

Extinction and quiescence in marine animal genera

Michael Foote

Abstract.—If last appearances of marine animal genera are taken as reasonable proxies for true extinctions, then there is appreciable global extinction in every stage of the Phanerozoic. If, instead, backsmearing of extinctions by incomplete sampling is explicitly taken into consideration, a different view of extinction emerges, in which the pattern of extinction is much more volatile and in which quiescent time spans—with little or no global extinction for several million years—are punctuated by major extinction events that are even more extreme than is generally thought. Independent support for this alternative view comes from analysis of genus occurrence data in the Paleobiology Database, which agrees with previous estimates of sampling probability and implies that offsets between extinction and last appearance of one or more stages are quite probable.

Michael Foote. Department of the Geophysical Sciences, University of Chicago, Chicago, Illinois 60637.
E-mail: mfoote@uchicago.edu

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What characterizes the probability distribution of extinction event sizes? Since the pioneering work of Raup and Sepkoski (1982) and Van Valen (1984), two enduring aspects of this question have been how to designate mass extinctions (Raup and Sepkoski 1982, 1984, 1986) and whether mass extinctions constitute a separate statistical population (reviewed by Wang [2003]). Most paleontologists would now recognize roughly the same handful of stages as major mass extinctions for marine animals, although there is still debate as to their ecological significance (Boucot 1983; McGhee et al. 2004), the relative roles of origination and extinction in depleting diversity (Foote 2000b, 2006; Bambach et al. 2004; Bambach 2006), and the extent to which mass extinctions represent something more than aggravated background extinction (Jablonski 1986, 2005; Wang 2003).

An important point, made most explicitly by Stigler (1987; see also Quinn 1983; Raup et al. 1983), is that questions concerning the temporal pattern of extinction events often involve an underlying model of the statistical distribution of extinction magnitudes and processes. Other tacit assumptions are also common. For example, the studies cited above, while they treat a diversity of issues from different perspectives, all assume that last appearances are reasonable proxies for extinctions. Incomplete sampling, however, has real

potential to distort the record of extinction in predictable ways (Signor and Lipps 1982; Foote 2001a, 2003, 2005; Peters 2006). Of particular interest, any extinction event will be smeared backward, so that last appearances are spread over some span of time even if true extinctions were more clustered temporally.

The treatment of the smearing problem has mainly focused on the limited span of time leading up to an extinction event (Signor and Lipps 1982; Raup 1989; Marshall and Ward 1996), with the offset between extinction and last appearance tacitly assumed to be well within the stage of actual extinction and therefore negligible for data compiled at the stage level of resolution. Subsequent work, by contrast, has suggested that offsets may commonly extend for one or more stratigraphic stages, potentially complicating the numerous analyses that have been conducted at this level of temporal resolution (Foote 2003, 2005).

The purpose of this paper is to reconsider the statistical and temporal distribution of extinction events in a way that attempts to take incomplete and variable sampling into consideration. Whereas incomplete sampling tends to smear true events, sequence-stratigraphic architecture and other sources of variable sampling have the potential to create spurious peaks in first and last appearances (Holland 1995, 2000; Foote 2000a; Holland and Patzkowsky 2002). Previous work suggests that,

for global data at the genus level, spurious peaks in extinction are generally less of a problem than is smearing (Foote 2003; Peters 2005, 2006). The focus of this discussion is therefore on smearing, although the method used here can counteract both biases. Maximum-likelihood estimates of extinction rates suggest considerable Signor-Lipps smearing even beyond the stage level. The distribution of event sizes is more highly skewed than suggested by the face-value data, with many stages having negligible extinction but appearing to have substantial turnover because of this smearing.

Secular Pattern and Frequency Distribution of Extinction

Global stratigraphic ranges for Phanerozoic marine animal genera were taken from Sepkoski (2002). A total of 30,528 genera have first and last appearances resolved to 80 basic stratigraphic divisions (hereinafter *stages*) (see Foote 2005).

Two models were used to estimate extinction rates:

(1) *Face-value Model*.—A model of effectively complete sampling was assumed, so that stages of first and last appearance were taken as equivalent to stages of origination and extinction. Taking the data at face value in this way is by far the most common approach used in the study of extinction (but see Alroy 1996, 1998; Miller and Foote 1996; Alroy et al. 2001; Connolly and Miller 2001a,b, 2002; Foote 2001a, 2003, 2005; Smith et al. 2001; Krug and Patzkowsky 2004; Lu et al. 2006; and Crampton et al. 2006b for a few exceptions).

