

Power spectra of extinction in the fossil record

M. E. J. Newman^{1*} and Gunther J. Eble^{1,2}

¹*Santa Fe Institute, 1399 Hyde Park Road, Santa Fe, NM 87501, USA*

²*Department of Paleobiology, Smithsonian Institution, Washington, DC 20560, USA*

Recent Fourier analyses of fossil extinction data have indicated that the power spectrum of extinction during the Phanerozoic may take the form of $1/f$ noise, a result which, it has been suggested, could be indicative of the presence of ‘critical dynamics’ in the processes giving rise to extinction. In this paper we examine extinction power spectra in some detail, using family-level data from two widely available compilations. We find that although the average form of the power spectrum roughly obeys the $1/f$ law, the spectrum can be represented more accurately by dividing it into two regimes: a low-frequency one which is well fit by an exponential, and a high-frequency one in which it follows a power law with a $1/f^2$ form. We give explanations for the occurrence of each of these behaviours and for the position of the crossover between them.

Keywords: extinction; fossil record; power spectra; Fourier analysis

1. INTRODUCTION

In a recent paper, Solé *et al.* (1997) have studied the power spectra of extinction intensity in the fossil record, using family-level data for the Phanerozoic (approximately the last 550 million years (Myr)) drawn from the compilation by Benton (1993). Such power spectra measure the degree to which extinction at one time is correlated with extinction at another. Intriguingly, Solé *et al.* (1997) find that for a variety of groups of organisms and extinction metrics, the variation of the power spectrum $P(f)$ with frequency f appears to follow a power law:

$$P(f) \sim f^{-\beta}, \quad (1)$$

where the exponent β is in the vicinity of unity. This result has provoked considerable interest, because it indicates that extinction at different times in the fossil record is correlated on arbitrarily long time-scales—that there is some mechanism by which extinction events at all times throughout the Phanerozoic are linked together. This would be a startling discovery if true, because there are no known processes, either biotic or abiotic, which act on time-scales of 100 Myr or greater. The time-scale on which families in the fossil database become extinct and are replaced by new ones ranges from about 30 Myr in the Palaeozoic to about 80 Myr in the Mesozoic and Cenozoic, so one might reasonably expect correlations in the extinction profile to be absent at times longer than this. Solé *et al.* discuss a number of different possible explanations for their results, particularly the idea that long-time correlations in extinction intensities might arise through so-called ‘critical’ processes in the evolution of species.

The results of Solé *et al.* (1997) have, however, been questioned. In a recent paper, Kirchner & Weil (1998)

have argued that the $1/f$ form may be an artefact of the particular method used to calculate the power spectrum. The method used was a combination of the standard Blackman–Tukey autocorrelation technique (Davis 1973) with a linear interpolation scheme, and it appears that this combination generates a $1/f$ spectrum regardless of any correlations in the data. In this paper, therefore, we take a different approach to the power spectrum of fossil extinction, performing a direct Fourier analysis of the fossil data without any intermediate steps. This method should, we believe, be free of the $1/f$ artefacts seen in the Blackman–Tukey method. As we will show, although the overall form of the spectrum calculated in this way roughly obeys equation (1), closer inspection reveals two different regimes, one approximately following an exponential law with no long-time correlations, and one following a steep power law which, we will argue, is a result of the way the power spectrum is calculated rather than an indicator of any real biological effect.

The outline of this paper is as follows: in §2 we describe how the power spectra are calculated; in §3 we give the spectra for a number of different data sets; in §4 we offer an explanation of the form of these spectra; and in §5 we give our conclusions.

2. CALCULATION OF POWER SPECTRA

Extinction intensity can be measured in a variety of different ways. In this paper we use data at the family level, as did Solé *et al.* (1997). This makes a direct comparison with their results more straightforward. Four metrics of extinction are in common use:

- (i) number of families becoming extinct in each stratigraphic stage;
- (ii) number of families becoming extinct in each stratigraphic stage divided by the length of the stage in Myr;

* Author for correspondence.

- (iii) fraction (or equivalently percentage) of families becoming extinct in each stage;
- (iv) fraction of families becoming extinct in each stage divided by the stage length.

