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Periodicity of Extinctions in the Geologic Past: Deterministic Versus Stochastic Explanations

Abstract. The temporal spacing and the magnitude of major extinctions over the past 250 and 570 million years, based on the use of different metrics of extinction probability, are analyzed by comparing deterministic and stochastic explanations. The best-fitting time series model is a stochastic autoregressive model that displays a pseudoperiodic behavior with a cycle length of 31 million years for the past 250 million years, regardless of the metric of extinction probability. The periodicity lengthens and weakens when the analysis is extended to the entire Phanerozoic. The history of the probability of extinction for the entire Phanerozoic, based on time series analysis, does not support the reported bipartite distribution of Van Valen. Rather, the probability of extinction has decreased uniformly over Phanerozoic time whereas the inertia or stability of the biotic system after the Late Permian crisis has increased.

The probability of extinction is known to have been nonconstant over geologic time (1). Fischer and Arthur (2) proposed that major extinction events (3) have occurred periodically. Raup and Sepkoski (4) recently applied statistical tests for periodicity to a data set of 567 extinct marine families whose origination and extinction times can be resolved to a geologic stage (mean duration, 6.2 million years). These analyses, restricted to the window of geologic time from 253 to 11.3 million years ago, identified 12 extinction peaks whose temporal spacing was significantly periodic at 26 million years. Raup and Sepkoski interpreted these results as a signal of an unknown event that appears uniformly and suggested astrophysical causes.

The periodicity described by Raup and Sepkoski compels attention. Our objectives are threefold: (i) to broaden the statistical analysis and thereby the interpretation of these data by comparing deterministic versus stochastic explanations, including models with and without external forcing functions; (ii) to focus on a neglected aspect of the data-namely, the striking feature that the magnitude of extinction peaks varies from 7.6 to 66.3 percent; and (iii) to broaden the empirical support by applying these alternative models to Van Valen's metrics (5), which differ substantially in the method of calculating the probability of extinction.

An observed periodicity in a given time series, evidenced as a peak in the spectrum or autocorrelation function of the series, could be the result of three very different causes (6): (i) a determinis-

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tic impulse which affects the evolution of the series only at specific times with fixed periodicity; (ii) a deterministic cycle in which some external variable follows a periodic wave which affects the evolution of the series; or (iii) a stochastic dynamic system (the stochastic behavior may be the result of multiple unknown causal factors operating to produce the observed series). In the first two cases, the periodic behavior observed can only be explained as a result of the effect of some exogenous variable. In the third case, to restrict our search to an external cause may be misleading, whereas attention to the internal structure of the system might increase our understanding of the observed behavior.

To test these alternatives statistically, we have first applied a series of models

to the data of Raup and Sepkoski. The results are summarized in Table 1. Model 1A represents the series modeled as a response to a deterministic impulse function. The parameter value that takes into account this deterministic effect is not significant. To allow for the observed autocorrelation in the series, model 1B adds a stochastic term. Although the capacity of explanation of the model increases, this is not due to the deterministic component which is still not significant. We also checked the presence of deterministic sinusoidal components fitting autoregressive-integrated-movingaverage (ARIMA) models (6) that allow for cancellation of the roots in the autoregressive polynomials (7), but we have not detected any indication of this kind of behavior. Model 2 is the best stochastic representation of the series, based on the use of ARIMA time-series models, that we have obtained and displays periodic (pseudoperiodic) behavior (8). This model is a fifth-order autoregressive model, that is, a model in which the current value of the series is explained as a linear combination of its values in the five previous periods. In this case, the parameter values obtained from maximum likelihood estimation are such that they produce pseudocyclic behavior. To test robustness to the apparent outlying observation (the Late Cretaceous extinction event), we also fitted the models using intervention analysis (9). These conclusions were also robust, and model 3 represents the best-fitted model. Although such an intervention model has a greatly increased capacity of explanation $(R^2 = 0.71)$, taking into account this effective outlier does not change the basic pseudoperiodic behavior referred to above. Figure 1 illustrates the observed series, including the variable magnitudes

Table 1. Models for the Late Permian-Middle Miocene time series of extinction probability, using the Raup-Sepkoski metric (4). Abbreviations: B is the backshift operator $B^k Y_t = Y_t$ and $\nabla = 1 - B$ is the difference operator; Y_t is the observed series; X_t is some deterministic series of zeros and ones with the ones separated by five stages; a_t is a white-noise process of uncorrelated variables with zero mean and constant variance. The parenthetical numbers under the estimated parameters are the t-statistics for these parameters. Q is the Ljung-Box statistic (11 degrees of freedom); δ is the residual estimated variance of the model; R^2 is the percentage of explained sum of squares; and I is an intervention variable that takes the value 1.0 in period 30 (Late Cretaceous) and 0 elsewhere.