(2) *Optimized Model*.—Maximum-likelihood estimates were derived from survivorship modeling that takes incomplete and variable sampling into consideration. This approach uses numerical optimization to find the time series of origination, extinction, and sampling rates that have the strongest statistical support, given the observed first and last appearances and assumed models of evolution and sampling. Briefly: X_{ij} is the observed number of genera with first appearance in stage i and last appearance in stage j ; m is the number of stages; p_k , q_k , and R_k are the genus-level origination rate, extinction rate, and sampling

probability in stage k ($k = 1, \dots, m$); $P_{\rightarrow ij}$ is the expected forward survivorship probability for a candidate time series of p , q , and R , i.e., the proportion, of those genera with first appearance in stage i , that are expected to have a last appearance in stage j ; and $P_{\leftarrow ij}$ is the expected backward survivorship probability, i.e., the proportion, of those genera with last appearance in stage j , that are expected to have a first appearance in stage i . (See Foote 2003 for the calculation of these probabilities.) For a candidate time series of rates and the corresponding predicted values of $P_{\rightarrow ij}$ and $P_{\leftarrow ij}$, the likelihood is calculated as

$$L = \prod_{i=1}^m \prod_{j=i}^m P_{\rightarrow ij}^{X_{ij}} \times \prod_{j=1}^m \prod_{i=1}^j P_{\leftarrow ij}^{X_{ij}}.$$

The time series of p , q , and R that maximize L are the maximum-likelihood estimates. The likelihood function was maximized with the intrinsic `optim()` function in the R software environment (R Development Core Team 2006), using the limited-memory Broyden-Fletcher-Goldfarb-Shanno method with bounds (option "method=L-BFGS-B") (see Foote 2005 for more detail). Variance in the rate estimates was assessed with a bootstrap resampling procedure (Efron and Tibshirani 1993). For each of 100 bootstrap replicates, 30,528 stratigraphic ranges were drawn with replacement from the available pool and the optimization procedure was repeated.

For the optimized model, pulsed turnover is assumed, in which origination and extinction are concentrated at stage boundaries (Foote 2003, 2005). Results obtained with an alternative assumption, namely that turnover is spread uniformly throughout stages, are consistent with those of the pulsed turnover model (Appendix). In addition, all genera are assumed to be governed by the same taxonomic and sampling rates within a given stage, although these rates are allowed to vary from stage to stage. Previous work suggests that temporal variation in rates can be adequately detected even if there is taxonomic heterogeneity in the average levels of origination, extinction, and sampling rates, provided that the various taxa have similar temporal patterns (Foote 2001a).

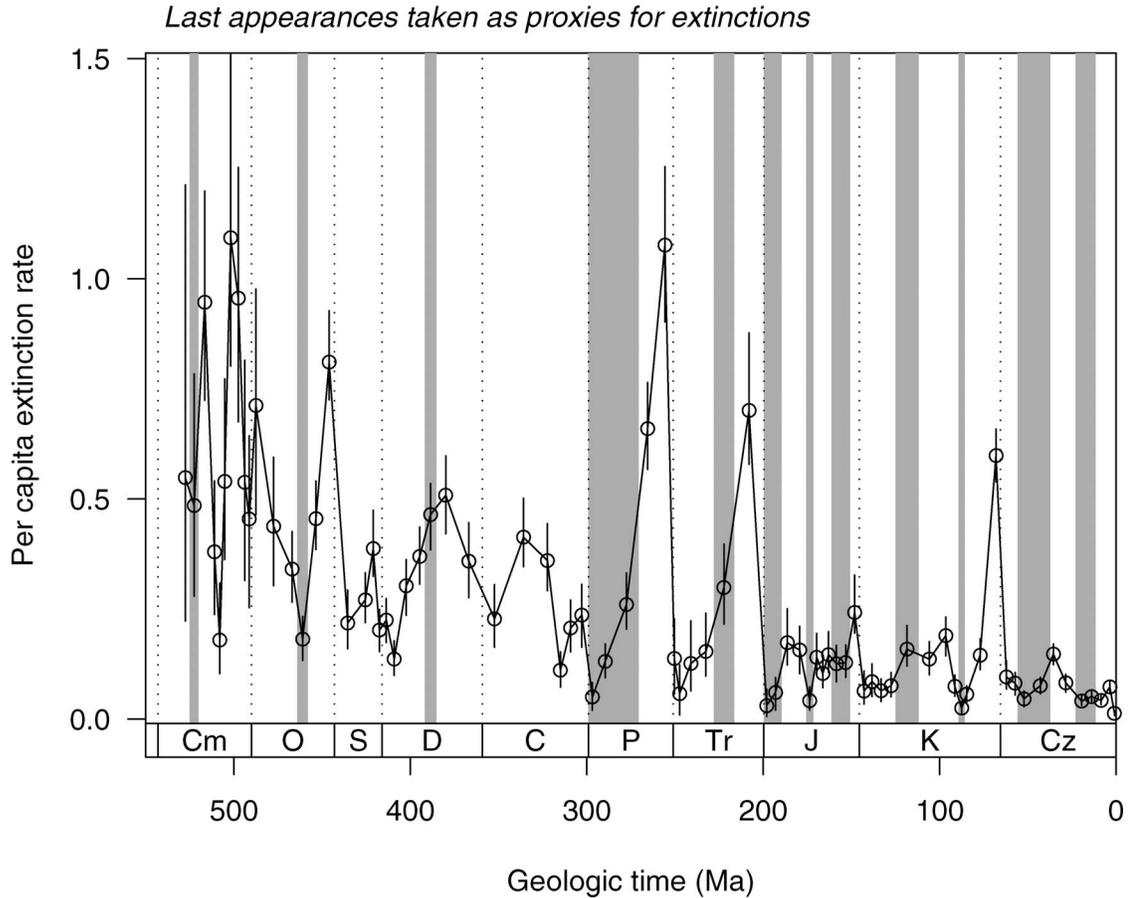


FIGURE 1. Per capita extinction rates under the conventional, face-value model, in which first and last appearances are taken as proxies for originations and extinctions. Vertical bars show the full range of values obtained for 1000 replicates of a bootstrap resampling procedure. Note that these values never reach zero. Time intervals in gray are explained in Figure 3.