Solé *et al.* looked at data for marine and land-dwelling organisms separately, and also combined data covering all organisms. Their data were taken from the compilation by Benton (1993). In the present paper we use data both from the Benton compilation, and also from the compilation by Sepkoski (1992). We concentrate, however, on marine organisms, partly because the marine fossil record is considerably more detailed than the terrestrial one, and partly because Sepkoski's database does not contain data for terrestrial organisms. In both databases the data extend approximately from the start of the Cambrian to the end of the Pliocene. To curb the worst excesses of systematic bias, such as monograph and sampling effects (Raup & Boyajian 1988) the data have been culled of all families which appear in only a single stage. The time-scale used for stage boundaries is essentially that of Harland *et al.* (1990). However, because this time-scale is believed to be in error where some of the earlier stage boundaries are concerned (Bowring *et al.* 1993) we have updated it with corrections kindly supplied by J. J. Sepkoski, Jr and D. H. Erwin. (In fact, we have experimented with a number of different time-scales, with and without these corrections, and find that the principal results of this paper do not depend on which one we use.)

The power spectrum $P(f)$ is defined to be the square of the magnitude of the Fourier transform of the extinction intensity. Denoting extinction intensity as a function of time by $x(t)$, we have

$$P(f) = \left| \int_{t_0}^{t_1} x(t) \exp(-i2\pi ft) dt \right|^2, \quad (2)$$

where t_0 and t_1 are the limits of time over which our data extend. In the case of data such as extinction records which are sampled at discrete time intervals, we should use the discrete version of this equation:

$$P(f) = \left| \sum_{t=t_0}^{t_1} x(t) \exp(-i2\pi ft) \right|^2. \quad (3)$$

In order to generate valid results however, this equation requires extinction data which are evenly spaced over time. The stratigraphic stages are not evenly spaced, so some interpolation scheme is necessary to generate a suitable set of values of $x(t)$. Here we make use of two different schemes. The first is the linear scheme employed by Solé *et al.* (1997), which we have adopted to facilitate comparison with their work. This scheme is a simple linear interpolation to intervals of 1 Myr. In other words, they placed straight lines between the known data points to generate extra points in between at intervals of 1 Myr. Our other interpolation scheme is, in a sense, the scheme which assumes least about the data. In this scheme we assume that we know the number of families becoming extinct in a particular stage, but that we have no more accurate information than this about when exactly during the stage any particular family became extinct. (This in

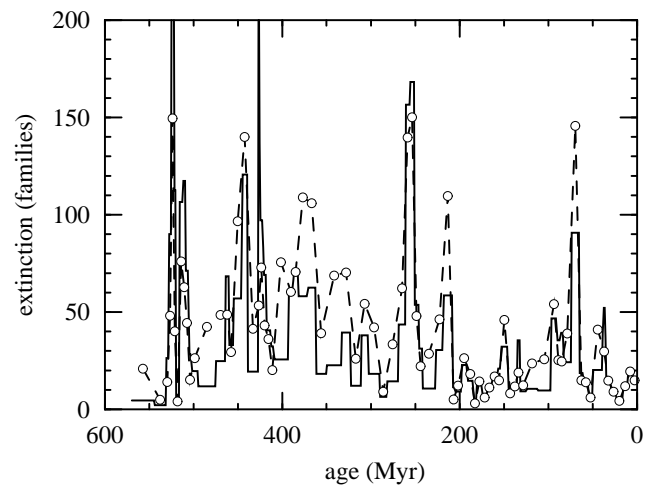


Figure 1. Illustration of the two different interpolation schemes described in the text. The points represent the total number of marine animal families becoming extinct in each of 77 stages, and are positioned at the centre of those stages. The dashed lines are a linear interpolation between them and the solid lines are a result of distributing the extinction events evenly over their corresponding stages.

fact is true; we don't have any more accurate information.) In this case, the best assumption we can make is that the probability of a family becoming extinct is uniformly distributed throughout the corresponding stage. This gives a kind of steplike form to the interpolated extinction data. The two interpolation schemes are illustrated in figure 1.

