Visibility of the impact of environmental noise: a response to Kaitala and Ranta

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Based on simulation modelling, Kaitala and Ranta (2001 *Proc. R. Soc. Lond. B* **268**, 1769–1774) have argued that detecting the statistical relationships between environmental variability and population fluctuations will be difficult. However, their study was limited in that only one pattern of density dependence and one detection method were used. Here, we show that their conclusion is in part a consequence of their choice of population model and in part a consequence of using relatively weak or inappropriate statistical methods. Other patterns of density dependence respond differently to environmental fluctuations, and the impact of the disturbance on these is clearly visible using their methods. For some patterns of population dynamics, environmental impacts are more readily detectable by correlating running-average environmental conditions with the population time-series or by correlating the first differences of the population time-series with environmental noise. When more appropriate statistical methods are used, environmental forcing is detectable in the majority of cases used by Kaitala and Ranta. The interplay between environmental stochasticity and density-dependent population growth means that there is no single best method to detect the influence of environmental forcing, even when population dynamics are approximately linear. But environmental forcing will often be detectable, contrary to Kaitala and Ranta's assertions.

Keywords: noise; population dynamics; density dependence; environmental stochasticity; age structure; perturbations

1. INTRODUCTION

The impact of environmental fluctuations, particularly climatic variation, on populations is of major interest to ecologists (e.g. Sugihara 1996; Dixon *et al.* 1999; Pascual *et al.* 2000). Detecting the effects of environmental variability on populations is difficult, at least in part because density-dependent population processes may interact in nonlinear ways with environmental forcing (e.g. Pascual & Ellner 2000; Turchin & Ellner 2000). It can be particularly difficult to detect the impact of noise on systems that have deterministic non-equilibrium dynamics. In what circumstances will the effects of environmental forcing on a population be detectable? Based on analysis of a mathematical model in which all of the model parameters and the noise terms were specified, Kaitala & Ranta (2001) have argued that this task will be difficult or impossible for age-structured density-dependent populations. If true, this assertion has serious implications for our abilities to understand the population dynamics of field populations and to detect the impacts on them of processes such as climatic change. If it is not possible to see the perturbations in a simulated population where all of the details of the system are known then there will be little hope of seeing them in a real population where there are many unknowns and sampling errors.

Kaitala and Ranta perturbed a density-dependent age-structured model with red, white and blue noise. They assessed the visibility of the impact of noise by calculating the cross-correlation coefficient (CCF) between the

population fluctuations of each age group and the input noise. Higher correlation coefficients were interpreted as an indicator of higher visibility of the impact of the noise. When noise was applied to the first age group, environmental forcing was never visible for a semelparous life history. For an iteroparous life history, only the effects of red noise were visible. Impacts of red noise became more visible as the noise was applied to more age groups. Kaitala and Ranta commented that further analysis of the visibility of external forcing was necessary, but summarized their results as 'cast[ing] doubts on the possibility of detecting' (2001, p. 1769) the effects of environmental noise on structured populations.

Here, we show that their conclusion is unduly pessimistic. The results on which Kaitala and Ranta base their conclusions are in part a consequence of their choice of population model and in part a consequence of using inappropriate statistical methods. Other population models respond differently to stochastic environmental fluctuations, and the impact of environmental perturbations is clearly visible. Even with their iteroparous population model, the effects of all colours of environmental forcing can be detected if more appropriate statistical methods are used.

2. MODEL FORMULATION

Kaitala & Ranta (2001) used a density-dependent Leslie-matrix model:

$$\mathbf{n}_{t+1} = V_t Q^{-1} M \mathbf{n}_t, \quad (2.1)$$

where $\mathbf{n}_t$ is a column vector giving the number of individuals in each age class at time t . M is a 10×10 matrix

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Table 1. Demographic parameters for the four populations studied.

model	age	1	2	3	4	5	6	7	8	9	10
iteroparous, $\lambda = 1.1$	fecundity	0.9	1.8	1.8	1.8	1.7	2	2	2	2	2
	survival	0.1	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2
iteroparous, $\lambda = 3$	fecundity	2.2	2.2	2.2	2.2	2.2	2.2	2.1	2.1	2.1	2.1
	survival	0.8	0.8	0.8	0.8	0.8	0.8	0.8	0.8	0.8	0.8
semelparous, $\lambda = 1.1$	fecundity	0	0	0	0	0	0	0	0	0	20
	survival	0.8	0.8	0.8	0.8	0.8	0.8	0.79	0.79	0.793	0.8
semelparous, $\lambda = 3$	fecundity	0	0	0	0	0	0	0	0	0	152 400
	survival	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9