Assuming pulsed turnover, the extinction parameter in the optimized model could be expressed equivalently as either a per capita rate per stage, q , or an extinction probability per genus per stage, Q , where $Q = 1 - e^{-q}$. I have chosen to represent both the face-value and optimized models with the per capita rate because the long-term mean is expected to be the same in both models (Foote 2000a), which in turn facilitates comparison of other aspects of the probability distribution. This is not the case for other extinction measures such as percent extinction, in which the biasing effect of singletons inflates the average extinction value in the face-value model (see Figure A4 in the Appendix). Using the per capita rate reduces the difference between the two models and so is conservative. In the optimized model, ex-

tingtion rate is a fitted parameter. For the face-value model, it is calculated as $q = -\ln(X_{bt}/X_b)$, where X_{bt} is the number of genera with first appearance sometime before the stage and last appearance sometime after the stage, and X_b is the number of genera with first appearance before the stage and last appearance during or after the stage (Foote 2000a).

The time series of face-value extinction rates is depicted in Figure 1. This shows the familiar secular decline with several excursions superimposed. Given that a number of the observed rates are rather low, one may reasonably ask whether they stand meaningfully above zero. This was explored by bootstrap resampling of the stratigraphic range data. For each of 1000 replicates, 30,528 ranges were drawn with replacement from the available

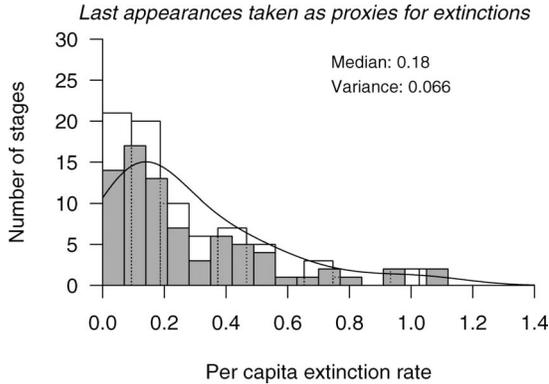


FIGURE 2. Two alternative histograms, with different bin widths, depicting face-value extinction rates from Figure 1, with a kernel density estimator (KDE) superimposed (see Wang 2003). In this and subsequent figures, a normal kernel is used and the bandwidth of the KDE is set to 10% of the range of values on the abscissa. Although the distribution is skewed, there is some indication of a mode at an extinction rate between 0.1 and 0.2.

pool and the entire extinction history recomputed. The vertical bars for each stage show the full range of resulting values. These never reach zero; the sample is large enough to conclude safely that each stage has some measurable global turnover. The gray intervals in Figure 1 and subsequent figures denote stages in which extinction rates are substantially lower under the optimized model than under the face-value model (q.v.).

The frequency distribution of extinction magnitudes at the stage level is clearly skewed, as seen in the histograms of Figure 2 and in similar depictions of the data using alternative extinction metrics (Wang 2003). As emphasized by Wang (2003), one's impression of the shape of the distribution can be influenced by the binning of the histogram. For example, a coarser binning (white bars) in Figure 2 suggests a hollow curve, whereas a finer binning (gray bars) suggests a distinct mode. Superimposed on this histogram is therefore a smoothed depiction of the probability distribution using a kernel density estimator. Rather than assuming a particular parametric form of the overall probability distribution, for example that it is normal or lognormal, this density estimator models the probability distribution as the sum of a series of probability curves (the kernel functions), each one

centered at an observed data point. An advantage of this approach is that virtually any continuous probability distribution can be modeled (see Wang 2003 for further discussion). The main goal here is to provide a graphical depiction that is not sensitive to the binning choice in a histogram. I have used a normal kernel and a bandwidth of 10% of the range of values depicted on the abscissa, and have implemented this using the `density()` function in the R programming language (R Development Core Team 2006). Although the bandwidth is somewhat arbitrary, this and other bandwidths indicate a mode in the distribution, at a per capita extinction rate between 0.1 and 0.2 per genus per stage.

The picture is different if we make allowances for incomplete sampling. Figure 3 shows the median of the 100 optimized rate estimates for each stage and the inner 68% of the distribution (from the 16th to the 84th percentile). (The median was used because some of the distributions of optimized values within a stage are skewed; the range of percentiles is meant to be roughly comparable to ± 1 standard error.) The timing of the resulting extinction peaks largely agrees with that of the face-value model. A conspicuous difference between the two models, however, is in the stages leading up to local maxima in extinction. In the face-value model, these preceding stages often have moderate to high extinction, whereas the optimized model in effect interprets many of these times of appreciable last appearance as backsmearing from the later events (Table 1). The frequency distribution of extinction rates in Figure 3 is strongly right-skewed, with 16 (20%) of the stages having an estimated extinction rate of zero (Figs. 4, 5). Because of this predominance of low rates, the leftmost bar on the histogram has the highest frequency irrespective of the binning used. The overall variance in rates is over 70% higher than in the face-value model.