3. RESULTS FOR POWER SPECTRA

In figure 2 we show the power spectra of fossil extinction, calculated using equation (3), for data taken from the compilation by Sepkoski (1992). In this case we used total extinction as our metric of extinction intensity (number (i) on the list given in § 2), although the results are similar for other metrics. The lower curve makes use of the linear interpolation scheme of Solé *et al.* (1997) and the upper one our own 'flat' interpolation scheme. In both cases the data were interpolated to 1 Myr intervals, just as in the studies of Solé *et al.* As we can see, the two curves are similar in appearance; the choice of interpolation scheme makes little difference to the results, except at very high frequencies. For each curve we have marked with a dotted line the slope expected of a $1/f$ power spectrum. As the figure shows, the average line of the curves follows the $1/f$ form reasonably well, but also displays marked systematic deviations from it, being clearly convex: it is shallower than $1/f$ at low frequencies and steeper than $1/f$ at high frequencies. In fact, at high frequencies the power spectra approximately follow power laws with forms $1/f^2$ and $1/f^4$ for the two different interpolation schemes. (These forms are also marked in figure 2.) In § 4 we propose an explanation of these results.

In figure 3 we show a similar power spectrum for data drawn from the compilation by Benton (1993). In fact, the data used to produce this figure were precisely the data used by Solé *et al.* in their calculations, having been

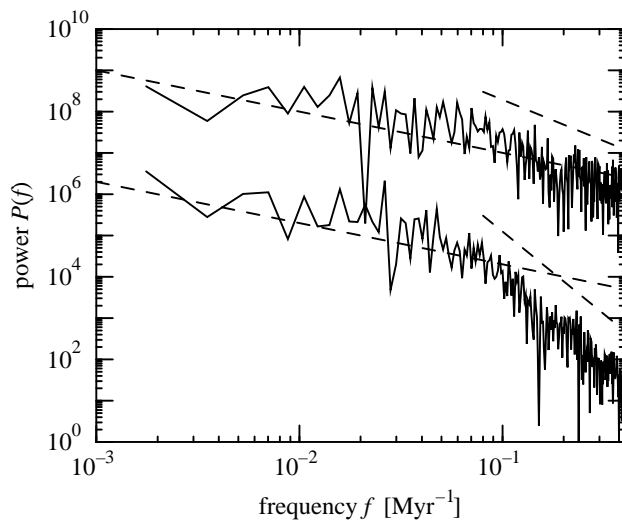


Figure 2. Power spectra of total familial extinction of marine organisms calculated using equation (3) with data drawn from the compilation by Sepkoski (1992). The lower spectrum uses the linear interpolation scheme employed by Solé *et al.* (1997) and the upper one the flat interpolation scheme described in the text. The long dotted lines indicate the form expected for a $1/f$ spectrum. The shorter dotted lines indicate $1/f^2$ (top) and $1/f^4$ (bottom).

kindly provided to us by Ricard Solé who also performed the linear interpolation between the stages to eliminate the possibility of any discrepancy in the way the interpolation was carried out. As figure 3 shows, the spectrum again follows an average $1/f$ form, but is in general shallower than $1/f$ at low frequencies and approximately $1/f^4$ in form at high frequencies.

4. DISCUSSION

Whilst it is true that on average the power spectra of figures 2 and 3 follow a $1/f$ form, we believe that there are clear deviations from this form visible in the figures and that the spectra each possess two distinct regimes, a low frequency regime in which the curve falls off approximately exponentially, and a high frequency one in which it falls off as a relatively steep power law. We now discuss the explanation of each of these regimes.

First, let us look at the high frequency behaviour of the power spectra. Consider the top spectrum in figure 2, which was produced using the flat interpolation scheme outlined in §2. We now demonstrate that the power spectrum of *any* function which has the step-like form produced by this interpolation scheme should fall off as $1/f^2$ at high frequencies. To do this, we observe that the power spectrum $P(f)$ may also be regarded as the Fourier transform of the two-time autocorrelation function $\chi(t)$ of the extinction intensity. For very short times, this autocorrelation has only a constant term and a contribution from the boundaries between stages which goes linearly with the time difference t , so that $\chi(t) = A + Bt$, where A and B are constants. It is straightforward to show that the Fourier transform of such a function varies with frequency f as $1/f^2$. This result is familiar to physicists studying X-ray scattering, who know it as Porod's law (Guinier & Fournet 1955). The $1/f^2$ form of the power spectrum is clearly visible in figure 2.

