gaston 1994; McKinney 1997; Purvis et al. 2000), and is frequently used to assess extinction risk among extant species (IUCN 2001). Although extinction must be preceded by population reduction it remains unclear to what extent interspecific differences in abundance accurately predict extinction dynamics. Support for a link between abundance and extinction in present-day biotas comes primarily from modeling and small-scale experiments (references above and reviewed in Gaston 1994), with most empirical studies conducted over relatively short time spans with a focus on local turnover rather than global extinction. The fossil record provides an opportunity to assess the relationship between abundance and extinction rates globally over much longer time scales and over a broader array of environmental conditions. However, few analyses of this sort have been conducted because of a paucity of fossil abundance data and because sampling biases will tend to

truncate the stratigraphic ranges of rare taxa preferentially (Signor and Lipps 1982; Mel-dahl 1990; Holland and Patzkowsky 2002), potentially yielding artificial differences in extinction rates.

Here we use a model-selection approach (Burnham and Anderson 2002) to investigate the influence of abundance on genus extinction rates globally for marine bivalve mollusks over the Mesozoic and Cenozoic eras. In our analyses, we compare the support for a model in which abundance was a factor in extinction rates with a simpler model in which abundance played no role. Bivalves are an ideal group to assess the relationship between abundance and extinction rates because they are diverse and abundant members of present-day and post-Paleozoic benthic marine faunas and have a comparatively complete fossil record (Kidwell and Flessa 1995; Kidwell 2005; Valentine et al. 2006). Furthermore, recent meta-analyses have found that skeletal concentrations of marine mollusks in present-day soft-sediment environments can, statistically speaking, preserve the relative abundance distributions of the live communities from which they are

derived (Kidwell 2001, 2002). Assuming no further bias during diagenesis, the fossil record provides a means to examine bivalve relative abundances over geologic time scales and their relationship to extinction rates.

Using abundance and occurrence data from the Paleobiology Database (PBDB) we reveal a well-supported nonlinear relationship between abundance and extinction rates. Increasing abundance is associated with declining extinction rates yet abundant genera deviate from this negative relationship by exhibiting elevated extinction rates comparable in magnitude to those of much rarer genera. This U-shaped relationship between abundance and extinction rates is a persistent feature of the post-Paleozoic history of marine bivalves and may be one reason why previous studies have generally found little support for an influence of abundance on extinction over geologic time scales (Lockwood 2003; Harnik 2007).

Data and Methods

We use abundance and occurrence data for fossil bivalves from the PBDB to investigate the influence of abundance on extinction rates globally over the last 250 Myr. We restrict our temporal scope to the post-Paleozoic to control for the secular decline in extinction rates observed over the Phanerozoic (Van Valen 1984; Bambach et al. 2004; Wang and Bush 2008) and the shift from carbonate- to clastic-dominated sedimentary environments (Ronov et al. 1980; Foote 2006; Peters 2008). The PBDB is a publicly accessible global compilation of collection-based fossil occurrence and taxonomic data; general discussion of the structure and contents of the PBDB is summarized in Alroy et al. (2001) and is available online (<http://www.paleodb.org>).

Consistent with other global-scale studies of the fossil record (e.g., Miller and Foote 2003; Jablonski et al. 2006; Peters 2006; Payne and Finnegan 2007), our analyses were conducted using morphologically defined genera and subgenera (hereafter termed "genera"). Using the genus as our operational taxonomic unit should allow for greater consistency in identification among multiple workers and, given the comparatively broad

geographic distributions of genera (relative to their constituent species) may help mitigate stratigraphic biases that have been shown to influence patterns of extinction (Holland and Patzkowsky 2002). In several clades, including bivalve mollusks, monophyly is supported by molecular data in >60% of morphologically defined genera (Jablonski and Finarelli 2009). Macroecological data (body size and geographic range) are also significantly correlated for genera defined on morphological and molecular grounds (Jablonski and Finarelli 2009).

Data Download.—Data used to estimate the abundances of bivalve genera were downloaded from the PBDB on 4 June 2007 using the research group "marine invertebrate" and the following parameters: time intervals = "Induan" through "Gelasian" (251 ± 0.4 Ma through 1.806 Ma using the timescale of Gradstein et al. (2004)), geographic coverage = "global," collections " ≥ 100 individuals or specimens."

Data used to estimate the durations of bivalve genera were downloaded from the PBDB on 4 June, 2007 using the research group "marine invertebrate" and the following parameters: name of taxon = "Bivalvia," geographic coverage = "global." Because poor preservation may artificially lengthen the durations of fossil taxa (Jablonski 2005; Kidwell 2005; Plotnick and Wagner 2006), generically and specifically indeterminate occurrences were excluded.

Data used to classify bivalve genera by their shell mineralogy (aragonitic or calcitic) were downloaded from the PBDB on 21 November 2008 using the research group "marine invertebrate" and the following parameters: name of taxon = "Bivalvia," geographic coverage = "global," with the primary and secondary composition fields selected.

Data used to assign habitat affinities to genera were downloaded from the PBDB on 29 October 2008 using the research group "marine invertebrate" and the following parameters: time intervals = "Induan" through "Gelasian," geographic coverage = "global," name of taxon = "Bivalvia," with the primary lithology field selected.

Abundance.—The abundance of individuals of a given taxon varies over space and time, and estimates of abundance are also influenced by collecting methods. Data entered into the PBDB were originally gathered to address a variety of paleontological questions, resulting in entries with heterogeneous sample sizes and abundance measures. For this study, we control for methodological variability by analyzing only collections containing whole-fauna numerical abundance data with sample sizes ≥ 100 individuals or specimens; 1631 collections met those criteria, containing a total of 7,169,465 individuals or specimens, with a median sample size of 315 and mean of 1084.

Given the considerable variation in sample sizes among collections as well as the observation that numerical abundance data in fossil concentrations can be influenced by physical factors such as sedimentation rate (Kidwell and Bosence 1991; Tomašových et al. 2006), we used relative abundance in our analyses. In a given collection, the proportional abundance of each bivalve genus was calculated relative to the total sample size of that collection. Collections contained a diversity of taxa in addition to bivalves, and the whole fauna as reported was used to estimate the abundances of bivalve genera. The global proportional abundance of each genus was then calculated as the arithmetic mean over all collections in which that genus occurred. Most taxa are rare in most places they occur, and only some are common somewhere within their geographic range (Rabinowitz 1981; Gaston 1994). Because of this skew in abundance distributions, we use the arithmetic mean, weighting more heavily collections in which a taxon was more common. The results we present below for the relationship between abundance and extinction rates are qualitatively similar if the average abundance for a given genus is estimated by using the median rather than the mean. The global abundance value provides an estimate of the average abundance of a bivalve genus in those collections in which it was found.

Genus Durations.—Durations were calculated by using the center points of the standardized PBDB 10-Myr bins in which genera

exhibited their first and last occurrences. Extant taxa were identified from the compendium of fossil marine animal genera compiled by J. J. Sepkoski Jr. (2002), as updated by Jablonski et al. (2003, revised November 2006), and were either included or excluded depending on the analysis (described further below). The full data set consisted of 440 extinct and 272 extant genera with abundance data.