The secular decline in extinction complicates analyses of the frequency distribution of extinction events because high but typical rates in the early Phanerozoic have magnitudes similar to those of major excursions later on (Wang 2003; Bambach et al. 2004; Jablonski 2005). Given that this decline is evident un-

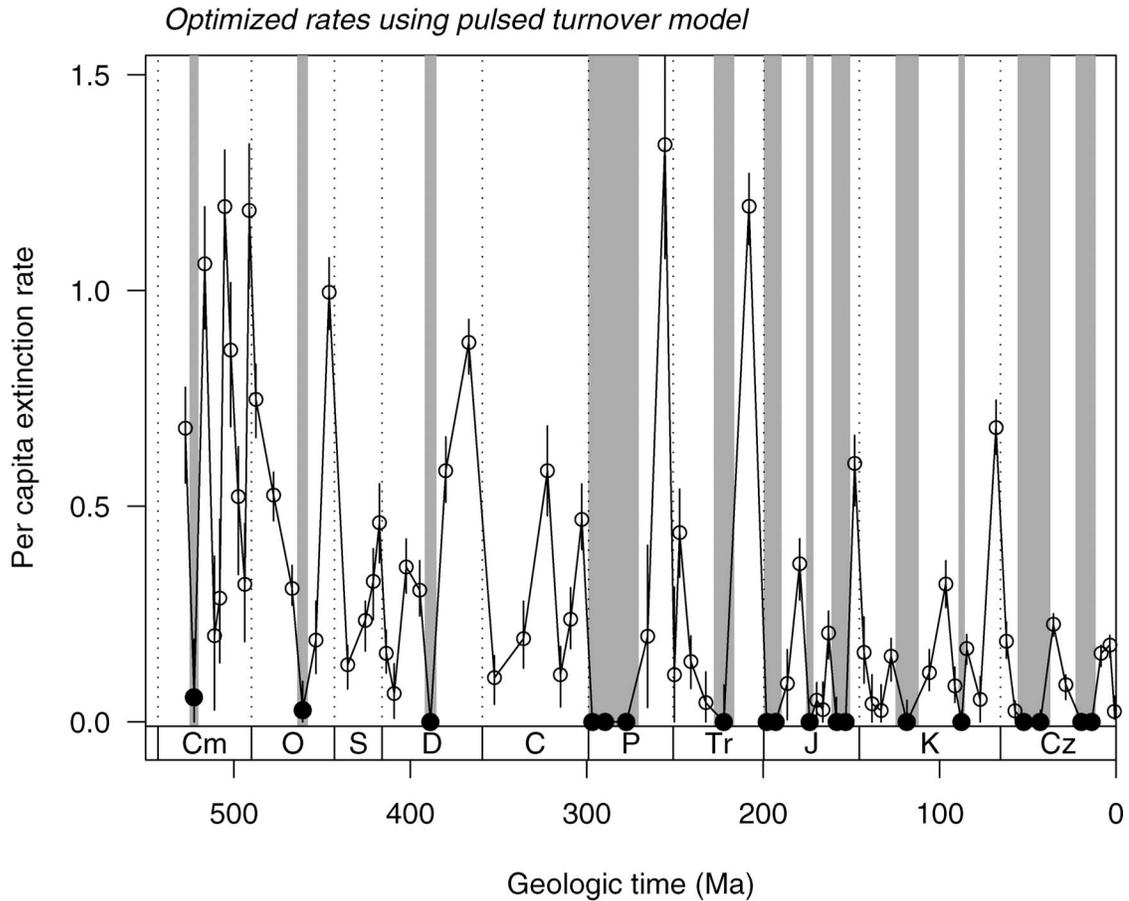


FIGURE 3. Per capita extinction rates under the alternative, optimized model, in which incomplete sampling is allowed, and in which origination, extinction, and sampling rates are simultaneously estimated from the time series of first and last appearances. The points denote the median values obtained from 100 bootstrap replicates, and the vertical bars show the inner 68% of the distribution of values (from the 16th to the 84th percentile). Time intervals in gray are those for which estimated rates are zero (16 stages) and those in which estimated rates are less than 25% as high as those obtained with the face-value model (two stages). The corresponding rates are indicated by filled circles. In contrast to the face-value model, the history of extinction is more volatile, with a greater tendency to oscillate between low and high rates. This difference arguably reflects backsmearing of extinction events in the face-value model.

der either model and represents an important component of the overall rate variance, some justification is in order for not detrending the data. First, there is a natural zero in the measurement of extinction, and I am interested in keeping that fixed point of reference to ask whether there are intervals of time that have the lowest conceivable rate of extinction. Second, detrending would, if anything, bring a number of the moderate Paleozoic values lower down in the distribution of rates. Because I mean to suggest that the extremely low rates in the optimized model are real, it is conser-

vative to exclude some potentially low rates by failing to detrend the data (see Appendix).

Extinction rates from the face-value and optimized models are compared directly in Figure 5. The closed symbols in this figure denote stages with optimized rates of zero (16 stages) or rates less than 25% as high as the face-value rates (two stages). One might have supposed that the zeroes in the optimized rates largely correspond to stages with little turnover in the raw data, and therefore represent but a minor adjustment. In fact, the zeroes come from a wide part of the spectrum of face-value ex-

TABLE 1. Stages with much lower extinction rate in optimized versus face-value model.