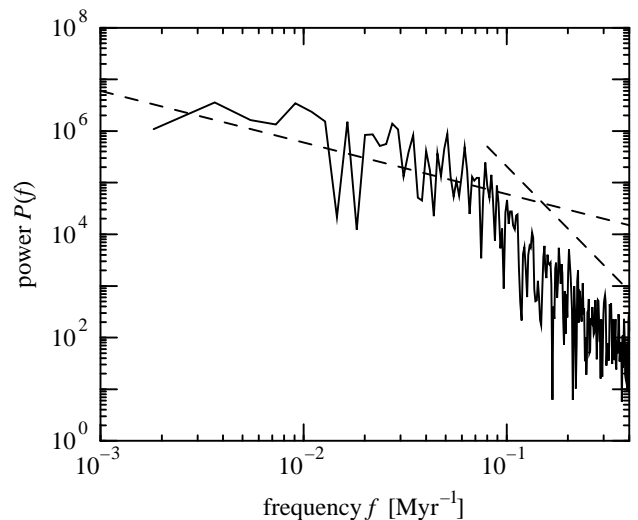


Figure 3. Power spectrum of total familial extinction of marine organisms calculated using data drawn from the compilation by Benton (1993). As in the preceding figure, the long dotted line denotes the $1/f$ form. The shorter one denotes the $1/f^4$ form.

This result does not apply to spectra generated using the linear interpolation scheme. However, in this case we notice that the interpolated function is piecewise linear between the data points at each stage (see figure 1) and hence that the derivative dx/dt of the extinction intensity is a step-like function of the form discussed in the previous paragraph. Thus the power spectrum of the derivative must fall off as $1/f^2$ at large frequencies. This being the case, we can then use integration by parts to show that the power spectrum of the intensity itself must fall off as $1/f^4$. This behaviour is visible in figures 2 and 3.

Thus we have demonstrated that the high frequency behaviour of the power spectrum is purely a mathematical artefact, and is not associated with any interesting biological phenomena. However, the arguments given above break down when we look at time-scales greater than the typical length of a stage, which means greater than about 10 Myr. This corresponds to frequencies in the power spectrum of less than about 0.1 Myr^{-1} . Indeed, we can see from the figures that the behaviour of the spectrum does change below this frequency. The behaviour below this point contains all the interesting biological information to be found in these spectra, and it is on this region that we now concentrate. In figure 4 we show this low-frequency region of the power spectrum replotted on semilogarithmic scales, both for the Sepkoski and Benton data. On these scales, the spectrum appears to follow a straight line, apart from statistical fluctuations. This implies that the spectra have an approximately exponential form. The slope of the exponential gives a 'correlation time' τ , which describes the time-scale on which the extinction data are correlated with one another. The best fits to the data are shown as the dotted lines in figure 4, and the corresponding correlation times are measured to be $\tau = 39.5 \pm 4.9 \text{ Myr}$ for the Sepkoski data and $\tau = 45.4 \pm 6.3 \text{ Myr}$ for the Benton data. Within the errors these two figures are the same.

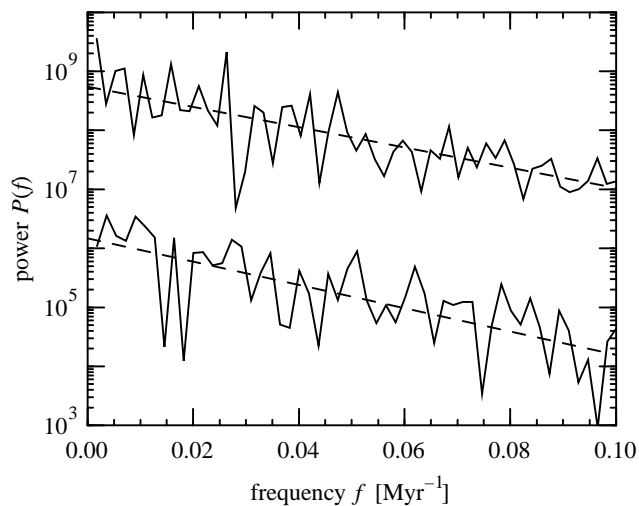


Figure 4. Power spectra for familial extinction in the Sepkoski (upper) and Benton (lower) databases, plotted on semi-logarithmic scales. The approximately straight-line form indicates that the spectra are falling off exponentially. The measured correlation times of the two spectra, extracted from a least squares fit (dotted lines) are $\tau = 39.5$ Myr and $\tau = 45.4$ Myr, respectively.