Extinction Rates.—Estimates of extinction rate (q) can be calculated in a variety of ways. For these analyses, we used two survivorship-based rate metrics: one for examining extinction rates for all post-Paleozoic genera and one for looking at interval-to-interval survivorship over finer temporal scales. For the calculation of both of these extinction rate metrics, abundance classes were defined by grouping taxa by order-of-magnitude similarity in proportional abundance: Very Rare = 0 to 0.001, Rare = 0.001 to 0.01, Common = 0.01 to 0.1, Abundant = 0.1 to 1. Using order-of-magnitude abundance classes should help minimize errors in abundance estimation arising from the heterogeneous sampling protocols of PBDB collections. For analyzing all genera that went extinct during the post-Paleozoic, the maximum likelihood extinction rate estimate (\hat{q}) for groups of genera (e.g., all Rare bivalve genera) was calculated as

$$\hat{q} = \frac{N_i}{\sum t_{ij}} \quad (1)$$

where N_i is the number of extinct genera and t_{ij} is the duration of genus j in group i (Van Valen 1973; Raup 1985); genera known only from a single 10 Myr interval were excluded (Foote and Raup 1996). Although excluding extant genera may elevate these extinction rate estimates (Foote 2000), it still allows relative differences in rates to be considered.

To determine the support for abundance in explaining extinction rate variations at finer temporal scales over the post-Paleozoic, we calculated extinction rates from survivorship through each 10-Myr interval. In this case, extinction rate (\hat{q}) was calculated as

$$\hat{q} = \frac{-\ln(N_{bt}/N_b)}{\Delta t} \quad (2)$$

where N_{bt} is the number of genera that range through a time interval, N_b is the number of genera that cross into an interval, and Δt is the length of the interval in millions of years (Foote 2000). Both extant and extinct genera were included in this finer-grained analysis and individual genera may be counted in more than one interval. The survivorship of extant as well as extinct genera is important to consider because these taxa contain information about patterns of survivorship that might otherwise be obscured if extinct genera were considered solely. By framing this analysis in the context of interval-to-interval survivorship, the problem that extant genera have yet to go extinct is no longer relevant, allowing us to consider an expanded sample size of genera for which quantitative abundance data have been gathered. Including extant genera will artificially depress extinction rates toward the Recent (Foote 2000); however, we are interested primarily in the relative differences in rates among genera varying in abundance within each interval.

Model Selection.—We use a model-selection approach (Burnham and Anderson 2002) to assess the role of abundance in bivalve extinction dynamics. We compare two classes of models, one in which there are multiple rates for groups of bivalve genera defined by their similarity in abundance, and another, in which there is a single extinction rate for all bivalve genera irrespective of their abundance. We use Akaike's Information Criterion (AIC) to evaluate the support for each model (Burnham and Anderson 2002). Qualitatively, AIC can be thought of as a measure of the fit of a given model to the data penalized by the complexity of the model. AIC is calculated as

$$\text{AIC} = -2\ell + 2k \quad (3)$$

where ℓ is the maximized log-likelihood and k is the number of estimated parameters. Log-likelihoods are additive, so ℓ is the sum of maximized log-likelihoods for all model parameters. A parameter in this study is an estimate of extinction rate. For the multi-rate model in which abundance is a factor in extinction, $k = 4$, representing the unique extinction rates estimated for the four abundance classes. In contrast, $k = 1$ for the model

in which a single extinction rate is estimated for all genera irrespective of their abundance.

AIC values decrease with increasing model fit but increase as the number of parameters increases. The model with the lowest AIC value is the best model among the candidate set of models considered. Because AIC is relative, we compare each model with the best model by calculating the AIC differences, Δ_i :

$$\Delta_i = \text{AIC}_i - \text{AIC}_{\min} \quad (4)$$

in which AIC_{\min} is the best model and AIC_i is the AIC value of the i^{th} model. The Akaike weights, w_i , are then used as a measure of the relative support for each model in the set of R models being considered. Akaike weights, w_i , are calculated as

$$w_i = \exp\left(-\frac{1}{2}\Delta_i\right) / \left[\sum_{r=1}^R \exp\left(-\frac{1}{2}\Delta_r\right)\right] \quad (5)$$

and sum to 1.

In our interval-to-interval analysis we use the small-sample Akaike's Information Criterion (AIC_c) to compare the support for the multi-rate model relative to the single-rate model. The small sample Akaike's Information Criterion (AIC_c) is recommended when the ratio of observations to parameters (n/k) is < 40 (Burnham and Anderson 2002). AIC_c is calculated as

$$\text{AIC}_c = \text{AIC} + \frac{2k(k+1)}{n-k-1} \quad (6)$$

where the relevant sample size (n) in this analysis is the number of bivalve genera in a given abundance class (e.g., Common genera) present at the start of each 10 Myr interval (N_b). Because the support for extinction-rate estimates equal to zero is undefined, only abundance classes with an estimated extinction rate greater than zero were considered in the multi-rate versus single-rate model comparison. The number of model parameters in the multi-rate model was modified accordingly to equal the number of abundance classes in a given interval for which $\hat{q} > 0$. The only time interval in which all abundance classes were estimated to have a rate equal to zero was Jurassic 4, which was excluded, as were the first and last time bins that have

undefined extinction rates, because of edge effects. All time bins contain genera of all abundance classes with the exception of Triassic 2 through Jurassic 1, from which Very Rare genera were absent. The AIC_c differences between the multi-rate and single-rate models and Akaike weights were calculated for 21 post-Paleozoic time bins. Note that these interval-to-interval survivorship analyses generate AIC_c values that are not independent between adjacent time bins because long-duration genera range through multiple bins.

Sensitivity of Results to Taphonomic Effects.—Various sources of error and bias may contribute to an observed relationship between abundance and extinction rate. First-order effects may include (1) the failure to sample rare taxa (rarity bias), and (2) biased estimates of abundance due to differences in shell durability or environmental preference. Rarity bias would artificially elevate extinction rates in poorly sampled abundance classes. Shell durability and habitat preference potentially influence estimates of abundance by taphonomic processes alone. For example, bivalve genera possessing calcitic shells may be less susceptible to dissolution and thus abundant in collections that have undergone such postmortem alteration. Abundance estimates for genera that prefer carbonate habitats may be similarly affected by dissolution as well as by the difficulties of collecting and identifying large numbers of individuals from lithified sediments. Unfortunately, the relationships between abundance and extinction rates predicted under several purely taphonomic scenarios are consistent with equally plausible biological explanations. Nevertheless, we conduct several sensitivity tests to investigate the potential contributions of rarity bias, shell durability, and habitat preference to the abundance-extinction rate relationship.

We use rarefaction to establish whether variations in the durations of genera grouped by their abundance are likely the result of sampling artifact. If short-duration genera were primarily the result of poor sampling, then the rarefaction curves of long- and short-duration genera will overlap when genus

occurrences are rarefied. In addition, we compare the durations of genera we analyze with those in the Sepkoski compendium (2002) as updated by Jablonski et al. (2003, as revised November 2006) to determine whether the durations of genera calculated using occurrences in the PBDB are under-sampled relative to previous estimates. The occurrence data in the PBDB were compiled from a variety of data sources with no systematic search for the range end-points of each genus in contrast to the Sepkoski compendium. Because of this, we may expect genus durations, particularly for rare taxa, to be underestimated in the PBDB relative to the Sepkoski compendium.