Stage	Face-value rate*	Optimized rate†	Possible source of backsmeearing
Atdabanian	0.486 (0.414, 0.558)	0.057 (0, 0.192)	Botomian
Llandeilian	0.182 (0.166, 0.198)	0.028 (0, 0.094)	Caradocian, Ashgillian
Givetian	0.465 (0.441, 0.489)	0 (0, 0)	Frasnian, Famennian
Asselian	0.05 (0.041, 0.059)	0 (0, 0.018)	Guadalupian, Changhsingian
Sakmarian	0.131 (0.117, 0.145)	0 (0, 0)	Guadalupian, Changhsingian
Leonardian	0.26 (0.241, 0.279)	0 (0, 0)	Guadalupian, Changhsingian
Carnian	0.299 (0.272, 0.326)	0 (0, 0.086)	Norian (including Rhaetian)
Hettangian	0.031 (0.022, 0.04)	0 (0, 0)	Pliensbachian, Toarcian
Sinemurian	0.06 (0.048, 0.072)	0 (0, 0)	Pliensbachian, Toarcian
Aalenian	0.042 (0.034, 0.05)	0 (0, 0)	Callovian
Oxfordian	0.126 (0.114, 0.138)	0 (0, 0.057)	Tithonian
Kimmeridgian	0.128 (0.116, 0.14)	0 (0, 0.015)	Tithonian
Aptian	0.159 (0.146, 0.172)	0 (0, 0.05)	Albian, Cenomanian
Coniacian	0.025 (0.021, 0.029)	0 (0, 0.027)	Santonian
Lower Eocene	0.046 (0.041, 0.051)	0 (0, 0)	Upper Eocene
Middle Eocene	0.076 (0.07, 0.082)	0 (0, 0.027)	Upper Eocene
Lower Miocene	0.041 (0.037, 0.045)	0 (0, 0)	Upper Miocene
Middle Miocene	0.051 (0.047, 0.055)	0 (0, 0)	Upper Miocene

* Numbers in parentheses are the limits of the observed value \pm one standard error.

† Numbers in parentheses are the limits corresponding to the 16th and 84th percentiles of the distribution of optimized values.

tion rates. Moreover, the optimization approach is not constrained to drive estimated rates to zero. A number of optimized rates are substantially lower than their face-value counterparts but still well above zero.

In the conventional extinction model (Figs. 1, 2), something is always happening in the world. In the alternative view (Figs. 3, 4), the process of taxonomic turnover is concentrated in a smaller proportion of available geologic time. On the whole, the optimized extinction model yields a more volatile record of extinction intensity, with periods of quiescence—sometimes quite extended—punctuated by substantial extinction events. Extreme quiescence is much more pronounced in roughly the second half of the Phanerozoic, when average extinction levels are already lower.

Why Take the Optimized Model Seriously?

The more volatile model of Figures 3 and 4 implies a substantial revision of the history of extinction. It is therefore worth asking whether there is any reason to prefer it over the conventional view, or at least to give it equal standing. At least three lines of reasoning are relevant to this question:

1. *First Principles*.—It hardly needs stating that stratigraphic ranges are incompletely sampled. To accept the face-value record of extinction requires that the offset between ex-

tion and last appearance generally be sufficiently small as to be negligible when data are binned at the stage level. The expected offset therefore needs to be empirically scaled on the basis of temporal occurrence data (Paul 1982), geological reasoning (Holland and Patzkowsky 2002), or other approaches (Foote and Raup 1996).

2. *Empirical Scaling of Sampling Probabilities*. A simple way to estimate sampling probabilities, based on analysis of gaps in stratigraphic ranges, was initially developed by Paul (1982; see Foote 2001b for modification). The number of taxa known to range through a stage, because they are sampled sometime before and sometime after the stage, is compared with the number of these taxa actually sampled from the stage.

To develop estimates of sampling probability, occurrence data on marine animal genera were downloaded from the Paleobiology Database (www.pdb.org; accessed 27 July 2006). The following options were specified in the download: Data were restricted to marine invertebrate collections; subgenera were elevated to genus rank; genus names were replaced with senior synonyms; occurrences that are determinate at the genus level but not the species level were included; genus names qualified by “aff.,” “sensu lato,” and quotation marks were excluded; informal names were

