Evidence for periodicity and nonlinearity in a high-resolution fossil record of long-term evolution

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ABSTRACT
The application of new signal analysis techniques provides increased insight into the study of the fossil record and processes of evolution. The fossil record of 622 planktic foraminifera contains data from 200 stratigraphic stages of the past 127 m.y. Time-series analyses (wavelet and Fourier transform) of the planktic foraminifera fossil record were used to discern periodic components in long-term evolution. The correlation function analysis was used to distinguish between random and deterministic behavior of the fossil record. The analyses show that stationary ~30 m.y. periodicity and complex deterministic patterns occur in the long-term planktic foraminifera evolution, in particular in the extinction record. Our results suggest that the occurrence of intense diversity fluctuations with ~3-10 m.y. periodicity after major extinction events may be attributed to nonlinear, self-organized evolutionary response to the availability of new ecospace. This coupled nonlinear-periodic scenario may explain the repetitive appearance of similar morphotypes in ~30 m.y. intervals.

Keywords: foraminifera, evolution, fossil record, periodicity, self organization.

INTRODUCTION
Two ideas regarding the interpretation of the fossil record and mechanisms of long-term evolution have been contended topics during the past two decades. Catastrophic models explain evolution, especially mass extinction, as being forced by 26-35 m.y. periodic events, such as bolide impacts (e.g., Rampino and Stothers, 1986; Raup, 1992) or terrestrial events such as sea-level changes, flood basalt volcanism, and magnetic field reversals (e.g., Hallam, 1989; Stothers, 1986, 1993). Alternatively (e.g., Bak et al., 1988; Plotnick and McKinney, 1993), nonlinear models based on self organization describe ecosystems as highly cross-linked webs supporting only a restricted number of species. Internally generated instabilities may cause extinctions to propagate through the ecosystem opening habitats to persistent forms, which radiate rapidly. Such self-organized systems produce naturally organized patterns and series that are deterministic, not random.

We chose to study long-term evolution using the planktic foraminiferal fossil record because (1) planktic foraminifera are widely distributed and well preserved in marine rocks, (2) their abundance is relatively high even in small samples, and (3) an extensive, well-established database exists (e.g., Bolli et al., 1989; Hart, 1990; Kennett and Srinivasan, 1983; Pearson, 1998). The planktic foraminifera evolutionary record utilized here comprises 622 species recording extinction and origination events in 200 stratigraphic levels from Barremian to Holocene, and is an update of the study of Patterson and Fowler (1996). The complete record used for this study is available as a downloadable biostratigraphic chart in pdf-format at: http://www.carleton.ca/~t-patters. Relative planktic foraminifera extinction is calculated by division of the number of species that became extinct during a stratigraphic interval with the total number of species at the previous level. Relative planktic foraminifera origination is calculated in a similar manner. The relative planktic foraminifera diversity change/m.y. is calculated from the difference in the 1 m.y. average of species diversity of two successive zones divided by the total number of species at the beginning of the 1 m.y. time interval.

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For determination of the stationarity and wavelength of periodicity, and long-term secular trends in the planktic foraminifera record, we use the continuous wavelet transform (e.g., Rioul and Vetterli, 1991) (Appendix 1) and Fourier analysis (e.g., Davis, 1986). The coefficients of the wavelet transform are coded in four levels of gray, and allow the tracing of periodicities as dark gray or black bands in the scalograms through geological time series. In this way, possible discontinuities in periodicity can be detected and localized (Prokoph and Barthelmes, 1996). Equidistant data entries at 1 m.y. intervals were taken for Fourier analysis, while wavelet transform can process the original, unevenly spaced fossil record.

PERIODICITY IN THE FOSSIL RECORD
The conspicuous dark gray horizontal bands (Fig. 1A and 1F) in the wavelet scalograms represent high wavelet coefficients for stationary ~30 m.y. periodicity of planktic foraminifera diversity (Fig. 1B) and relative diversity changes/m.y. (Fig. 1E).

Additional pronounced ~4.7 m.y. and 10 m.y. periodicities (gray bands in Fig. 1F) are apparent from the Aptian-Albian and Campanian to Eocene, respectively. The gray patches at wavelengths at ~3 m.y. in the scalograms of Figure 1 (A and F) correspond to the sharp reduction in planktic foraminifera diversity at the Cretaceous-Tertiary (K-T) boundary, and strong diversity increase at early Aptian and Miocene.