To assess the effects of shell durability and habitat preference on abundance estimates we compared the frequency of genera of each shell mineralogy and habitat preference across the four abundance classes. We used the primary and secondary composition fields in the PBDB to classify genera as having either aragonitic or calcitic shells. The primary lithology reported for each collection in the PBDB was used to assign habitat preference. Habitats were classified into two primary types, clastic or carbonate, with a third "mixed" category denoting genera of equivocal preference. Clastic habitats were those identified as "shale," "siliciclastic," claystone, conglomerate, mudstone, phyllite, quartzite, sandstone, siltstone, or slate in the primary lithology field. Carbonate habitats were those identified as "carbonate," "limestone," "reef rocks," bafflestone, bindstone, dolomite, framestone, grainstone, lime mudstone, packstone, rudstone, floatstone, or wackestone in the primary lithology field. Marls and other mixed lithologies were excluded from the analysis.

Habitat preference was estimated for each genus with more than four occurrences. Preference was calculated by using the Bayesian posterior probability of a genus occurring in carbonate habitats. This posterior probability is a function of the prior probability, given by the ratio of carbonate to clastic occurrences over the stratigraphic range of a genus, and the null hypothesis that a genus has no habitat preference. This approach

allows us to test the null hypothesis that a genus is equally likely to prefer carbonate or clastic habitats, despite variation in the availability of carbonate and clastic habitats over time. Even if the null hypothesis is true, variation in the occurrences of carbonate and clastic habitats over time leads to a potential bias in the estimated probability of preferring a particular habitat (Kiessling and Aberhan 2007). To distinguish between the null hypothesis and the potential sampling bias we use Bayesian inference. Bayes' Theorem is computed as

$$P(H_1|E) = \frac{P(E|H_1)P(H_1)}{P(E|H_1)P(H_1) + P(E|H_2)P(H_2)} \quad (7)$$

in which $P(H_1|E)$ is the probability that a genus prefers carbonate habits given the prior probability $P(E)$ which is the proportion of all collections that are carbonates. The null hypothesis of equal affinity remains $P(H_1) = P(H_2) = 0.5$. For the conditional probabilities for each hypothesis—that a genus prefers $P(E|H_1)$ or dislikes $P(E|H_2)$ carbonates—we use the binomial probability of sampling the observed number of carbonate occurrences, k , (or for $P(E|H_2)$, clastic occurrences) out of the total number of occurrences, n . In this case, p equals the proportion of all collections that are carbonates. The conditional probability for the carbonate preferring hypothesis is

$$P(E|H_1) = \binom{n}{k} p^k (1-p)^{n-k} \quad (8)$$

The posterior probability, $P(H_1|E)$, easily classifies genera by their habitat preference into three classes: those that prefer carbonates ($P(H_1|E) < 0.5$), those that prefer clastics ($P(H_1|E) > 0.5$), and those of equivocal or mixed affinity ($P(H_1|E) = 0.5$).

A 3×2 contingency table is constructed for each abundance class by tabulating the number of genera of each shell mineralogy and habitat preference. Using Fisher's exact test we compare the 3×2 contingency tables for the four abundance classes to determine if they are pulled from the same underlying distribution. If shell mineralogy and habitat preference affect abundance, the contingency tables are predicted to be significantly different at the $p = 0.05$ significance level.

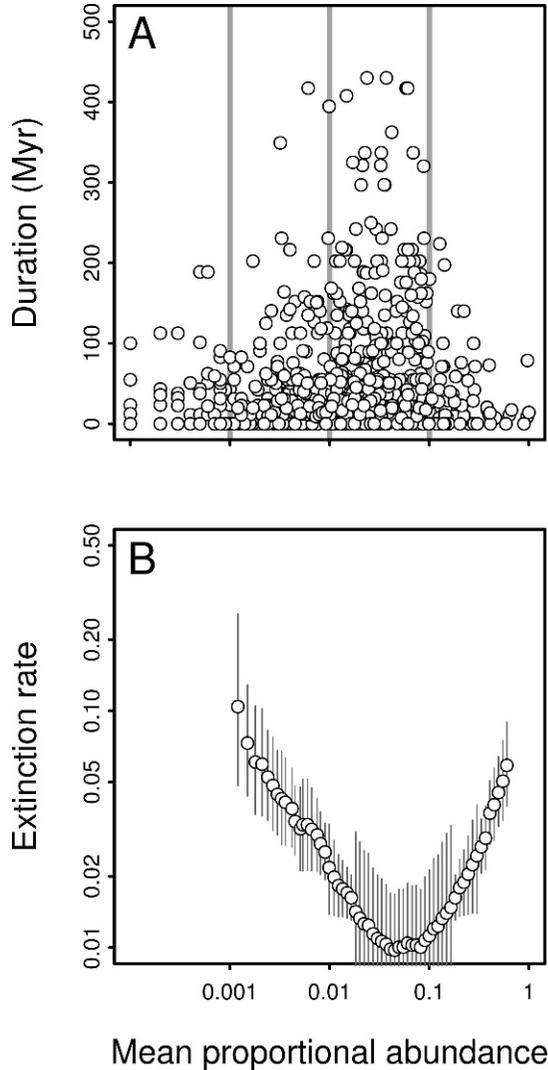


FIGURE 1. Genus abundance-duration and abundance-extinction rate relationships. A, Relationship between genus abundance and duration (Myr); abundance classes are separated by vertical lines. B, Extinction rates estimated by using a moving window of $\frac{1}{2}$ order of magnitude of abundance, incremented logarithmically. The last point, at 0.5 mean proportional abundance, is the rate for all genera between 0.1 and 1 mean proportional abundance. Bars are 2 units of support. AIC values strongly support the multi-rate abundance model over a single-rate model estimated from pooling all bivalve durations.

Results

Rare bivalves tend to have shorter durations than more common bivalves, with a mean duration of 31.8 Myr for Very Rare genera, in contrast to 47.6 Myr and 75.4 Myr for Rare and Common genera, respectively (Fig. 1A). Surprisingly, Abundant genera,

TABLE 1. Support for multi- versus single-rate models depending on whether mean versus median genus abundance is used in the analysis. K is the number of model parameters, Δ_i is the AIC difference, and w_i is the Akaike weight. All subdivisions are better supported (have a lower Δ_i) than the single-rate model, in which abundance is not a factor in extinction rates.

	Model	K	Δ_i	w_i
Mean	Single rate	1	31.56	<0.001
	Multi rate	4	0	>0.999
Median	Single rate	1	38.31	0
	Multi rate	4	0	1

with a mean duration of 38.6 Myr, exhibit durations comparable to those of much rarer genera. Genera with the minimum duration possible (≤ 10 Myr) exhibit the complete range of observed proportional abundance values.

