THE COLOR OF ENVIRONMENTAL NOISE

DAVID A. VASSEUR¹ AND PETER YODZIS

Department of Zoology, University of Guelph, Guelph, Ontario, Canada N1G 2W1

Abstract. Biological populations are strongly influenced by the random variation in their environment. The spectrum of frequencies in noise is particularly important to dynamics and persistence. Here we present an analysis of the variance spectra of a wide variety of long-term time series of environmental variables. Spectra were well approximated by the inverse power law $1/f^{\beta}$ within the appropriate range of frequencies *f*; however, the majority of spectra were "flattened" at low frequencies. With some qualification we found the spectral exponents (β) to corroborate an earlier suggestion that terrestrial noise tends to be "white" ($\beta < 0.5$), while marine environments tend to be "red" ($\beta \approx 1$) or "brown" ($\beta \approx 2$). As well, we found a tendency for whiter noise in temperate latitudes than in either high or low latitudes. These results have wide-ranging consequences for ecosystem fragility and species conservation.

Key words: environmental noise; noise color; power spectrum; time series.

INTRODUCTION

Biological populations exist in a noisy world of random variation in the environmental parameters that affect their dynamics. For some populations, this natural variability merely superimposes noise on the time series of population abundance (exclusive of noise introduced by measurement error). But there is also a class of systems for which external forcing by environmental noise alters the qualitative nature of the dynamics. The best studied case is when environmental fluctuations are so large or the population is so small that the population is driven to local extinction (e.g., Ripa and Lundberg 1996, Johst and Wissel 1997). More recently, awareness has been growing, particularly but not exclusively concerning marine systems, that environmental variability may cause fundamental alterations in the dynamics and structure of communities, such as changes in the dominant taxa present (NRC 1996, Holmgren et al. 2001). In order to model these phenomena, we must start by modeling the noise in environmental variables.

An important characteristic of environmental noise is its spectrum, which describes the variance as a sum of sinusoidal waves of different frequencies. For many years, theoretical work on environmental noise uncritically assumed a white spectrum, partly for want of a more general model of noise, partly for want of guidance from data. In order to theoretically study the phenomena mentioned in the preceding paragraph, it is crucial that we move beyond white noise to something more realistic. This paper is a survey and analysis of time series data for a wide variety of environmental variables, which confirms and sharpens the emerging paradigm of "colored noise."

In white noise, the variance is the same at all frequencies. This is by far the most thoroughly studied and applied form of noise. The reason for this is that it is a simple and easily articulated model for noise. However, it is not necessarily a good description of the time series of environmental variables in nature. We need to move beyond the assumption of white noise in modeling environmental variability, but in order to do so, we need another relatively simple and easily articulated hypothesis.

Building on work scattered in the literature, with some of it his own, Mandelbrot (1983) suggested that the family of noise forms whose variance scales with frequency according to an inverse power law, $1/f^{\beta}$, may describe many instances of noise in nature. In this setting, white noise is a special case, $\beta = 0$, in which there is an equal mix of cyclic components at all frequencies in the variance, while "colored" noises are dominated by frequencies in a certain range. Specifically, red noise ($\beta = 1$) is dominated by low-frequency (or long-period) cycles and has residuals that are autocorrelated. In the time domain, this produces an increased probability of having long runs of above (or below) average conditions (Fig. 1). More intense slopes have been termed brown ($\beta = 2$), which is by no coincidence, the color of noise generated by a Brownian process. The family of $1/f^{\beta}$ noise models seems, with a caveat discussed later, to describe well the fluctuations of a wide range of environmental variables.

Colored noise was brought to the attention of ecologists by Steele (1985), who suggested that terrestrial noise should be white, while marine noise should be brown, based upon a few empirical records and simple forcing models. Based on this, noise color has been examined in a wide variety of climatological and hy-

Manuscript received 18 September 2002; revised 10 February 2003; accepted 25 August 2003. Corresponding Editor: S. R. Lele.