Fourier analysis of the relative planktic foraminifera extinction (Fig. 2A and 2B) and origination data (Fig. 2C and 2D) reveals that only the power of ~31 m.y. periodicity is above the red and white noise level calculated after the method of Mann and Lees (1996). The spectral power of the ~31 m.y. periodicity remains significant above the noise levels even after removal of data associated with the extremely high mass extinction and the subsequent speciation burst from the K-T event (ca. 65 Ma) (Fig. 2B and 2D). The strong ~3 m.y. and the weaker 4.7-4.9 m.y. and 10-15 m.y. periodicities in the fossil record may coincide with relative high planktic foraminifera speciation and extinction rates during the Paleocene (Fig. 1C and 1D). During that interval extinct planktic foraminifera species were often replaced by newly originated species of similar morphotypes in <1 m.y. (Hart, 1990). The 3.2 m.y. period also remains in the planktic foraminifera extinction record after removal of the K-T boundary event data (Fig. 2B). Consequently, the major planktic foraminifera extinction event at the K-T boundary was not necessary to retain the observed ~30 m.y. and ~3 m.y. periodicity in the fossil record.

A plot of shuffled relative planktic foraminifera diversity changes/m.y. (Fig. 3B) was constructed, which preserves the statistical moments and data entries of the original planktic foraminifera diversity change data but is randomized in time. Wavelet and Fourier analysis of this data set indicates that no stationary periodicity such as the ~30 m.y. period can be formed by a random configuration of planktic foraminifera diversity change. Long periods of 30 m.y. and 10 m.y. of the planktic foraminifera record disappeared in the shuffled data set (Fig. 3C). Nonstationary periodicity can appear randomly in some time intervals, in particular for wavelengths <5 m.y. (dark gray and black patches in wavelet scalogram of Fig. 3A), while long periods >20 m.y. are nonstationary and weak (light gray bands in scalogram).

TEST FOR NONLINEARITY
From wavelet and Fourier analysis, we can distinguish an ~30 m.y. periodicity as statistically significant and stationary throughout the past 127 m.y. The question remains whether the nonstationary high-frequency
cyclicity in the planktic foraminifera record is due to randomness (e.g., imperfection of the fossil record and time scale, random evolution at short time intervals) or due to determinism, because wavelet or spectral analysis cannot separate them (e.g., Prokoph and Barthelmes, 1996). Nonlinearity in planktic foraminifera extinction has been suggested based on sequential event size distribution (Patterson and Fowler, 1996) and a 1/1 trend in the power spectra (Sole et al., 1997). Accordingly, we test the planktic foraminifera fossil record, and models that implement nonlinearity, randomness, and periodicity for time, \( t = 1 \)–127 in 1 m.y. intervals.

A periodic forced random model is based on a 30 m.y. periodicity (according to the periodicity in the planktic foraminifera record) coupled with the white noise amplitudes \( F_t \) from 0 and 1 to obtain:

\[
x_t = -0.5 F_t \sin(1/30) + 1. \tag{1}
\]

The random walk model, which adds a memory (red noise) to a random time series

\[
x_{t+1} = 0.5 x_t + F_t, \tag{2}
\]

represents a lag-one memory function of a random process, the white noise \( F_t \) ranging from 0 to 1 to bound the output series between \(-1 \) and 1.

The output series is bound between 0 and 1 and fluctuates between periodic and chaotic behavior (May, 1976).

Our nonlinear model is one of three coupled nonlinear equations used to describe the chaotic, but deterministic character of atmospheric turbulence by Lorenz (1963):

\[
\frac{\Delta x}{\Delta t} = -10x + 10y, \tag{4}
\]

We used 127 data entries with time increments \( \Delta t = 0.01 \) representing a chaotic, steady stage with \( y = \sqrt{8/3(1.2 - 1)}^{0.5} \) (Turcotte, 1997).