To examine the relationship between abundance and extinction rates in a semi-continuous fashion, we used a moving-window incremented along the abundance axis, binning genera within the window and calculating an extinction rate (Fig. 1B). Although adjacent rates share genera and are thus not independent, this allows the overall shape of the abundance-extinction rate relationship to emerge. Qualitatively, as abundance increases extinction rate drops, with the most abundant genera deviating from the expected pattern by exhibiting elevated extinction rates. To compare quantitatively the support for the multi-rate versus single-rate extinction models we used the model-selection criteria described above, and calculated extinction rates based on the four independent (i.e., nonoverlapping) abundance classes. The more complex multi-rate model—in which each abundance class exhibits a unique extinction rate—was substantially better supported over the simpler model in which the extinction dynamics of all bivalve genera were characterized by a single rate irrespective of their abundances ($\Delta_{i(\text{single-rate})} = 31.56$, $w_{(\text{single-rate})} < 0.001$; $\Delta_{i(\text{multi-rate})} = 0$, $w_{(\text{multi-rate})} > 0.999$). Support for the multi-rate model remains if the median rather than the mean is used to calculate the global abundances of genera (Table 1), though the rate differences decrease as expected as the range of variation

in abundance is diminished and more genera become restricted to the Rare abundance class.

The strong relationship between abundance and extinction rate summarized in Figure 1 represents a long-term average over the post-Paleozoic. However, some previous analyses of the abundance-extinction rate relationship during critical intervals in the geologic past have not found support for a relationship (e.g., Lockwood 2003), and the nonlinear relationship revealed in our pooled analysis runs counter to the expected linear decline in extinction rate with increasing abundance. Is it possible that temporal variation in selectivity underlies the form and strength of the abundance-extinction rate relationship? For example, selectivity may have varied between background and mass extinction intervals, with the expected linear relationship weakening with increasing extinction magnitude and the elevated extinction rates of abundant genera driven by short-lived “bloom taxa” present during the recovery intervals following large extinction events (e.g., Hansen 1988; though see Miller and Foote 2003). To examine the abundance-extinction rate relationship at a finer temporal scale we calculated the differences in support between the multi-rate and single-rate extinction models for 21 post-Paleozoic time bins, including in these analyses both extinct and extant genera. All time intervals show greater support for the multi-rate model relative to the single-rate model, with 62% of intervals characterized by an Akaike weight > 0.95 for the multi-rate model.

Support for the multi-rate model over time can be interpreted as support for heterogeneous rates among classes of genera differing in abundance, yet the Akaike weights do not describe the relationship among these rates. The relationship between abundance and extinction rate can be summarized by fitting a linear model to the unique extinction rates in each interval. Using linear regression to summarize the role of abundance in extinction does discard information but is justified by considering the role of abundance as a directional selection process. In directional selection, the change in the mean phenotype

is the result of the product of the slope of the linear regression between fitness and phenotype, in this case survivorship and abundance respectively, and the variance of the phenotype (Rice 2004). The linear regression of extinction rate on abundance is precisely what we are interested in when studying extinction selectivity. However, if the abundance-extinction rate relationship is U-shaped as observed in the pooled data (Fig. 1), the slope of a linear regression through all of the unique extinction rates in each time interval may mask a nonlinear relationship if it exists.

To describe the abundance-extinction rate relationship in each interval we use values for three linear slopes: a slope fit to all of the rates (β_{all}) to assess the overall strength of directional selection, a slope through the rates for the Very Rare, Rare, and Common abundance classes ($\beta_{\text{VR-C}}$) to assess the negative decline with increasing abundance, and a slope through the rates for the Common and Abundant classes ($\beta_{\text{C-A}}$) to assess the upturn in extinction rates among the most abundant genera. The signs and relative magnitudes of the slopes $\beta_{\text{VR-C}}$ and $\beta_{\text{C-A}}$ are used to assess the U-shape in each interval.

A single linear regression through the rates for all abundance classes in each time interval suggests that abundance does not influence extinction rate, with the average β_{all} equal to 0.03 (Figs. 2, 3A). The apparent lack of relationship between abundance and extinction rate is further strengthened by examining the equal frequency of positive versus negative slopes for β_{all} (11 positive and 9 negative slopes out of 20 time bins with measurable slope) (Fig. 3A). However, when the data are partitioned to either confirm or reject the nonlinear relationship, we find that the U-shape is observed in approximately two-thirds of the intervals, with Very Rare and Abundant genera having higher extinction rates than Rare and Common genera (Figs. 2, 3C). Whereas, the average β_{all} for all abundance classes equals 0.03, the average $\beta_{\text{VR-C}}$ for the least abundant classes equals -0.36 , and average $\beta_{\text{C-A}}$ for the most abundant classes equals 0.26. These statistics are qualitatively similar to those in our pooled analysis (Fig. 1) in which $\beta_{\text{all}} = -0.02$, $\beta_{\text{VR-C}}$

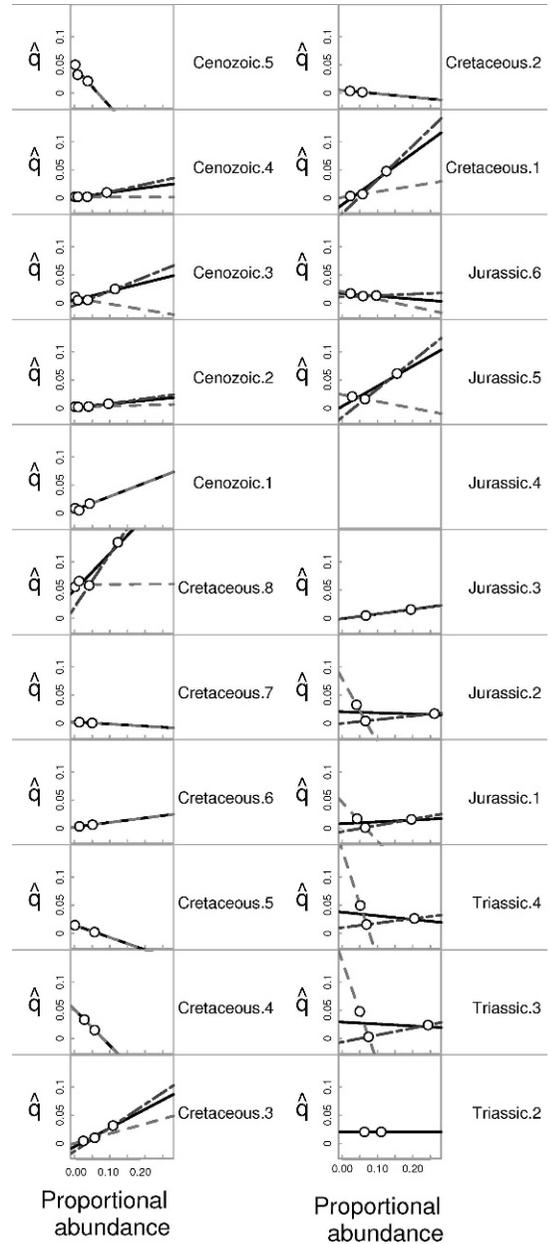


FIGURE 2. Estimates of the extinction selectivity of abundance during each time interval as measured by three linear slopes: β_{all} (solid line) is the slope through all the rates; $\beta_{\text{VR-C}}$ (light-gray dashed line) is the slope through the rates for the Very Rare through Common abundance classes; $\beta_{\text{C-A}}$ (dark-gray dashed line) is the slope between the rates of the Common and Abundant classes. All intervals show greater support for the multi-rate model over the single-rate model.