Estimated model	Q(11)	δ_a^2	R^2
1A. $Y_t = 16.88 + 4.5 X_t + a_t$ (6.82) (0.82)	19.6	190.0 (169.5)	0.02
1B. $Y_t = 16.7 - 1.29 X_t + (1 - 0.32B)^{-1}a_t$ (5.62) (0.29) (2.33)	10.0	145.0	0.25
2. $(1 + 0.66B + 0.56B^2 + 0.71B^3 + 0.38B^4) \nabla Y_t = a_t$ (4.2) (3.8) (4.6) (2.56)	6.2	122.8	0.45
3. $Y_t = 42.68I_{30} + \frac{a_t}{\nabla(1 + 0.32B + 0.56B^2 + 0.45B^3 + 0.22B^4)}$	4.1	63.65	0.71
(6.71) (1.94) (3.75) (2.71) (1.55)			

of extinction peaks, and the predicted or the explained part of the series based on the use of model 3.

The results shown in Table 1 demonstrate that the deterministic impulse model, model 1, provides the poorest fit to the data, even when a stochastic component is added. This result is not surprising in light of the fact that the time series of extinction probability is nonstationary (that is, no fixed mean), and there are both peaks of heightened probability of extinction and peaks of diminished probability of extinction; such data are in contradiction with model 1. Results for the second type of model, model 1B, assuming a fixed component of periodicity, also indicate a poor fit. These results suggest that the periodicity, if present, is changing in amplitude or phase, or both, and consequently cannot be adequately modeled by deterministic components. The best-fitting model for the series is the stochastic dynamic model, model 2 (and 3), with a dominant periodicity at 31 million years (8). To test the robustness of these conclusions, we also repeated the analysis with both a logit transformation and logarithm transformation for the series. In both cases the conclusions were the same.

These results indicate that neither the deterministic impulse explanation nor the fixed cycle wave provides a consistent representation of the observed periodicity in both timing and magnitude of extinction. Hence, a hypothesis of strict determinism is rejected by the data. The



Fig. 1. The observed time series of extinction probability (solid line) based on the Raup-Sepkoski (4) metric and the explanation of the series provided by model 3, Table 1 (dashed line). There are 39 geologic stages extending from the Late Permian to the Middle Miocene representing the interval of geologic time from 253 to 11.3 million years.

observed series can be represented adequately by an autoregressive process that displays a pseudoperiodic behavior. This strongly supports an interpretation that the history of extinction was a dynamic phenomenon.

We also would like to point out that endogenous periodic oscillations are a characteristic feature of equilibrium systems such as the system previously described for the diversification history of family-level taxa (10, 11). The simple logistic equation of diversification (11) can generate periodic behaviors in the known absence of an external forcing function. The resultant periodicity in the rate of extinction is regular in temporal spacing but can be either homogeneous or nonhomogeneous in the magnitude of the extinction peaks (12). Consequently, periodicity in a time series is insufficient evidence that a periodic external force is causally responsible. Causality must be evaluated with independent evidence, such as the iridium anomaly coincident with the Late Cretaceous peak (13).

There is also some empirical support for such an interpretation. We have compiled origination data to complement the Raup-Sepkoski extinction data. The most obvious feature of the origination data are two "origination bumps" following the massive Late Permian and Late Cretaceous extinction events; these bumps suggest that the severity of these extinctions allowed the rate of successful originations to substantially increase in the lagged recovery periods. If successful origination rate is depressed when diversity is high but is enhanced when diversity is low, then waves in extinction are predicted (14). Such waves would persist indefinitely if all families had the same duration, but, since duration times are variable, such waves would dampen. We suggest only that the interrelationship between origination and extinction bears additional analysis.