¹ Present address: Department of Biology, McGill University, 1205 Avenue Docteur Penfield, Montreal, Quebec, Canada H3A 1B1. E-mail: David.Vasseur@mail.mcgill.ca



FIG. 1. Residual time series for (a) a white noise model and (c) a red noise model (generated using an AR[1] process), and (b, d) their respective power spectra. The mean and variance for the data are identical. In panel (b), the contribution to the variance is equal across all frequencies ($\beta = 0$; white noise), while in panel (d), the variance is dominated by low-frequency periodic components ($\beta = 1$; red noise). Straight lines represent the $1/f^{\beta}$ approximation.

drological variables (e.g., Pelletier and Turcotte 1997, Cyr and Cyr 2003). Recent theoretical work has shown that population dynamics, particularly population persistence and extinction, are influenced by noise color (Steele and Henderson 1984, Ripa et al. 1998), but that the effect of noise can be masked by periodic or chaotic dynamics (Ranta et al. 2000).

Lawton (1988) predicted an increased risk of extinction in populations experiencing red noise relative to those experiencing white noise, based upon the simple observation that in red noise long runs of 'poor' conditions for survival are more likely than they are in white noise. Recent work has to some extent supported this observation using discrete-time population models tracking colored variation generated by a firstorder autoregressive process (Johst and Wissel 1997, Petchey et al. 1997, Cuddington and Yodzis 1999). However, this trend is sensitive to the underlying dynamics of the modeled population (Ripa and Lundberg 1996, Petchey et al. 1997, Cuddington and Yodzis 1999), and to the noise model employed (Cuddington and Yodzis 1999, Halley and Kunin 1999).

In this study, we analyzed the noise spectra of longterm time series of a variety of environmental data from different geographic regions. Our object was to be as thorough as we could manage, attempting a catalog with enough breadth and depth to serve as a test for colored noise in environmental data, and as a guide for interested modelers wishing to investigate the effect of environmental noise, but lacking the appropriate data.

Methods

We searched the print literature and the Internet for time series of environmental data satisfying a number of requirements. Firstly, there had to be enough points to permit a meaningful spectral analysis. We chose 2^7 as the minimum number of points that could be of use. As well, we sought data with regularly spaced points, with <10% missing. Finally, and importantly (in our view), we tried to find data for as wide a variety of environmental variables as we could, including aggregate quantities such as averages and extrema of temperature and precipitation, degree days (number of days per month exceeding a certain threshold), and other seasonal indices (such as area of ice cover, number of days with snow, etc.), located over a wide variety of geographic locations.

One hundred fifty-two data sets incorporated a variety of environmental variables (Table 1), with lengths ranging from 128 to 4056 samples (median 774) taken at monthly intervals. Exceptions were eleven data sets classified as seasonal indices, which were sampled annually, or at 10-year intervals. Geographical origin of the data was recorded, and sites were classified as "marine" or "terrestrial." Terrestrial sites were subclassified as "coastal" or "inland" depending on their proximity to a marine coast (coastal data originated from cities located directly on a marine coast, all others were designated inland). Time series had on average 1.5% of data points missing (range = 0-10%). Missing data were filled in using linear interpolation.

Variable	Description	Origin	Source
Air temperature mean	monthly mean air temperature data	North America and Europe	1–9
Air temperature maxi- ma and minima	monthly maximum and minimum air temperature	globally distributed	9–11
Precipitation	total monthly accumulation	globally distributed	3, 7–9, 11, 12
Sea surface temperature mean	monthly mean sea surface temperature data	Atlantic and Pacific oceans	5, 13, 14
Sea surface temperature maxima and minima	monthly maximum and minimum sea surface tem- perature	Atlantic and Pacific oceans	14
Degree days	number of days per month with average air temper- ature exceeding 15°C	generaed from daily data	9
Seasonal indices	various aggregate measures of climate sampled an- nually: area of ice cover, number of days with snow, date of ice clearance, drought index, winter severity index	Europe	12, 15, 16

TABLE 1. Summary of variables used in this study.