$= -0.21$, and $\beta_{\text{C-A}} = 0.03$. Examining the frequency of positive versus negative slopes for $\beta_{\text{VR-C}}$ and $\beta_{\text{C-A}}$ in the interval-to-interval analysis further corroborates the presence of a

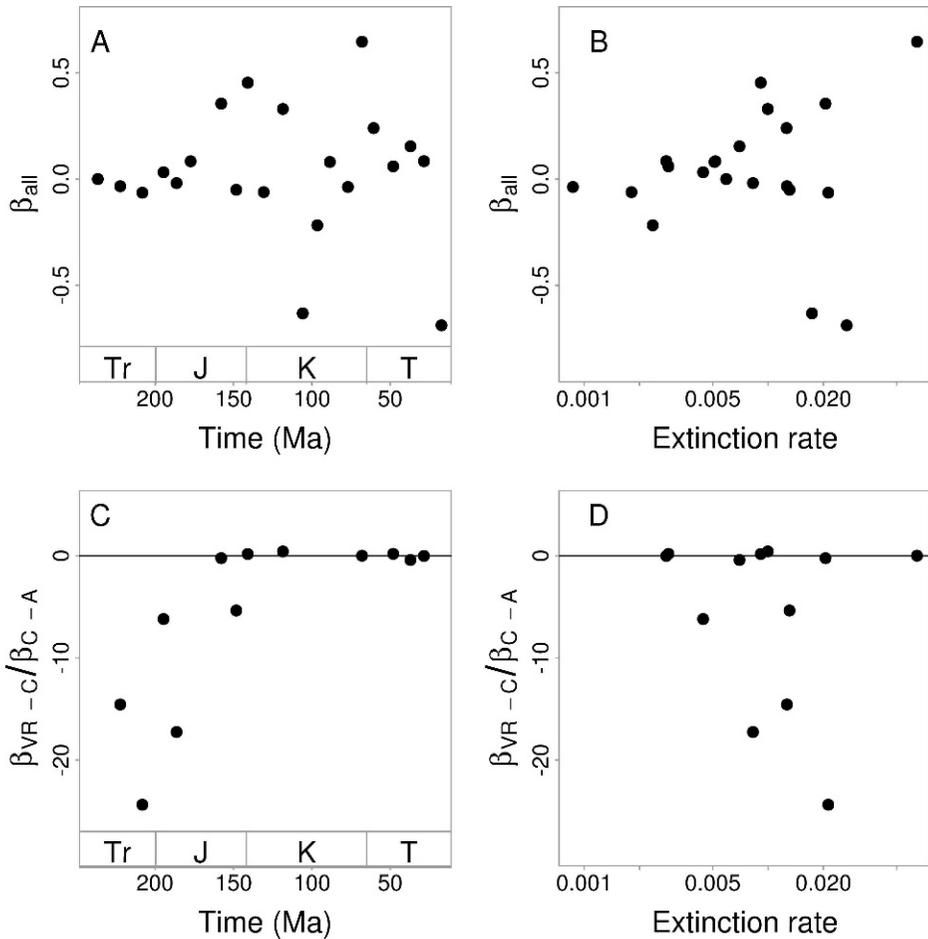


FIGURE 3. Abundance as a factor over time and relative to varying extinction intensities. A, Time series of the linear slopes (β_{all}) fit to the extinction rates for all abundance classes in each interval. B, Extinction rates calculated for all bivalves in each time bin plotted against β_{all} . No correlation is observed between extinction rate and either the strength or direction of selection as measured by β_{all} , though there is a general tendency for more severe extinction events to exhibit greater variance in the strength and direction of the abundance-extinction rate relationship. C, The ratio of β_{VR-C}/β_{C-A} plotted against time. All values of β_{C-A} are positive. Negative values of β_{VR-C}/β_{C-A} indicate intervals in which the U-shaped relationship is observed, whereas positive values indicate positive abundance-extinction rate relationships for both subsets of data. Approximately two-thirds of intervals exhibit a U-shaped abundance-extinction rate relationship. D, Extinction rates calculated for all bivalves in each time bin plotted against β_{VR-C}/β_{C-A} indicates no systematic variation in the structure of the abundance-extinction rate relationship with extinction severity.

U-shaped abundance-extinction rate pattern with 68% of β_{VR-C} of negative slope and 100% of β_{C-A} of positive slope (Figs. 2, 3C).

Model selection results for finer temporal subdivisions over the post-Paleozoic show that abundance was an important factor in extinction rates over all of the time intervals examined; however, the strength and direction of this effect fluctuated over time (Figs. 2, 3). Patterns of selectivity have been shown to vary between background and mass extinction intervals, particularly for variables such as geographic range (Jablonski 1986, 2005;

Payne and Finnegan 2007). To assess whether extinction magnitude was mediating the relationships we observe we plot β_{all} and the ratio of β_{VR-C}/β_{C-A} against the extinction rate calculated for all bivalves in each interval (Figs. 3B,D). Despite fluctuations in the strength and sign of the abundance-extinction rate relationship, temporal variability in these measures of selectivity do not covary with extinction magnitude, although elevated extinction rates are associated with increasing variance in the sign and strength of the abundance-extinction rate relationship (Fig. 3B,D). There is

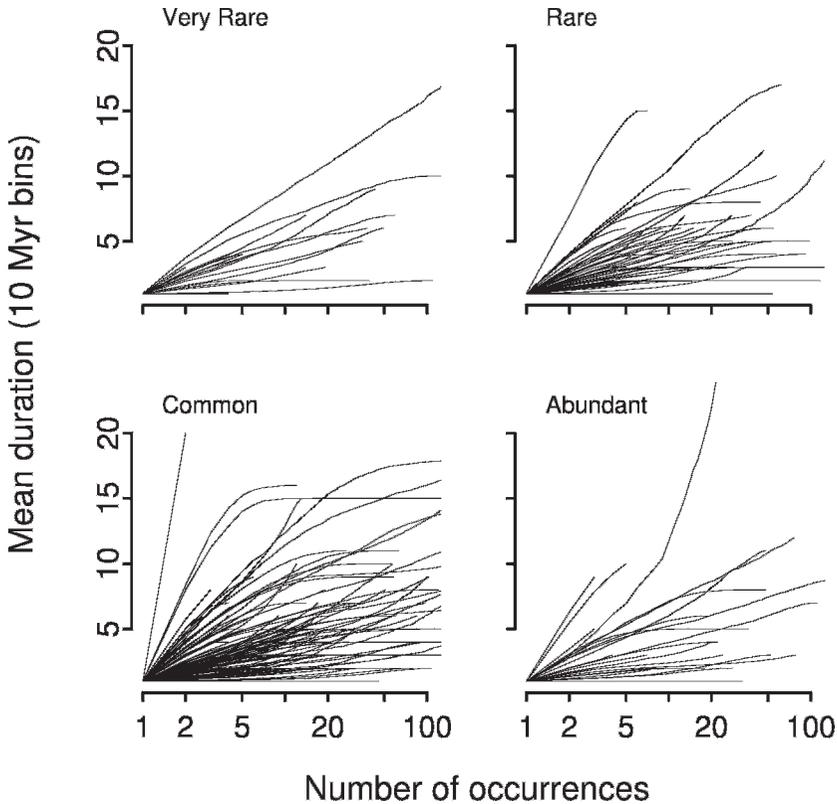


FIGURE 4. Rarefaction curves for genera in each abundance class. Generic occurrences are rarefied and the mean duration for 1000 replicates is shown. Duration units are the number of PBDB 10-Myr bins. The curves for short- and long-duration genera exhibit considerable variation as do those for genera from different abundance classes, suggesting that there is no systematic tendency for short-lived taxa to result from undersampling.

some suggestion that the magnitude of the negative relationship (β_{VR-C}) relative to the positive upturn in rates (β_{C-A}) was strongest in the early Mesozoic.