To further investigate the source of the detected pseudoperiodicity, we next analyzed the series using Van Valen's (5) metric of extinction probability. The denominator (taxa at risk) in the Raup-Sepkoski data set excludes all marine

Table 2. Models for the entire Phanerozoic time series of extinction probability, based on the use of the Van Valen metric (5). P_1 refers to probabilities of extinction per stage; P_2 refers to the same probabilities normalized for stage interval length; *T* is the number of stages; and *d* is the damping factor of the cycle. Other abbreviations are explained in Table 1.

Model	Variance	R^2	Comments
p	art A	0.71	
1. $(1 + 0.38B + 0.44B^2 + 0.24B^3 + 0.30B^3) \lor \ln P_1 = -0.144 + a_t$ (3.0) (3.3) (1.8) (2.3) (1.9)	0.399	0.71	Cycles of $T = 5.4/, d = 0.75$ T = 8, d = 0.72
2. $\nabla \ln P_1 = -0.044 + (1 - 0.49B - 0.51B^2) a_t$ (9.1) (4.6) (4.9)	0.376	0.73	No cycles
3. $\ln P_1 = 3.64 - 0.04t + (1 + 0.50B) a_t$ (14.2) (9.8) (5.0)	0.371	0.74	No cycles
4. $(1 + 0.46B + 0.31B^2 + 0.22B^3 + 0.24B^4)$ $\forall \ln P_2 = -0.102 + a_r$ (4.1) (2.6) (1.8) (2.1)	0.481	0.57	Cycles T = 5.65, d = 0.75 T = 9.46, d = 0.69
5. $\nabla \ln P_2 = -0.04 + (1 - 0.49B - 0.17B^2) a_t$ (1.4) (4.4) (1.5)	0.481	0.57	No cycles
6. $\ln P_2 = \frac{1.41 - 0.035t}{(5.0)} + \frac{1}{(1 - 0.45B)} a_t$ (4.2)	0.435	0.61	No cycles
I	Part B		×
First division: $\ln P_2 = 1.71 - 0.064t + (1 - 0.17B)^{-1}a_t$ Paleozoic (7.5) (6.1) (1.0)	0.267	0.61	4
Second division: $\ln P_2 = 0.914 - 0.063t + (1 - 0.38B)^{-1}a_t$ Mesozoic-Cenozoic (2.3) (6.0) (2.5)	0.408	0.64	
Total $\ln P_2 = 1.75 - 0.066t + 1.67I_t + (1 - 0.30B)^{-1}$ (8.2) (8.2) (4.6) (2.8)	$a_t = 0.348$	0.69	

families that persist beyond the Middle Miocene. Such a restriction is substantial. For example, the Raup-Sepkoski data set excludes 64.9 percent of the Mesozoic-Cenozoic Bivalvia families, 83.3 percent of the Mesogastropoda families, and 95.4 percent of the Neogastropoda families despite Sepkoski's (15) demonstration that Bivalvia and Gastropoda are the dominant components of the Mesozoic-Cenozoic record of marine life. Such omissions are potentially significant when one is interested in drawing general conclusions regarding the history of life. Moreover, by causing the denominator to become increasingly small, one runs a risk that noise may be greatly magnified. Van Valen's denominator, by contrast, includes nonextinct families and thereby provides a means of determining if the observed periodicity is robust to the metric of extinction probability.

The results of these analyses (restricted for comparison to the Late Permian-Middle Miocene interval) indicate that the stochastic autoregressive model continues to provide the best fit. The periodicity is still present and with the same cycle length of 31 million years when the Van Valen metric is substituted. Interestingly, the capacity of explanation of the stochastic autoregressive process increases significantly from $R^2 = 0.45$ with the Raup-Sepkoski metric to $R^2 = 0.71$ (0.70 if the data are normalized by stage length) when the Van Valen metric is used. The model is globally less robust, however. Deletion of the first observation (the Late Permian extinction event) results in a second-order moving-average model, with no cycle at all, providing an almost equally good representation of the data (16). This tendency is even more clear when the data are normalized by length of the stage interval.