containing the demographic parameters of the population. The first row of M gives the age-specific fecundities, and the first subdiagonal gives the age-specific survival rates. V_t is a 10×10 matrix in which the diagonal values give the age-specific environmental noise. If more than one age class is being perturbed by noise, each age class is perturbed by the same noise series. The scalar value of the environmental noise, v_t , is generated by a first-order autoregressive process, with the colour of the noise being determined by β , the autocorrelation parameter. A positive value for β gives red noise, a negative value gives blue noise and $\beta = 0$ gives white noise. Following Kaitala and Ranta, $\beta = 0.8$ was used for red noise and $\beta = -0.8$ was used for blue noise. The non-zero diagonal elements of V_t are then $1 + v_t$ and are truncated within the range $(1 - w, 1 + w)$. Kaitala and Ranta used $w = 0.5$ to generate their results but state that using $0.05 < w < 0.8$ gives very similar results. Q^{-1} is a 10×10 matrix representing the effect of density dependence on the demographic parameters in M . The diagonal of Q^{-1} contains q_t^{-1} . The density-dependence function giving q_t is

$$q_t = 1 + \left[\frac{\lambda - 1}{K} \right] N_t, \quad (2.2)$$

where N_t is the total population abundance at time t , K is the carrying capacity and λ is the average growth rate. Kaitala and Ranta used a value of $K = 5000$. Two basic life histories were studied: iteroparous, in which all age classes reproduce, and semelparous, in which reproduction takes place only in the final age class. Two density-independent growth rates, 1.1 and 3, were tested for each model. The pattern of density dependence in the model can be classified as compensatory and keeps the net growth rate asymptotically equal to 1 (Caswell 2001). The density dependence is unusual in that the equilibrium population depends only on K and is unaffected by other demographic parameters. The density dependence makes the population very resilient to perturbations. For example, when the growth rate is high, if the population is perturbed by an impulse that takes the population down to only a tenth of the carrying capacity, the population effectively recovers in only three time steps. Correspondingly, population sizes greater than the equilibrium size are rapidly reduced. This fast recovery from environmental perturbations is one of the reasons why the impact of the noise can be hard to detect.

Kaitala and Ranta do not state the values of the demographic parameters that they used. We have chosen four sets of demographic parameters, corresponding to

iteroparous and semelparous life histories with growth rates of 1.1 and 3 (see table 1). However, altering the parameter values while keeping the growth rate constant did not significantly affect the behaviour of the model. This is partly because the equilibrium population is unaffected by the demographic parameters.

The density dependence affects all of the fecundity and survival terms in the projection matrix. To explore the effects of other patterns of density dependence on the visibility of the noise we examined the CCFs when the density dependence is applied only to the fecundity terms. When density dependence is applied to the fecundity terms alone, K is no longer the carrying capacity and the equilibrium population abundance is determined by the demographic parameters as well as by the value of K . Red, white and blue noise was applied to the first age group only, and growth rates of 1.1 and 3 were tested using the same life histories as in the original model. This offers a direct comparison with the first set of Kaitala and Ranta's results. The effect on the visibility of the noise of using different growth rates that lie between these values was also briefly explored. In line with the original paper the simulations were run for 5000 time steps and these transients discarded. The following 1000 time steps were then used. We have also examined the consequences of applying Ricker and Beverton–Holt density functions to the fecundity only. The results were similar to those obtained by applying the original density function to the fecundity only, so are not discussed in detail.

3. PATTERNS OF POPULATION DYNAMICS

Populations with different vital rates and patterns of density dependence can respond differently to environmental forcing. Consequently a range of statistical methods may be necessary to detect the impacts of the environmental forcing. To help decide which statistical methods are most appropriate it is useful first to examine the dynamics of the population. Kaitala & Ranta's (2001) model was replicated using an iteroparous life history, density dependence as described by equation (2.2) and disturbance applied to the first age group only, with truncation at $w = 0.5$. Two distinct patterns of total population dynamics were observed. When the population growth rate was high ($\lambda = 3$), the total population abundance fluctuated around the carrying capacity (figure 1a–c). The magnitude of these fluctuations depended on the colour of the environmental noise, with white and red noise producing larger fluctuations than blue noise. The total population abundance tracked the noise closely.

Figure 1. Sections of the total population abundance time series for Kaitala & Ranta's (2001) original iteroparous model with (a–c) high and (d–f) low growth rates perturbed with (a,d) blue, (b,e) white and (c,f) red noise.

When the population growth rate was low (figure 1d–f), the population showed a pattern of ‘outbreaks’, in which periods of high density were interspersed with periods of very low density. The population was much less resilient to noise, and the density dependence was unable to overcome the effects of the environmental disturbance. The most extreme example occurred with red environmental noise, when the population had long periods during which it was practically extinct. During locally good environmental periods, the average population growth rate was greater than 1 and the population was able to exceed the equilibrium size. During locally bad periods, the average population growth rate is less than 1 and the population heads towards extinction. In these cases, the correlation between population numbers and environmental conditions will be low, particularly with the red input, although the relationship with time-averaged environmental conditions will be stronger.

The three alternative models of density dependence (Leslie density dependence, Ricker density dependence and Beverton–Holt density dependence on the fecundity only) were tested in the same manner and showed similar patterns of time-series to the original model. However, we shall see later that applying density dependence to the fecundity only can make the impacts of noise easier to detect.