It is well known that abundance influences sampling probability (Preston 1948; Hayek and Buzas 1997; Thompson 2004), and as a result rare taxa may artificially exhibit shorter durations and higher extinction rates simply because of a failure of the sampling process (Signor and Lipps 1982; Meldahl 1990). Through the use of rarefaction, we assess whether a paucity of long-duration rare genera in our data is a sampling artifact. If short-duration genera were primarily the result of poor sampling, then the rarefaction curves of long- and short-duration genera will overlap when genus occurrences are rarefied. Here we report genus durations as the number of 10-Myr bins. A comparison of rarefaction curves (Fig. 4) shows considerable

scatter, with a substantial number of short-duration genera with many occurrences falling off of the trajectories of long-duration genera. Abundance also does not influence sampling at this scale because the rarefaction curves for genera grouped by abundance classes do not form distinct families of curves, but rather exhibit considerable variation. Although sampling undoubtedly influences the durations we observe, these results (Fig. 4) indicate no systematic bias of a given duration or abundance class.

To determine whether the durations we analyzed are undersampled relative to previous estimates, we compare the durations of genera recorded using occurrences in the PBDB with those in the Sepkoski compendium (2002) as updated by Jablonski et al. (2003, as revised November 2006). A strong positive correlation between the two databases would be indicated by a slope of one, with some

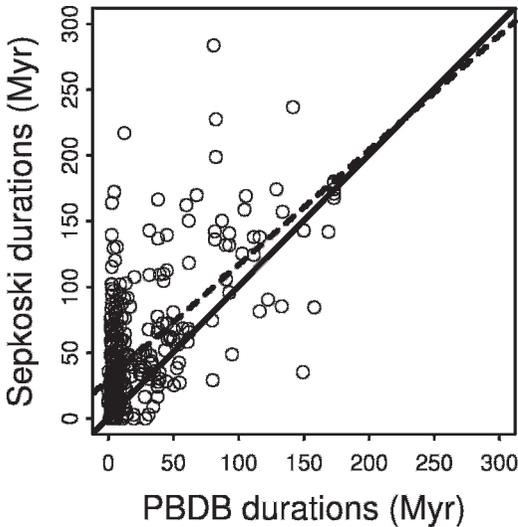


FIGURE 5. Completeness of PBDB genus durations with respect to previous estimates. Comparison of genus durations estimated from the updated Sepkoski compendium for bivalves and the PBDB. Solid line has a slope of unity; the dashed line is a linear regression. A strong positive correlation is observed, with dispersion due, in part, to differences in the time bins used.

dispersion expected due to uncertainties in the placement of occurrences in the PBDB into sub-stage level time bins. Genus durations in the two databases are strongly correlated (slope = 0.65, $p < 0.0001$) (Fig. 5), as has been shown in other groups such as Paleozoic brachiopods (Powell 2007). If the residual variance is distributed randomly with respect

to our variables of interest, namely abundance and occurrence, then the differences between the data sets will not affect our results. In Figure 6, the duration residuals from Figure 5 are plotted against mean proportional abundance (Fig. 6A) and occurrence (Fig. 6B), and in neither case is a relationship observed. The analyses presented in Figures 5 and 6 suggest that the method of data compilation in the PBDB did not influence the durations of genera analyzed here.

Both shell mineralogy and habitat preference potentially affect abundance estimates for fossil taxa owing to taphonomic factors alone. To assess these potential biases, we compare the frequency of genera of each shell mineralogy and habitat type across the four abundance classes (Table 2). A total of 371 extant and extinct genera have sufficient data to determine their habitat preference and shell mineralogy. All four abundance classes are represented, although the proportion of Very Rare genera is lower than in our extinction analyses because few of these genera have sufficient numbers of occurrences to distinguish their habitat preference with confidence. Using Fisher's exact test, we compare the contingency tables for the four abundance classes and find that abundance classes differ significantly in how genera are

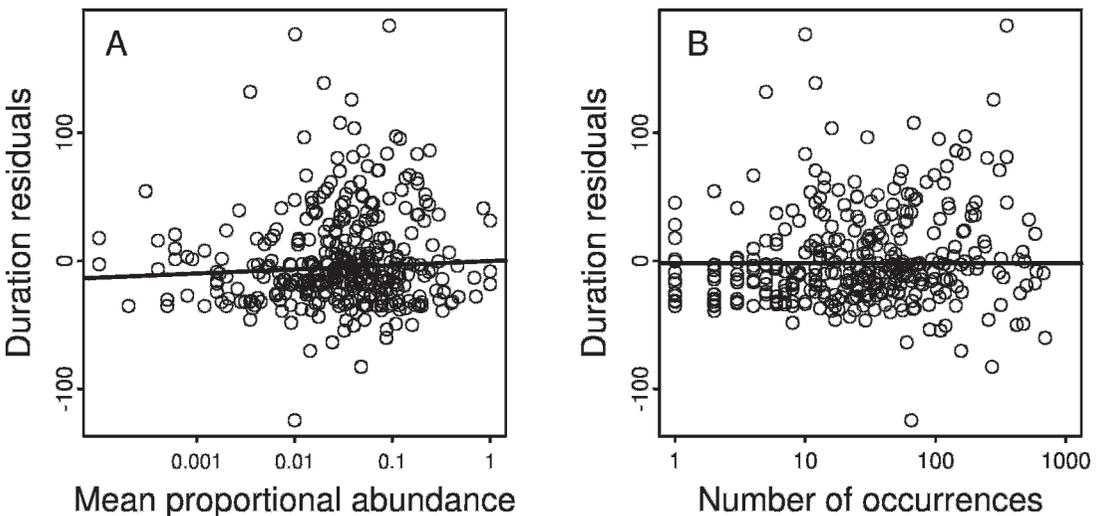


FIGURE 6. Duration residuals from Figure 5 plotted against mean proportional abundance (A) and number of occurrences (B). The dashed linear regression line indicates no relationship between either of these two variables and the duration residuals. In A, slope = 3.24, $p = 0.83$. In B, slope = 0.02, $p = 0.10$.