Note: Sources are: (1) Linacre 1992; (2) Manley 1974; (3) Landsberg et al. 1968; (4) National Climate Archive, Environment Canada (online, URL: (http://www.climate.weatheroffice.ec.gc.ca)); (5) NOAA/National Weather Service, Climate Prediction Center (online, URL: (http://www.cpc.ncep.noaa.gov/)); (6) Fisheries and Oceans Canada, data from BC Lighthouses (online, URL: (http://www.cpc.ncep.noaa.gov/)); (6) Fisheries and Oceans Canada, data from BC Lighthouses (online, URL: (http://www.cpc.ncep.noaa.gov/)); (6) Fisheries and Oceans Canada, data from BC Lighthouses (online, URL: (http://www.cpc.ncep.noaa.gov/)); (6) Fisheries and Oceans Canada, data from BC Lighthouses (online, URL: (http://www.cpc.ncep.noa/searchfools/Searchlighthouse.e.htm)); (7) University of East Anglia, Central England Data Sets (online, URL: (http://www.cru.uea.ac.uk/~mikeh/datasets/uk/engwales.htm)); (8) Southeast Regional Climate Center, Historical Climate Summaries and Normals for the Southeast (online (URL: (http://www.dnr.state.sc.us/climate/sercc/climateinfo/historical/historical.html)); (9) National Climate Data Center (online, URL: (http://www.ndr.state.sc.us/climate/sercc/climateinfo/historical.html)); (11) British Antarctic Survey, Natural Environment Research Council (online, URL: (http://www.inmu.cdavis.edu/WEATHER/wxretrieve.html)); (11) British Antarctic Survey, Natural Environment Research Council (online, URL: (http://www.mlrg.ucsd.edu/shoresta/index.html)); (14) NEMO, Oceanographic Data Server, Scripps Institution of Oceanography Shore Stations (online, URL: (http://csweb1.ucsd.edu/shoresta/index.html)); (15) Lamb 1966; and (16) Manley 1978.

Seasonal variability was removed from monthly samples by subtracting from each data point the mean for the corresponding month taken over the total record (see Chatfield 1989). This process was visually verified to eliminate the spike in the spectral density function at the annual frequency. Spectral densities were calculated as in Priestley (1981) using a Parzen window over the frequency interval $n^{-1} - 0.5 \text{ month}^{-1}$ [year⁻¹ or $(10 \times \text{year})^{-1}$ for seasonal indices], where *n* represents the number of samples in the data set. The spectral exponent, β , was estimated as the negative slope of the linear regression of \log_{10} spectral density against log₁₀ frequency. Slopes of all regressions were significantly different than zero (P < 0.05). We tested for pairwise differences in the distribution of spectral exponents (B) for environmental variables (and locations) using the Wilcoxon rank-sum test (see Zar 1999).

We adopted the following terminology for noise color in an effort to state patterns simply: "white" for $0 \le \beta \le 0.5$, "red" for $0.5 < \beta \le 1.5$, and "brown" for $1.5 < \beta \le 2$.

RESULTS

The air temperature data span a wide range from white to brown noise (Fig. 2). However, if we partition the data sets for monthly mean temperature according to proximity to the seas, we find white spectra at inland (terrestrial) locations, red-brown noise at coastal locations, and for comparison, mostly brown noise for sea-surface temperature (Fig. 3a). On the other hand, monthly minima and maxima have mostly red spectra at both coastal and inland locations, as well as in sea surface temperature (Fig 3b, c).

Quite a variety of other environmental parameters possess white, or at most "pink" ($0.5 \le \beta \le 1$), noise in terrestrial environments (Fig. 2). These include total monthly precipitation, degree days, and several seasonal indices.