The correlation function analysis is used to distinguish between randomness and determinism in time-series data, and can provide the number of parameters controlling the underlying processes (Grassberger and Procaccia, 1983). The attainment of constant values of the correlation dimension \( d \) with changing embedding dimension \( E \) is indicative of deterministic behavior, whereas a continuous increase in \( d \) with \( E \) is indicative of random processes (Appendix 2). The output from the computer generated deterministic and random signals allows us to discriminate signals for small sets and low dimensional systems.

Figure 4 demonstrates that two models (Lorenz equation, periodic forced nonlinear model) and the planktic foraminifera record (relative diversity changes/m.y., relative extinction) all have evidence of stabilization of the dimensionality \( d \), i.e., deterministic behavior. The correlation function technique is very sensitive to sample size (Essex, 1991). However, correlation function analysis can give good approximations estimates for smaller time series, if the major dynamics of the process are completely represented by the data. For example, the Lorenz equation (nonlinear model with one parameter) saturates at \( d = 1 \) with a maximum error range of \(+0.45\) at \( E = 3 \), and the periodic forced nonlinear model saturates at \( d = 2 \) due to a periodic and a nonlinear parameter (Fig. 4).
Even though the planktic foraminifera fossil record is probably the best time series available from the fossil record, the results of correlation function analysis are not unambiguous for relative planktic foraminifera diversity changes/m.y. The saturation at a high dimensionality $d = \sim 6$ (Fig. 4) suggests that complex deterministic behavior is involved in long-term evolution. The planktic foraminifera fossil record is still sparse and the dimensionality is not completely stable, suggesting that some stochastic randomness may be present. However, the shuffled relative planktic foraminifera diversity changes/m.y. output has a strong continuous increase of dimensionality consistent with random behavior (Fig. 4), thus setting its behavior apart from the planktic foraminifera record. The result of correlation function analysis therefore suggests that determinism and not randomness dominates in the evolutionary record. Consequently, the nonstationary periods of $\sim 15$ m.y. in the planktic foraminifera record (Figs. 1 and 2) can be due to complex nonlinearity, and not randomness.

**EXTERNAL VERSUS INTERNAL CONTROL MECHANISMS OF LONG-TERM EVOLUTION**

The $\sim 26$–32 m.y. periodicity in geological events recognized from a 250 m.y. record (Rampino and Caldeira, 1992; Yabushita, 1998) has almost the same periodicity as the planktic foraminifera record. External forcing by periodic sea-level changes (Hart, 1990), bolide impacts (Rampino and Stothers, 1986), or flood basalts (Yabushita, 1998) are all potential control mechanisms for the $\sim 30$ m.y. periodicity of planktic foraminifera evolution. The validity of the $\sim 26$–30 m.y. periodicity of the fossil record has been questioned because of limited statistical significance due to uncertainties of the stage ages, culling of data, preservation constraints, and statistical methods used (e.g., Hoffman, 1989; Benton, 1995). However, our planktic foraminifera database provides a detailed record in comparison to previous mass-extinction studies having 24 stage boundaries from Holocene to the Barremian (Rampino and Caldeira, 1992) or the 2 m.y. time resolution of the planktic foraminifera extinction record (Sole et al., 1997).

Because variations in the time scales used by others over the years vary, the $\sim 30$ m.y. periodicity could coincide with the $\sim 26$–30 m.y. periodicity in the mass-extinction record (e.g., Rampino and Caldeira, 1992; Sepkoski and Raup, 1986). The $\sim 30$ m.y. periodicity is probably also comparable to the $\sim 26$ m.y. periodicity found in the rapidity of the planktic foraminifera origination by Hart (1990). At the current recognizable resolution of geological events and time series recording, nonstationary periodicities of $<15$ m.y. detected in the fossil record cannot be attributed to any periodic external forcing.

Throughout the planktic foraminifera group similar structures and ecology have evolved repeatedly, and appear to be related partly to intrinsic features of the foraminifer genome as well as to the limitations imposed by their existence in a low Reynolds’ number environment (Warhaft, 1998). Planktic foraminifera are good examples of iterative evolution and show only a limited repertoire of phenotype variation (Lipps, 1979). Representative for the influence of external control, some phenotypes, such as forms with a single peripheral keel, are typical invaders of relatively deep water, evolving at $\sim 30$ m.y. intervals from simple globular phenotypes following an oceanic anoxic event (Hart, 1980). In contrast, the iterative evolution following the major extinction events may indicate internal, self-organized control mechanisms.