Raup and Sepkoski (4) reported that periodicity was not detectable if the time window was expanded to include the \sim 350 million years of the Paleozoic. To determine if this conclusion was robust, we expanded the series to examine the entire Phanerozoic record using Van Valen's metric. Cyclicity in extinction probability is demonstrable. Time-series analysis with stochastic autoregressive models results in longer cycles (T = 5.47stages, model 1, Table 2A, or T = 5.65stages, model 4, Table 2A, if extinction probability is normalized by stage length). Models with fewer parameters (models 2, 3, 5, and 6, Table 2A), however, provide better fits and lack cycles. Such findings underscore Raup and Sepkoski's contention that the periodicity is best observed when geologic time is restricted to the Late Permian (Dzhulfian)-Middle Miocene interval. We have shown that this generalization is true regardless of whether deterministic or stochastic models are used. Within this interval of geologic time, however, the periodicity determined with the use of stochastic models remains fixed at 31 million years, regardless of the alternative metrics of extinction probability.

Van Valen's (5) major contention, utilizing the entire Phanerozoic record, was that the probabilities of extinction had a bipartite distribution: the probability of extinction decreased regularly throughout two divisions of the Phanerozoic (the Paleozoic and the Mesozoic-Cenozoic), but the slope of this decrease was higher in the latter division. Van Valen obtained this result by fitting regression lines to each division of the Phanerozoic. Because these data are strongly autocorrelated, a time-series analysis is more appropriate and yields quite different results. Model 3 (Table 2A) indicates that the entire Phanerozoic series (17) can be well represented as the addition of a decreasing linear trend and an autocorrelated component. Similar effects are shown when the data are normalized. Table 2B shows the result of applying a covariance analysis of the time series to test if the deterministic component that represents the rate of decrease in the probability of extinction is actually the same for both divisions. The two slopes estimated are the same (0.064). Hence, there is no doubt about the permanency of the observed decrease, a finding contrary to Van Valen's principal result. Such a decrease is consistent, however, with the result of an earlier report by Raup and Sepkoski (18) and their speculation of progressive change in evolutionary dynamics. What is also observed is that the autoregressive component that measures the inertia of the system increases when one compares the first division of Phanerozoic time to the second, indicating more stable biotic responses to post-Paleozoic environments. The history of the probability of extinction for the entire Phanerozoic consequently can be modeled as the sum of three terms: (i) an exponential decrease in the probability of extinction that occurs uniformly over the whole Phanerozoic, with a relative reduction of 6.6 percent per stage; (ii) a step-effect, which describes an event in the Late Permian that produced a substantial increase in the probability of extinction; and (iii) a stochastic component that reflects the inertia in the system and follows a first-order model.

In summary, our results show that a stochastic autoregressive process provides a better description than a deterministic process of the pseudoperiodicity in temporal spacing of extinction peaks and the variability in their magnitudes. Consequently, we must broaden our attention to include endogenous causes of periodicity, and we must continue the search for independent evidence of exogenous causes. Second, we have shown that the periodicity is robust to an alternate metric of extinction probability but steadily weakens when the series is normalized by stage interval length or is extended to include the whole Phanerozoic. However, the entire Phanerozoic record can be well represented as the net effect of an exponentially decreasing rate of extinction plus an autocorrelated component. Third, the hypothesis suggested in the literature (5) of a change in the deterministic decrease of the rate of extinction has been tested and rejected and a model has been built that allows a simpler interpretation of the evolution of life. Over Phanerozoic time, the slope of extinction rate has remained constant, whereas-as evidenced by increased autocorrelation-the stability of the biotic system has increased.

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Covariance Patterns of Foraminiferal δ^{18} O: An Evaluation of Pliocene Ice Volume Changes Near 3.2 Million Years Ago

Abstract. Oxygen isotope data for a Pliocene interval from 3.6 to 2.8 million years ago show a mean increase (0.5 per mil) of benthic $\delta^{18}O$ at about 3.2 million years ago, whereas planktic $\delta^{18}O$ does not increase. This lack of covariance indicates that the event at 3.2 million years did not result in a permanent increase in the ice budget of either the Northern or the Southern Hemisphere.

The history of continental ice sheets and their effect on the composition and climates of the ocean is a pervasive theme in paleoceanography. For example, within the Neogene, much of the evidence for the magnitude and timing of the initiation of major ice sheets in the Northern Hemisphere has come from analysis of the stratigraphy of ice-rafted deep-sea sediments (1, 2) and increased δ^{18} O of benthic foraminifera (3, 4). Although the first major glaciation in the Northern Hemisphere has traditionally been placed in the Pliocene (5), some investigators have suggested that ice sheets were present as early as the late Miocene (6). In this report I examine the oxygen isotope evidence for major glaciation at 3.2 million years ago (Ma) a date often cited for the initiation of Northern Hemisphere glaciation (1-5).