The exponential form of the power spectrum at low frequencies indicates that there is correlation between the extinction intensity at different times in the fossil record, but that it falls off quite quickly, in a way which is not consistent with, for example, the critical processes considered by Solé *et al.* (1997). The mean lifetime of families in the Sepkoski database (again excluding single-stage records) is 58.5 ± 1.3 Myr. Thus the time-scale τ on which there are correlations is similar to (in fact slightly shorter than) the time-scale on which the families present turn over. It is therefore not surprising that we see correlations on these time-scales.

We should note that the data presented in figure 4 are also consistent with a power-law hypothesis. Using an *F*-test, we find that there is no statistically significant advantage of one fit over the other. (Other authors (e.g. Baskaran *et al.* 1996) have also found that it can be hard to distinguish the two forms in data such as these which are subject to large statistical fluctuations.) Thus we have not ruled out the possibility of a power-law power spectrum, but we have shown that there is no statistical evidence in its favour. The form of the power spectrum of fossil extinction data can be explained as the result only of normal, short-time correlations and does not require us to invoke critical phenomena or similar explanations, at least in this case.

5. CONCLUSIONS

In this paper we have calculated power spectra of extinction intensity in the Phanerozoic fossil record of marine families, using data from two independent compilations. These spectra show two distinct regimes of behaviour: one at low frequency (below about 0.1 Myr^{-1}) in which the spectrum is consistent with an exponential form with a time-scale of the order of the typical lifetime of a family, and another for high frequencies which falls off either as $1/f^2$ or as $1/f^4$ with frequency, depending on the interpolation scheme used in calculating the spectra. The exponential form is typical of most power spectra, and denotes short-time correlations in the extinction data, but no long-time ones such as might be typical of the critical systems which Solé *et al.* (1997) suggested to explain their results. The high-frequency behaviour of the spectrum is the result solely of the fact that the databases used record the time of extinction of families to the nearest stage, and does not reflect any real biological phenomena.

We would like to thank Jim Kirchner, Jack Sepkoski, Kim Sneppen and Ricard Solé for useful discussions, and Doug Erwin, Jack Sepkoski and Ricard Solé for providing data used in the calculations and figures. This work was supported by the Santa Fe Institute, the Smithsonian Institution and DARPA under grant number ONR N00014-95-1-0975.

REFERENCES

- Baskaran, S., Stadler, P. F. & Schuster, P. 1996 Approximate scaling properties of RNA free energy landscapes. *J. Theor. Biol.* **181**, 299–310.
- Benton, M. J. 1993 *The fossil record 2*. London: Chapman & Hall.
- Bowring, S. A., Grotzinger, J. P., Isachsen, C. E., Knoll, A. H., Pelechaty, S. M. & Kolosov, P. 1993 Calibrating rates of early Cambrian evolution. *Science* **261**, 1293–1298.
- Davis, J. C. 1973 *Statistics and data analysis in geology*. New York: Wiley.
- Guinier, A. & Fournet, J. 1955 *Small angle scattering of X-rays*. New York: Wiley Interscience.
- Harland, W. B., Armstrong, R., Cox, V. A., Craig, L. E., Smith, A. G. & Smith, D. G. 1990 *A geologic time scale 1989*. Cambridge University Press.
- Kirchner, J. W. & Weil, A. 1998 No fractals in fossil extinction statistics. *Nature* **395**, 337–338.
- Raup, D. M. & Boyajian, G. E. 1988 Patterns of generic extinction in the fossil record. *Paleobiology* **14**, 109–125.
- Sepkoski Jr, J. J. 1992 *A compendium of fossil marine animal families*, 2nd edn. Milwaukee Public Museum Contributions in Biology and Geology 83.
- Solé, R. V., Manrubia, S. C., Benton, M. & Bak, P. 1997 Self-similarity of extinction statistics in the fossil record. *Nature* **388**, 764–767.