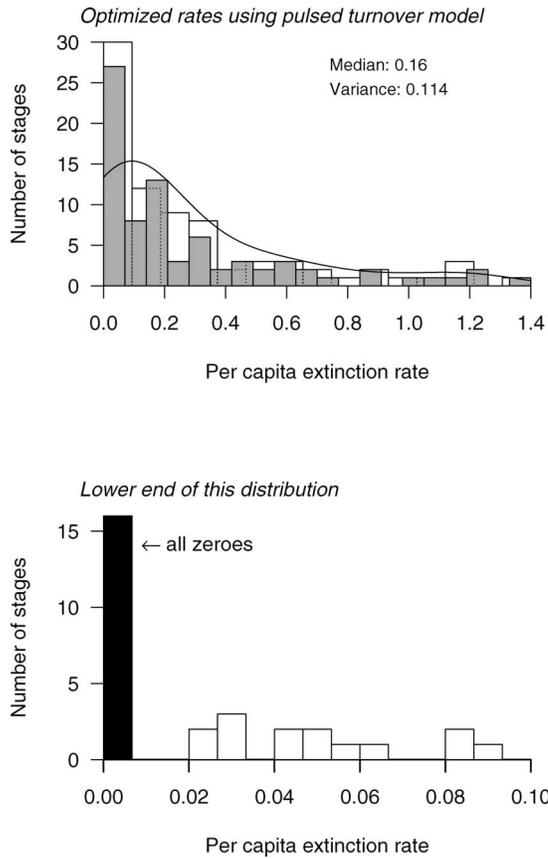


FIGURE 4. Histograms of optimized extinction rates from Figure 3, with a KDE superimposed as in Figure 2. Note the greater concentration of extinction rates near zero and the higher variance compared with the face-value model. The bottom panel shows the detail of the lower end of the distribution.

excluded; ranges were based only on fossil collections and were not extended to the Recent.

The stratigraphic information associated with each collection was used to assign each occurrence to one of Sepkoski's stages, relying on the definitions of stages given by Sepkoski (2002) and on correlation charts between regional and global stages given by Harland et al. (1990) and Gradstein et al. (2004). For certain intervals of time, many collections could not be adequately resolved. Some of Sepkoski's stages were therefore combined into broader units used by the Paleobiology Database: Cambrian 2 (Lower Cambrian exclusive of Nemakit Daldynian); Cambrian 3 (Middle Cambrian); Cambrian 4 (Upper Cambrian); and Llanvirn+Llandeilo. This resulted in

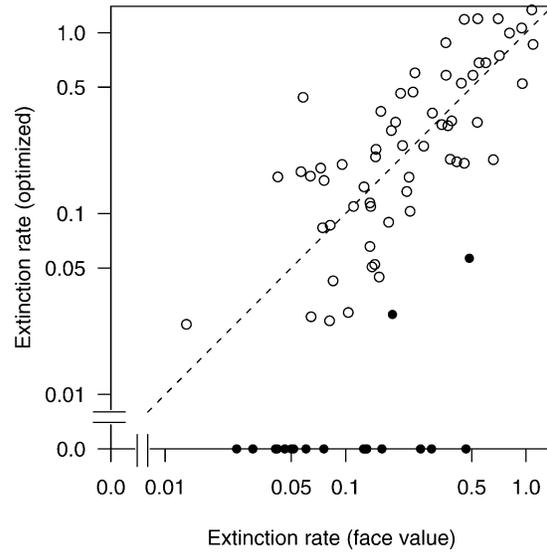


FIGURE 5. Stage-by-stage comparison between face-value and optimized models, plotted on dual logarithmic axes. Stages corresponding to the gray bars in Figure 3 are shown as closed circles, other stages as open circles. Note that the zeroes in the optimized model come from a wide part of the range of extinction rates in the face-value model. The dashed diagonal is the 1:1 line.

17,867 genera with occurrences assigned to 72 operational stages.

For each stage, let X_{bt} denote the number of genera observed to cross both the bottom and top stage boundaries (i.e., the number sampled anytime before and anytime after the stage), and let $X_{bt,samp}$ denote the number of these that are also sampled in the stage. Then the overall average sampling probability per genus per stage is estimated as

$$R = \frac{\sum_{i=1}^m X_{bt,samp}(i)}{\sum_{i=1}^m X_{bt}(i)},$$

where m is the number of stages. For these data, the estimated sampling probability is 0.37 per genus per stage. This implies that, on average, just over one-third of all genera are expected to be sampled in their stage of extinction. Offsets of one or more stages between extinction and last occurrence should be rather common.

Of course, the sampling probabilities estimated from the Paleobiology Database could

conceivably be too low, because the Database includes only a sample of available collections. Other estimates of sampling probability are roughly compatible with these, however. Foote and Sepkoski (1999) reported estimates per genus per 5 Myr ranging from less than 0.1 to nearly 1.0, with many higher taxa having per-genus sampling probabilities near 0.5, namely Porifera, Anthozoa, Crinoidea, Echinoidea, Gastropoda, Bivalvia, and Ostracoda. Thus we should not be surprised if half or more of all genera make a last appearance in one of the stages leading up to their stage of true extinction.

3. Concordance between Empirical and Model Results.—Previous studies (Foote 2001a, 2003; Crampton et al. 2006a) have shown that the sampling probabilities estimated from the optimization approach tend to be broadly correlated with those estimated from independent sources and different methods. This lends additional credence to the entire optimization effort.

In summary, we expect some degree of offset between extinction and last appearance; empirically calibrated sampling probabilities suggest that offsets of a stage or more are quite plausible; and the optimization approach yields sampling probabilities that agree with independent calibrations. That global extinction rates were at or near zero for extended periods of time may seem incredible at first, but a priori arguments for backsmearing and empirical calibration of sampling probabilities suggest that it should not be dismissed out of hand and in fact may be more reasonable than the face-value model.