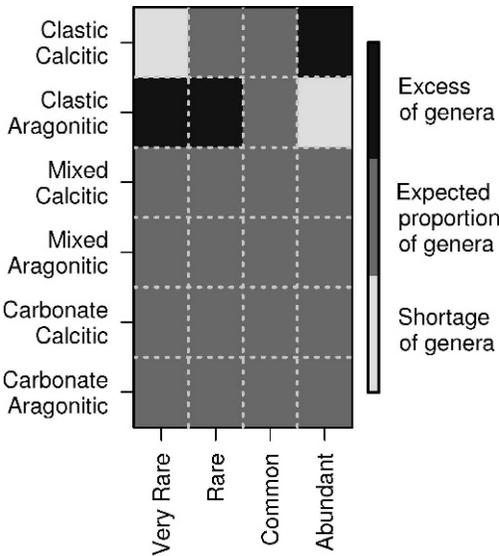


FIGURE 7. Differences between the expected and observed proportions of genera for each grouping of shell mineralogy, habitat preference, and abundance. Expected proportions were calculated by pooling all genera irrespective of their abundance. Deviations are observed in some abundance classes, specifically between calcitic and aragonitic genera that prefer clastic habitats (discussed in the text).

distributed among mineralogy-habitat groups ($p < 0.001$). Therefore, for these data there is some evidence of variation in abundance according to mineralogy and/or habitat preference. To examine where these differences are manifest we calculate the difference between the expected and observed proportions of genera for each combination of mineralogy and habitat preference for all four abundance classes (Fig. 7). Consistent with taphonomic expectations, we find an excess of

TABLE 2. Distribution of potential taphonomic factors among abundance classes. The frequency distributions of genera grouped by abundance class, habitat preference, and mineralogy were compared across abundance classes using Fisher's exact test to determine if they were drawn from the same underlying sampling distribution. The null hypothesis that each abundance class is pulled from the same distribution was rejected ($p < 0.001$).

Taphonomic bias		Abundance			
		Very Rare	Rare	Common	Abundant
Clastic	Calcitic	0	6	32	18
Clastic	Aragonitic	3	62	169	13
Mixed	Calcitic	0	0	10	0
Mixed	Aragonitic	0	0	10	2
Carbonate	Calcitic	0	0	7	3
Carbonate	Aragonitic	0	2	33	1

Abundant calcitic genera and a shortage of Abundant aragonitic genera in clastic habitats. This pattern is reversed in the Rare and Very Rare abundance classes, which contain an excess of aragonitic genera in clastic habitats. The first association we observe between mineralogy and abundance in clastic habitats (an excess of Abundant calcitic genera in clastic habitats) may be driven by the effects of dissolution in some collections, whereas the second association (an excess of Rare and Very Rare aragonitic genera) may be attributable to the larger sample sizes and/or the greater identifiability of specimens in some clastic collections. It is important to note that these differences are slight; Abundant genera contain only four more calcitic than aragonitic genera and Very Rare genera contain three aragonitic and no calcitic genera. The biggest anomaly is that most rare genera are aragonitic and prefer clastic habitats. Given these potential taphonomic biases, we reran our pooled analysis of abundance versus extinction rate using only extinct, aragonitic genera with a preference for clastic habitats. These 124 genera are distributed across three of the four abundance classes (Rare through Abundant); mineralogy and habitat preference could be assigned with certainty only to three Very Rare genera, all of which were extant and thus excluded from this analysis. Qualitatively, we recover the same U-shaped relationship between abundance and extinction rate (extinction rates for the Rare, Common, and Abundant classes are 0.0129, 0.0136, and 0.0236). However, for this taphonomic control the single-rate model is better supported than the multi-rate model ($\Delta_{i(\text{single-rate})} = 0, w_{(\text{single-rate})} > 0.999$; $\Delta_{i(\text{multi-rate})} = 1051.825, w_{(\text{multi-rate})} < 0.001$). Rerunning our finer-grained time-series analysis including only aragonitic genera with a preference for calcitic habitats reveals equivocal support for either single- or multi-rate models. Out of the 17 intervals where comparisons between the single-rate and the multi-rate can be made, eight exhibit a slight preference for the single-rate model and seven a slight preference for the multi-rate model, with each model best supported in only a single bin. These results suggest that

taphonomic factors may contribute to some extent to the U-shaped relationship observed in the full analyses but are unlikely to be the primary driver.

Discussion

Abundance was a significant factor in marine bivalve extinction rates globally over the post-Paleozoic. Extinction rates calculated for bivalve genera with last occurrences during the post-Paleozoic decline with increasing abundance as expected, demonstrating that the relationship hypothesized for present-day biotas existed as a long-term average over the last 250 Myr. Surprisingly, however, this relationship is nonlinear: Abundant genera, those with mean proportional abundances greater than 10%, reverse this trend by exhibiting elevated extinction rates.

Although a negative relationship between abundance and extinction rates is expected biologically, and may also result from sampling biases, it is not readily apparent what factors would cause abundant genera to be at elevated risk of extinction. Abundant genera included in these analyses are not taxonomically restricted, but rather come from a diverse array of clades including corbulids, venerids, and pectinids, among others. Were these genera characterized by marked spatial and temporal variance in abundance and thus more prone to extinction due to population fluctuations not well characterized by the single abundance measure we used? Were abundant genera restricted environmentally and/or geographically? Or were the durations of these genera truncated because the facies in which they occurred were poorly preserved and/or because they were less likely to be sampled during intervals in which they occurred at low densities? None of these hypotheses are mutually exclusive and in several cases similar predictions are consistent with both biological and sampling hypotheses. It is worth noting that the pattern of elevated extinction rates among abundant taxa has been observed in other studies (Layou 2007; Lockwood and Barbour Wood 2007), and that many taxa used to correlate marine sedimentary rocks were both abundant and temporally restricted. Thus the

perplexing pattern we document here may be more general and warrants further work.

One of our reviewers suggested that the U-shaped relationship between abundance and extinction may be a function of community structure rather than taxon abundance. Perhaps genera that occur in communities with more even abundance distributions are more resilient to extinction than genera found in more uneven communities. This hypothesis, relating diversity and stability, has been tested previously using an array of neontological and paleontological data (McCann 2000; Kiessling 2005; Ives and Carpenter 2007). Although it deserves further investigation, this is an unlikely explanation for the U-shaped pattern we observe. Evenness is a measure of the numerical dominance of the most abundant taxa in any given assemblage, and qualitatively many communities characterized by high evenness contain long tails of rare taxa (Hubbell 2001; Harnik 2009) that span several of the abundance classes analyzed here. Uneven communities may contain genera of high extinction risk drawn from both ends of the abundance spectrum (e.g., Rare and Abundant), but communities of high evenness also contain a substantial fraction of taxa predicted to be at elevated extinction risk on the basis of their rarity.

The few existing analyses of the abundance-extinction rate relationship using fossil data have been somewhat equivocal. Some support exists for selective extinction during the Late Ordovician (Layou 2007) and the Neogene (Stanley 1986; Stanley et al. 1988), in contrast to weak or no support during the Eocene (Harnik 2007; Lockwood and Barbour Wood 2007) and at the Cretaceous/Paleogene extinction (Lockwood 2003; Lockwood and Barbour Wood 2007). Although other studies have considered the abundance-extinction relationship, many of these have used occurrence data as a proxy for abundance, which conflates population size and geographic distribution (e.g., Kiessling and Baron-Szabo 2004; Powell 2007), so they are not considered further here. In our analyses we find substantial support in both the pooled post-Paleozoic and time-series analyses for a relationship between abundance and extinction rates.