**CONCLUSION**

Results of our time-series analyses show that persistent $\sim 30$ m.y. periodicity coupled with other deterministic nonlinear processes approximates best the observed dynamics in the planktic foraminifera fossil record. In particular, we suggest the coexistence and possible interaction of externally long term periodic forcing and self organization. In other words, mass extinctions are likely forced by quasiperiodic external events, and the background evolution is self organized but less abrupt. Randomness may have a significant input to evolution only at short time scales. Self organization in planktic foraminifera evolution may dominate after externally forced events with $\sim 30$ m.y. periodicity (e.g., impacts, oceanic anoxic events, flood basalt volcanism) and lead to increased radiation and/or extinction rates and occupation of newly available ecospaces (e.g., deeper water, shelf seas). This coupled nonlinear- periodic scenario may explain the repetitive appearance of similar morphotypes in $\sim 30$ m.y. intervals shortly after major extinction events. Consequently, extraordinarily high planktic foraminifera extinction rates (e.g., K-T boundary) are unlikely to be purely the result of self-organized criticality (Sole et al., 1997). External factors are involved in the periodic pattern of the fossil record of planktic foraminifera, and it is difficult to view long-term evolution as being purely due to external causes, self organization, or randomness.
APPENDIX 1

The continuous wavelet transform performs analyses by convolving the time-series data $f(t)$ using an analyzing function $\Psi$, which has zero integral, is finite, and is centered about zero. The wavelet transform uses narrow analysis windows at short scales, and wide windows at long scales. The results are wavelet coefficients $W_\Psi(a, b)$ of continuous scale $a$ and position (e.g., time) $b$:

$$W_\Psi(a, b) = \frac{1}{a} \int f(t) \overline{\Psi} \left( \frac{t-b}{a} \right) dt. \quad (1)$$

The numerator term $t - b$ slides the analysis window to position $b$. Scaling is provided by variations of $a$, which is comparable to the period or wavelength in spectral analysis (Riou and Vetterli, 1991). The scalogram is a two-dimensional graphic representation of the wavelet coefficients in logarithmic spaced scale (or period) and its location. We used a four-step (0%–25%, 25%–50%, 50%–75%, 75%–100%) gray-level scale for coding the wavelet coefficients. As analyzing function $\Psi$ we use a sinusoidal function overlaid by the Gaussian probability density function, the so-called Morlet wavelet (Grossman and Morlet, 1984):

$$\psi_{a,b}(t) = \frac{1}{\sqrt{\pi a}} e^{-\frac{1}{2} \left( \frac{t-b}{a} \right)^2}.$$ \quad (2)

The parameter $l$ is representative of the relative size of the analyzing window and set to $l = 10$, which provides particularly good resolution in periodicity. Data were standardized to a mean = 0, and a fitted trend line was removed. Edge effects of $W$ were reduced by using zero padding on beginning and ends of the data series. The method was completely explained in Prokoph and Barthelmes (1996).

APPENDIX 2

Correlation function analysis (Grassberger and Procaccia, 1983) is accomplished by transformation of a time series $x(t)$ into an array of $E$-dimensional vectors $X_i$. The method requires evenly spaced data. A data interval $\Delta t = 1$ m.y. used for all data sets corresponds to the mean standard error of the time scale of ±0.5 m.y. (Gradstein et al., 1994). The correlation function $C(r)$ is estimated by:

$$C(r) = \frac{1}{N^2} \sum_{i,j=1}^{N} \theta \left[ r - ab \left| X_i - X_j \right| \right]. \quad (3)$$

with $\theta(x) = 0$ if $x < 0$, $\theta(x) = 1$ if $x > 0$.

Ten values of radius $r$ are used in the range from 0.05 to $2 \times r_{max}$, for each data set. Relatively small $C(r)$ varies approximately as $C(r) = r^{-d}$, implying that the dimensionality $d$ of the attractor is given by the slope of the log $C(r)$ versus log $r$ plot within the restricted range of values of $r$, where log $C(r) \sim d \log r$. $C(r)$ in the range from 0.0013 to 0.15 is used for approximation of $d$, to avoid depopulation regimes (i.e., <20 corelative events) and saturation effects (Fowler and Roach, 1993).

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