Discussion

The principal argument of this paper is that the history of extinction in the marine realm has been much more volatile over the course of the Phanerozoic than would be suggested by the face-value data. One aspect of this volatility is that new extinction excursions are evident that are not seen in the face-value model, for example in the Carboniferous (Fig. 3). More generally, quiescent intervals of little or no global extinction are punctuated by major events that are more severe than is generally thought to be the case. The extinctions asso-

ciated with these events are smeared back by incomplete sampling (Signor and Lipps 1982) to give the spurious appearance of a smoother history of extinction. This may in turn imply that the driving mechanisms of extinction are less frequent and more intense than suggested by the face-value model. The idea of quiescence punctuated by major extinctions is not new (Boucot 1983; Brett and Baird 1995; Sheehan 1996), but the model put forth here represents a more extreme version of this idea than is generally entertained.

The inference of significant backsmearing is by no means forced by the method. It is possible in principle for optimized extinction rates to be less variable than face-value rates, provided that sampling variability is the most important source of bias (e.g., Foote 2001: Fig. 3).

The reality of major extinction events has of course been questioned before (see MacLeod et al. 1997; Smith 2001; Smith et al. 2001; and Peters and Foote 2002 for just few examples). For the most part, however, it is not the major peaks that are at issue in this study, but rather the stages leading up to them. One interesting exception to this generalization is the Aptian, which has an extinction peak in the face-value model but not in the optimized model. The Aptian happens to be one of the stages singled out by Smith et al. (2001) as suspect on the basis of the biasing effects of sea level variation. A number of other peaks that are suspect according to Smith (2001), however, turn out to be evident even in the optimized extinction model; these include the end-Jurassic, end-Cretaceous, and end-Eocene events. Many inferences based on the major peaks, for example the periodicity of extinction (Raup and Sepkoski 1984, 1986), should not depend critically on which extinction model is adopted.

In contrast to the robustness of the major extinction peaks, conclusions that rest on the more subtle details of the timing of first and last appearances may need revision. For example, Lu et al. (2006; see also Foote 2003) have already used the optimized model to argue that a supposed lag between extinction events and origination events (Kirchner and Weil 2000) may well be an artifact of the for-

ward smearing of originations and backward smearing of extinctions.

Because the proposed extinction model includes many stages with little or no global extinction of genera, it is worth asking about rates and patterns of regional extinction and species-level extinction that are compatible with the model. There is abundant evidence that more broadly distributed genera are more likely to survive an extinction event, even one with a global reach (see Jablonski 2005). As long as a widespread genus survives somewhere, it can potentially endure substantial ecosystem perturbations on a regional scale. There is a complication here, however. Just as range-size distributions of living species tend to be skewed toward species with narrower ranges (see Gaston 2003 for an overview), many fossil genera are endemic. For example, Miller (1997: Fig. 3) found that a large plurality of Ordovician genera are confined to a single paleocontinent. For an endemic genus, regional extinction is effectively equivalent to global extinction. If endemics are quite common, and if many time intervals had little if any global extinction, then it follows that these intervals probably had little regional extinction as well.

Turning to the species level, a widely cited model of the frequency distribution of extinction rates is Raup's (1991) Kill Curve. Like the genus-level model proposed here, the Kill Curve is highly skewed, with a few large events that punctuate stretches of time characterized by low extinction probability (Raup 1991; see also Foote 1994: Fig. 4). The Kill Curve was motivated in part to explain the extreme variability in the slopes of genus-level cohort survivorship curves, but these in turn were based on the face-value genus data. Integrated over the length of a typical stratigraphic stage, the Kill Curve generally yields enough species-level extinction to extirpate some genera. The more volatile genus-level model proposed here would lead to a species-level extinction model in much the same spirit as the Kill Curve, but with an even greater disparity between background turnover and extinction pulses.

Summary

1. Consideration of incomplete and variable sampling suggests that apparent global extinction of marine animal genera in many Phanerozoic stages is greatly exaggerated by backsmearing of true extinction events in subsequent stages. Some 20% of stages, mainly in the latter half of the Phanerozoic, may have had true extinction rates at or near zero.

2. The history of extinction is more volatile than would be suggested by taking last appearances as equivalent to extinctions. If incomplete sampling is taken into account, an alternative model emerges in which longer intervals of quiescence are punctuated by more extreme extinction events.

3. The alternative model is supported by empirically scaled sampling probabilities, which predict that a high proportion of genera have offsets of one or more stages between extinction and last appearance.

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Appendix

Sensitivity Analyses

Appendix Figures A1–A4 present results using alternative protocols from those described in the main text. See figure legends for comments and explanations.

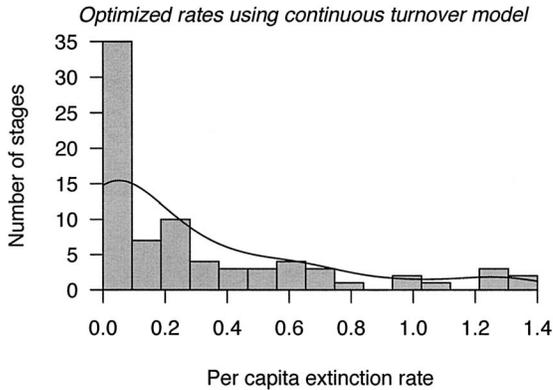


FIGURE A1. Histogram and KDE of optimized extinction rates obtained with the continuous turnover model. Note that there are even more zeroes and higher variance than with the pulsed turnover model. The pulsed model is therefore conservative.