We found enough information for precipitation and temperature extrema to group the data into latitudinal categories. While several of the differences are only marginally significant, we found a suggestive tendency for precipitation, minimum temperature, and maximum temperature to have the flattest spectra (smallest β) at temperate locations, with steeper spectra both at high and at low latitudes (Fig. 4).

DISCUSSION

To a considerable extent, our analysis upholds Steele's (1985) generalization that terrestrial noise is white, while marine noise is reddened (red to brown). In exception are locations proximal to a marine coast, which show more reddened spectra than inland locations, and monthly extrema, which show red noise, regardless of location. The first exception can be explained by the capacity of the sea to buffer much of the high frequency variation evident in coastal terrestrial locations, therefore reddening the environment. In an analysis of environmental measures associated with lakes and rivers, Cyr and Cyr (2003) found white, or at most pink ($\beta \approx 0.5$) spectra, which suggests that these systems are strongly coupled to the terrestrial



FIG. 2. Box plots of spectral exponents (β) for environmental variables (SST = sea surface temperature). Lines indicate the median, 75th, and 90th percentiles, with outlying points (\bullet), and sample sizes indicated below. Letters indicate significant differences in the distribution of spectral exponents (β), where A is significantly different from B, but BC is not significantly different than CD, etc. (Wilcoxon rank-sum test, $\alpha(2) = 0.025$). Environmental variables are described in detail in Table 1.

environment, as one would expect. The second exception to Steele's generalization provides an interesting similarity between extreme events in marine and terrestrial environments that may be as, or more, important to their inhabitants than averages.

Crucial though it is to the dynamics of populations, ecologists still have a rather limited understanding of how organisms perceive their environment, and thus how they respond numerically to changing environmental conditions. From a modeling perspective, it is likely that many, if not all, parameters that describe a population's rate of change may react to a change in the environment. Stochastic processes in birth and death rates (Johst and Wissel 1997), in carrying capacity (Ripa and Lundberg 1996, Petchey et al. 1997), and in an additive density dependent term (Dennis and Costantino 1988, Ripa and Lundberg 1996) have been used to model the influence of environment on population dynamics. However, it is likely that such quantities will have nonlinear dependencies on actual environmental variables (e.g., measured temperature), or will respond only outside a certain threshold, due to the ability of organisms to buffer small changes. In light of this, it is possible that extrema or aggregate indices, such as degree days, measured at a relevant time scale, will be more important to some organisms than averages.

Another pressing question is: What is a relevant time scale? Organisms with a short life span (e.g., one day) cannot perceive the environmental variance measured at monthly intervals, and alternatively, variance measured at the minute⁻¹ scale would be nearly inconsequential for organisms with long life spans (e.g., 10 years). One must also consider how indirect effects might alter an organism's perception of environmental noise: Responses developing elsewhere in the food web are passed through trophic relationships as numerical responses, with some associated time lag, and ultimately affect the entire food web. The issue of scale then further complicates the response of an individual or population to the environment, and makes that of a community exceedingly difficult to perceive. We show (mainly) monthly data here, not to imply that this time scale is predominantly important, but to allow a comparison across variables while providing a meaningful sample size.

The marginal trend in the latitudinally grouped data generally showed flatter spectra in temperate locations than in polar or equatorial regions. We cannot provide a reasonable explanation for this trend. Although we





FIG. 3. Box plots of spectral exponents (β) for (a) air temperature mean, (b) maximum air temperature, and (c) minimum air temperature at inland and coastal locations. Lines indicate the median, 75th, and 90th percentiles, with outlying points (\bullet), and sample sizes indicated below. For comparison, sea surface temperature mean, maximum, and minimum are shown. All differences in panel (a) are significant (α (2) = 0.025), whereas all differences in panels (b) and (c) are non-significant.

did not detect any differences between terrestrial and marine extrema, it is possible we are detecting an increased influence of terrestrial (flatter) noise in temperate locations. Nevertheless, further studies of this trend may provide interesting results.