Prior to the availability of Deep Sea Drilling Project (DSDP) hydraulic piston cores, the highest quality oxygen isotopic record relevant to the question of Pliocene glaciation was that of core V28-179 from the equatorial Pacific (7). At approximately 3.2 Ma, this record contains a steplike increase of about 0.4 per mil in the average δ^{18} O of benthic foraminifera. This baseline shift separates an interval of low variability and relatively low isotopic values, called the "preglacial" Pliocene, from an interval of higher and variable isotopic values (the "glacial'' Pliocene) (7). The increased δ^{18} O values were interpreted to indicate increased δ^{18} O of the ocean due to the presumed initiation of Northern Hemisphere ice volume. With one apparent exception (2), this pattern of benthic δ^{18} O is widely observed in all oceans (3, 4). A subsequent increase in the mean δ^{18} O at about 2.4 Ma has recently been



Fig. 1. Schematic records of planktic (P) and benthic (B) for a miniferal δ^{18} O. A steplike change in mean δ^{18} O is imposed on the normal variability, which is simulated by frequency components that are observed in paleoceanographic data. The low-latitude planktic record is simulated by a combination of 0.023-Ma (precession) and 0.041-Ma (tilt) cycles. The benthic record is simulated by the 0.041-Ma tilt cycle, which is predominant at high latitudes. Comparison of the P and B records shows the patterns expected from an increase in ice volume (a), a decrease in sea-surface temperature (b), and a decrease in bottomwater temperature (c). The pattern of covariation of P and B records allows one to distinguish between ice volume changes and other processes.

correlated with the onset of major ice rafting on Rockall Bank in the North Atlantic (2, 7). This 2.4-Ma isotopic event is also clearly recorded, although with lower amplitude, in a detailed planktic isotopic record from the equatorial Pacific (DSDP site 572) (8).

If these mean δ^{18} O increases (9) do represent a greater average volume of continental ice sheets, the isotopic composition of the entire ocean should be increased. Therefore, the change in mean $\delta^{18} O$ observed in benthic records should also be observed in the average $\delta^{18}O$ of surface-dwelling planktic foraminifera. At the 2.4-Ma event, the planktic and benthic δ^{18} O records do covary. However, preliminary data suggest that planktic and benthic δ^{18} O data do not covary across the 3.2-Ma event. I examine here simple models of foraminiferal isotopic variations and new data to identify the pattern of covariation between the planktic and benthic δ^{18} O data before and after 3.2 Ma.

Conceptual models for the expected covariation between low-latitude benthic and planktic δ^{18} O records are shown in Fig. 1 for three plausible changes in the ocean-climate system. An increase in oceanic δ^{18} O, due to increased ice volume, would increase both records equally, yielding covariation (Fig. 1a). A decrease in local sea-surface temperature would increase planktic δ^{18} O but would not affect the benthic δ^{18} O record (Fig. 1b). A decrease in bottom-water temperature would increase the benthic δ^{18} O but would not affect the planktic record (Fig. 1c). The δ^{18} O effect of these various processes may be estimated at about 0.23 per mil per degree Celsius (10), 0.11 per mil per 10 m sea level equivalent (11), and 0.11 to 0.29 per mil of salinity (12). Hence, the relative amplitude of these processes can be considered in the context of the three conceptual patterns of planktic-benthic δ^{18} O covariation.

To define the degree and pattern of benthic-planktic δ^{18} O covariance in the "preglacial" to "glacial" Pliocene, I compared isotopic time series over the interval from 3.6 to 2.8 Ma. This 0.8million-vear interval includes a significant length of record before and after the 3.2-Ma event so that reliable statistics can be calculated to characterize changes in the mean δ^{18} O. Figure 2 compares a representative benthic record (core V28-179) with planktic records from DSDP site 502 (Caribbean Sea), DSDP site 572 (equatorial Pacific), DSDP site 573 (equatorial Pacific), V28-179 (equatorial Pacific), and V20-163 (Indian Ocean) (13). All isotopic data were generated in the Benedum Stable Isotope