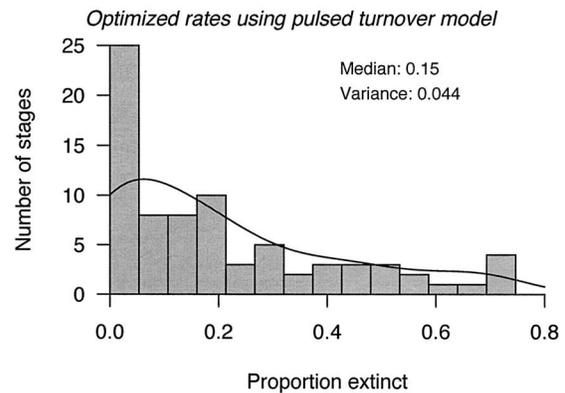
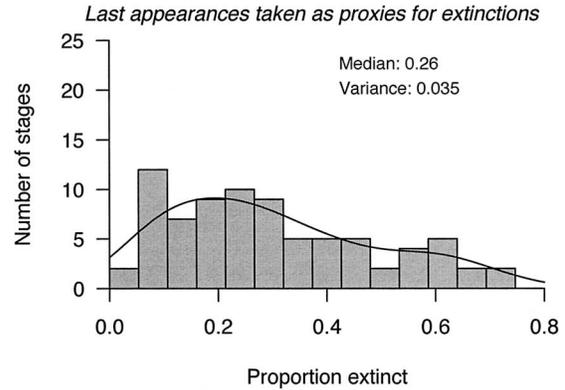


FIGURE A2. Histograms and KDEs of face-value and optimized extinction rates, using proportional extinction (total extinctions divided by total genera). The difference between the two models is at least as striking with this measure of extinction as with the per capita rate. Note that, for the optimized model, there is a simple monotonic transformation between proportional extinction (PE) and per capita extinction rate per stage (q): $PE = 1 - e^{-q}$. For the face-value model, there is no simple relationship between the two extinction metrics, because, with empirical data, single-stage genera may contribute substantially to PE , largely accounting for the higher average in the face-value model, but they play no role in the calculation of q (Foote 2000a). It is therefore probable that we are seeing here, in contrast to Figures 2 and 4, another manifestation of the distorting effect of singletons (Alroy 1998, 2000; Foote 2000a).

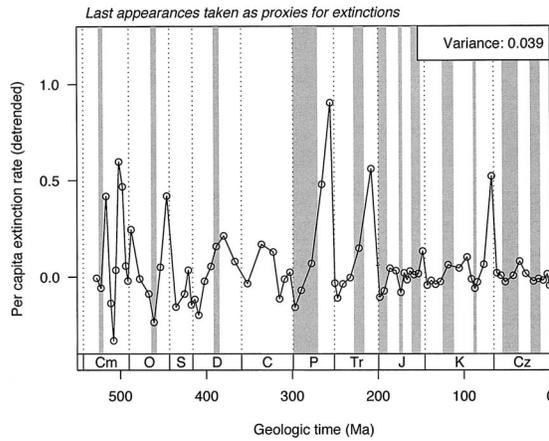


FIGURE A3. Detrended per capita extinction rates under the face-value model. A single exponential function is fitted to the rates in Figure 1; this has the form $q = 0.590 \exp[-0.00426(t_0 - t)]$, where t is the age at the stage midpoint and t_0 is the age at the base of the Cambrian (based on Gradstein et al. 2004; Bowring and Erwin 1998). The product-moment correlation coefficient is 0.73. The residuals, plotted here, have a variance of 0.039. See Figure A4 for further discussion.

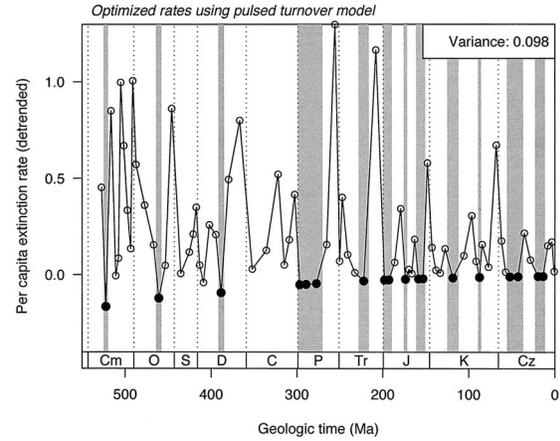


FIGURE A4. Detrended per capita extinction rates under the optimized model. A single exponential function is fitted to the rates in Figure 3; this has the form $q = 0.251 \exp[-0.00642(t_0 - t)]$ (see Fig. A3). The product-moment correlation coefficient is 0.42. The residuals, plotted here, have a variance of 0.098. Closed symbols correspond to those of Figure 3. The secular trend is stronger with face-value rates; i.e., a greater proportion of the total variance is attributable to the secular trend. The difference in variance between the two models is therefore even greater when the data are detrended (cf. Figures 2 and 4), and the decision not to detrend in the main analysis is conservative. Major features of detrending, in particular the higher correlation coefficient of the regression and lower variance of the residuals for the face-value model, are similar if the secular decline is fitted with a linear rather than an exponential function, or with separate exponential functions for the Paleozoic and post-Paleozoic (Peters and Foote 2002) (additional results not presented).