FIG. 4. Box plots of spectral exponents (β) for (a) precipitation, (b) maximum air temperature, and (c) minimum air temperature grouped into latitudinal categories. Lines indicate the median, 75th, and 90th percentiles, with outlying points (\bullet), and sample sizes indicated below. In general, temperate locations are different from equatorial and polar regions; however, some differences are only marginally significant, due in part to small sample sizes.

The ability of the $1/f^{B}$ power law to fully describe the variance spectra of our environmental time series is questionable; the majority of variance spectra analyzed here (60%) showed a distinct "flattening" at low frequencies (Fig. 5a, b). It is evident that an increase in the lower frequency boundary of variance spectra, from n^{-1} to $5n^{-1}$, can eliminate this flattening, indi-



FIG. 5. Illustrative spectral densities for (a) monthly mean temperature for a coastal terrestrial site displaying a distinct flattening at low frequencies, $\beta = 0.65$; (b) monthly mean temperature for an inland terrestrial site without flattening, $\beta = 0.41$; and (c) an autoregressive time series defined by $\phi_{t+1} = \alpha \phi_t + C(1 - \alpha^2)^{0.5} \times \varepsilon_{t+1}$ where $\alpha = 0.7$, C = 20, and ε_{t+1} is a random normal deviate with mean zero and unit variance, $\beta = 1.02$. Straight lines represent the $1/f^{\beta}$ approximation.

cating a possibility that variation at the lowest frequencies may be undersampled. Despite this, we have no theoretical reason to alter the lower boundary in our analysis, and the one we have used is customary in analyzing climate data (C. Chatfield, *personal communication*). The low-frequency flattening has a negligible effect on the significance of our regressions because log-transforming the (equally spaced) frequencies produces a concentration of points at higher frequencies.

While we cannot rule out the possibility that they may be artifacts of the analysis, it is equally conceivable that the flattened regions could indeed be a property of the data. Frankignoul and Hasselmann (1977) explained the observed "flattened" regions obtained from their surface sea temperature data using negative feedback in a stochastic model of atmospheric forcing; feedback enabled the ocean to influence atmospheric factors to stabilize the spectral densities at low frequencies. Furthermore, the first-order autoregressive stochastic process AR(1) is well known to have a spectrum that is "flattened" at low frequencies (Fig. 5c). This difference between AR(1) and $1/f^{\beta}$ spectra depends on the correlation between events; correlation decays exponentially with time in AR(1) processes, but more slowly according to a power law in $1/f^{\beta}$ processes. Recent work has suggested that the difference between true $1/f^{\beta}$ and autoregressive AR(1) noise is not trivial to population dynamics. Cuddington and Yodzis (1999) showed that populations experiencing true $1/f^{\beta}$ noise had an increased mean persistence time for red and brown noise, but that noise generated by an autoregressive process had the opposite effect of decreasing mean persistence time (for populations with undercompensatory dynamics). In contemplating the influence of environmental variation on population dynamics, it may be necessary not only to take noise color into account, but also to consider the presence or absence of a flattening at low frequencies.

On the whole, we find that $1/f^{\beta}$ noise, possibly with a flattening at low frequencies, is a good model for the stochastic variation of a wide range of environmental variables. It would be prudent for modeling exercises to examine a range of colors, as well as to distinguish "flattened" spectra (conveniently generated as AR[1]) from true inverse power spectra (generated, say, by spectral synthesis [Cuddington and Yodzis 1999]). Ultimately, we will have to address the really difficult issue of just which environmental variables are particularly important for each given taxon of interest.

ACKNOWLEDGMENTS

We thank Keith Brander, Chris Chatfield, Kim Cuddingon, Hélène Cyr, Mariano Koen Alonso, and Doug Larson for discussions, Brian Dennis and John Steele for comments on an earlier draft, and the Natural Sciences and Engineering Research Council of Canada for financial support (grant A7775 to PY).