What might explain the possible variation in results among these studies? One possible explanation that could reconcile our results with previous studies would be if there is temporal variation in selectivity patterns between background and mass extinction intervals as has been hypothesized for other variables such as geographic range (Jablonski 1986, 2005; Payne and Finnegan 2007). In our finer-grained time-series analysis we did observe substantial variation in the relative support for an abundance-extinction rate relationship over the post-Paleozoic. In contrast with previous studies, however, support for abundance as a factor in extinction appeared to vary largely independently of extinction intensity, with some suggestion that the role of abundance may have been more variable during extinction events of greater intensity.

Despite a variety of factors that might bias estimates of abundance or taxon duration, our sensitivity analyses reveal little evidence for taphonomic effect. Specifically, we find no systematic evidence for biased durations in these data, either in our rarefaction analysis or in comparison between durations in the PBDB and Sepkoski database. With respect to shell mineralogy and habitat preference, we find two associations that may in part be taphonomic. First, we find more Abundant calcitic genera in clastic habitats than expected—a result somewhat in contrast to those of a recent study (Behrensmeyer et al. 2005) that found no association between shell durability and frequency of occurrence. Second, we find that Rare and Very Rare genera are predominantly aragonitic. When we attempt to control for these effects by constraining our analyses post hoc to only those genera that are aragonitic and prefer clastic habitats, we find the U-shaped relationship between abundance and extinction rate qualitatively remains. Whereas the multi-rate model is no longer best-supported in the pooled analysis, the results of the finer-grained time-series approach show equivocal support for either single- or multi-rate models. These results suggest that taphonomic factors may strengthen the observed abundance-extinction rate relationship, but are unlikely to be the primary driver.

Another factor that might influence our abundance estimates is community composition. If a fauna contains poorly individuated, clonal and colonial organisms, such as bryozoans, the relative abundance estimates of highly individuated and countable organisms will be uncertain. There are no satisfactory sampling protocols to deal with faunas that are composed of organisms varying in their countability. Harper (1977) proposed counting genets (the number of genetic individuals) and ramets (the number of structural individuals) separately. These two counts bracket a vague intuitive notion of how many individuals there are in a population. Unfortunately, the number of genets cannot be estimated from the fossil record, and the number of ramets may be inflated by post-mortem fragmentation. Measuring the biomass of colonial organisms is possible, yet collections containing biomass estimates are fairly uncommon in the PBDB and this only partially addresses the problem. In order to estimate the strength of this bias, we tallied the number of collections containing bryozoans in our data and compared the relative abundances of bivalves estimated from the whole fauna with those estimated from a subset of the fauna excluding bryozoans. Of the 1631 collections we used for our abundance estimates only ~50 contain bryozoans, and abundances calculated with or without bryozoans are strongly correlated ($\rho = 0.99$; $p < 2.2e-16$).

Calculation of extinction rates requires delineation of groups and in the case of a continuous variable such as abundance, binning schemes require subjective decisions regarding where to place cutoffs. To examine the sensitivity of our results to varying definitions of abundance classes we partitioned our total data set post hoc into quartiles and found qualitatively no difference in our results (Table 3).

The data archived in the PBDB provide an unprecedented opportunity to investigate the relationship between abundance and extinction rate over Phanerozoic time scales. However, using such data, compiled from a diversity of studies each with its own idiosyncrasies, is not without risk. Our sensitivity

TABLE 3. Comparison of support for the multi- versus single-rate models using abundance classes defined in two ways. Data are split into nonoverlapping bins according to two subdivision schemes: (1) an equal distance between abundance bins on a log scale (order of magnitude bins); (2) equal proportions of data in each bin (quartiles). K is the number of model parameters, Δ_i is the AIC difference, and w_i is the Akaike weight. All subdivisions are better supported (have a lower Δ_i) than the single-rate model in which abundance is not a factor in extinction rates.

Model binning		K	Δ_i	w_i
Order-of-magnitude bins	Single rate	1	31.56	<0.001
	Multi rate	4	0	>0.999
Quartiles	Multi rate	1	22.25	<0.001

analyses suggest that the heterogeneity of PBDB data is unlikely to generate the abundance-extinction rate relationship we observe. Nonetheless, our results could be further tested by applying the methodological framework we have developed and used here to other data sets generated with more standardized protocols (e.g., Jackson et al. 1999). Whereas previous approaches to understanding extinction selectivity have generally focused on comparing the characteristics of victims and survivors, our approach allows one to compare the relative support for multiple rates among taxa partitioned a priori on the basis of their biological characteristics. Because genera of all abundances can (and do) go extinct, focusing on differential extinction rates is an important step toward assessing the contribution of abundance to survivorship. Our method is also flexible enough to detect nonlinear relationships in semi-continuous data which may have certain advantages over other linear modeling approaches. Although using standardized sampling protocols is ideal, it is important to consider that taphonomic processes cull the data before we do. Using standardized sampling protocols in the absence of models relating taphonomic processes to the biological distributions we observe in the fossil record may offer a false sense of security about data quality and runs the risk of changing the scale and structure of data such that they are no longer commensurate with the question being asked.

Conclusions

Empirical studies of extinction dynamics in present-day and fossil biotas have repeatedly demonstrated that species differ in their risk of extinction and that such differences may be

explained in part by variation in life history and other ecological factors (Pimm et al. 1988; Tracy and George 1992; Purvis et al. 2000, 2005; Harcourt et al. 2002; Cardillo 2003; Jones et al. 2003; Kotiaho et al. 2005). Geographic range size and habitat breadth have emerged as important contributors to extinction risk in present-day biotas and their importance over longer time scales has been demonstrated in a plethora of analyses of the fossil record. The role of abundance in extinction rates over geologic time has not been studied as intensively owing to limited abundance data and concerns regarding possible sampling biases, with existing studies providing equivocal support for abundance as a factor in extinction dynamics. Using the extensive data archived in the PBDB and a model-selection approach increasingly applied in paleobiology (e.g., Foote 2005; Hunt 2006; Wagner et al. 2006; Liow and Stenseth 2007) we show that abundance was an important factor in marine bivalve extinction rates over the post-Paleozoic. Contrary to our expectations, however, these analyses reveal a persistent nonlinear relationship between abundance and extinction rates that only in part corroborates neontological predictions. As abundance increases, extinction rate declines, yet more abundant taxa exhibit elevated rates. These results are robust and are not simply the product of variation in sampling probabilities among genera that differ in abundance, although they may be influenced by other taphonomic factors such as shell mineralogy. This U-shaped relationship emerges both in the pooled analysis of all post-Paleozoic genera and in our finer-grained interval-to-interval approach and may explain in part why other studies have found relatively weak support whereas we document considerable

support. A variety of biological processes are possible candidates for generating the U-shaped relationship between abundance and extinction rate, including the effects of other factors correlated with abundance and stabilizing or disruptive selection. Further work is needed to tease apart the underlying determinants of this anomalous yet persistent pattern.

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