LITERATURE CITED

- Chatfield, C. 1989. The analysis of time-series: an introduction. Chapman and Hall, London, UK.
- Cuddington, K. M., and P. Yodzis. 1999. Black noise and population persistence. Proceedings of the Royal Society of London, Series B 266:969–973.
- Cyr, H., and I. Cyr. 2003. Temporal scaling of temperature variability from land to oceans. Evolutionary Ecology Research 5:1183–1197.

- Dennis, B., and R. F. Costantino. 1988. Analysis of steadystate populations with the gamma abundance model: application to tribolium. Ecology **69**:1200–1213.
- Frankignoul, C., and K. Hasselmann. 1977. Stochastic climate models. Part II. Application to sea-surface temperature anomalies and thermocline variability. Tellus 29:289– 305.
- Halley, J. M., and W. E. Kunin. 1999. Extinction risk and the 1/f family of noise models. Theoretical Population Biology 56:215–230.
- Holmgren, M., M. Scheffer, E. Ezcurra, J. R. Gutierrez, and M. J. M. Godefridus. 2001. El Niño effects on the dynamics of terrestrial ecosystems. Trends in Ecology and Evolution 16:89–94.
- Johst, K., and C. Wissel. 1997. Extinction risk in a temporally correlated fluctuating environment. Theoretical Population Biology 52:91–100.
- Lamb, H. H. 1966. The changing climate. Methuen, London, UK.
- Landsberg, H. E., C. S. Yu, and L. Huang. 1968. Preliminary reconstruction of a long time series of climatic data for the eastern United States. Technical Note **BN-571.** University of Maryland, Institute of Fluid Dynamics, College Park, Maryland, USA.
- Lawton, J. H. 1988. More time means more variation. Nature **334**:563.
- Linacre, E. 1992. Climate data and resources. Routledge, London, UK.
- Mandelbrot, B. B. 1983. The fractal geometry of nature. W. H. Freeman, San Francisco, California, USA.
- Manley, G. 1974. Central England temperatures: monthly means 1659 to 1973. Quarterly Journal of the Royal Meteorological Society 100:389–405.

- Manley, G. 1978. Variation in the frequency of snowfall in east-central Scotland, 1789–1975. Meteorological Magazine **107**:1–16.
- NRC [National Research Council]. 1996. The Bering Sea ecosystem. National Academy Press, Washington, D.C., USA.
- Pelletier, J. D., and D. L. Turcotte. 1997. Long-range persistence in climatological and hydrological time series: analysis, modeling and application to drought hazard assessment. Journal of Hydrology 203:198–208.
- Petchey, O. L. A. Gonzalez, and H. B. Wilson. 1997. Effects on population persistence: the interaction between environmental noise color, intraspecific competition and space. Proceedings of the Royal Society of London, Series B 264: 1841–1847.
- Priestley, M. B. 1981. Spectral analysis and time series. Academic Press, London, UK.
- Ranta, E., P. Lundberg, V. Kaitala, and J. Laakso. 2000. Visibility of the environmental noise modulating population dynamics. Proceedings of the Royal Society of London, Series B 267:1851–1856.
- Ripa, J., and P. Lundberg. 1996. Noise color and the risk of population extinctions. Proceedings of the Royal Society of London, Series B 263:1751–1753.
- Ripa, J., P. Lundberg, and V. Kaitala. 1998. A general theory of environmental noise in ecological food webs. American Naturalist 151:256–263.
- Steele, J. H. 1985. A comparison of terrestrial and marine ecological systems. Nature 313:355–358.
- Steele, J. H., and E. W. Henderson. 1984. Modeling longterm fluctuations in fish stocks. Science 224:985–987.
- Zar, J. H. 1999. Biostatistical analysis. Fourth edition. Prentice Hall, London, UK.