4. DETECTION METHODS

The different patterns of population dynamics described above will require different approaches to detect the impact of the noise. For patterns showing the population dynamics when the growth rate is high (figure 1a–c), correlating age-class abundances with noise is a reasonable

strategy to detect the effects of environmental forcing. A population with a high growth rate would be expected to track the environmental noise well and so have high CCFs.

For populations showing the type of dynamics associated with very low growth rates (figure 1d–f) correlating the environmental perturbations with population size has some serious limitations. Population numbers are greater than the equilibrium population density when the mean environmental conditions over the past several time steps have been better than the long-term average. During locally unfavourable periods, population numbers are low. This means that the correlation between population size and environmental conditions during the time interval immediately before will be relatively low. The same would be true for populations in which there is no density dependence and population numbers follow a random walk, driven by the environmental noise. This explains why Kaitala and Ranta's methods failed to detect the effects of noise on the population in some cases.

What alternative detection methods are there? Populations with lower growth rates respond to running-average environmental conditions over longer averaging periods. A more appropriate method to detect the overall influence of the environment would be to correlate population size with environmental conditions averaged over several time steps. High frequencies of noise would require a shorter averaging window than low frequencies. However, there are limitations to this approach. Many real time-series of population abundance are short, making detection using average environmental conditions difficult. Also, this approach may increase the possibility of a ‘false alarm’ as averaging the environment will introduce

some serial correlation in the noise. That is, two different noise series of the same colour become more similar if both are averaged over several time steps.

While it is comparatively easy to detect the impacts of noise on the age that is being directly perturbed, detecting the impacts on the other ages can be more difficult. This is especially true if density dependence is operating on all age classes, as in Kaitala & Ranta's (2001) model. Here, the impacts of the noise can become 'blurred' by the density dependence over several time steps. An alternative strategy would be to isolate the short-term effect of the environmental noise by correlating it with the change in population abundance from one time step to the next (first differences of the population time-series). This technique will be most effective in detecting blue noise owing to the higher frequencies.

Useful information may also be gained by correlating the total population abundance with the noise even when correlations with the individual age abundances do not detect the noise. Although arguably less informative than the impacts on individual ages, the impacts on the total population are still important. For example, in the field, total population data are generally easier to gather than abundances of the individual age classes and so this approach has more practical value. This technique is more likely to work with populations with higher growth rates as they tend to track noise better.

There is a final situation in which Kaitala and Ranta's approach will not perform well. Correlation is used to determine the strength of the linear relationship between two or more sets of data (Bendat & Persol 1980). Some density-dependent models (for example the Ricker model) are capable of displaying non-equilibrium dynamics such as quasi-cyclic or chaotic behaviour. The response of a nonlinear system can be strong but not visible from simple correlations (Dixon *et al.* 1999). Attempts by Lundberg *et al.* (2002) to detect noise using correlation in a population regulated by Ricker density dependence showing anything other than equilibrium dynamics have unsurprisingly been unsuccessful. By using correlation, Kaitala and Ranta are making the assumption that there is a linear relationship between the input and the output of the model or that the population fluctuations around the equilibrium are approximately linear. For the model to be considered linear around the equilibrium, the equilibrium needs to be stable and the population must be ergodic. In the absence of noise the semelparous model is periodic. It cannot be considered to be behaving linearly, and using correlation methods is therefore not appropriate. The iteroparous population is ergodic, and calculation of its stability matrix (Nisbet & Gurney 1982) shows that the equilibrium point is stable. Consequently we have concentrated on testing the iteroparous models.

5. CAN THE PERTURBATIONS BE DETECTED?

In the light of the issues discussed in §§ 2 and 3, can we detect the impact of the environmental noise if we adopt more appropriate statistical methods? Kaitala & Ranta (2001) calculated the CCFs of the environmental forcing and the abundances of the individual age classes with lags of 0 to -10 time steps. The higher the value of the CCF, the more visible the impact of the noise was

assumed to be. Kaitala and Ranta present the values of CCFs graphically. Both axes of their plots are discrete but the shading of the plots treats the data as continuous and obscures the actual value of the CCF for each age group and time-lag. To assist comparison, we have presented our results in a similar style, but have kept the data discrete for the sake of clarity.

We first analysed the original iteroparous model, and Kaitala and Ranta's original results were reproduced. Kaitala and Ranta conclude that only red noise for the high growth rate is visible in the individual population stages. However, using the different methods of detecting noise described in § 4 we were able additionally to detect blue and white noise in the individual age classes for both growth rates and all colours of noise in the total population for both growth rates.

When the first differences of the individual population age classes were correlated with the environment it was possible to detect clearly the impact of the disturbance for blue and white noise for both high and low growth rates. Blue noise is more visible because this method will best detect higher frequencies. The irregular shapes of the results generated by Kaitala and Ranta are replaced by clear positive CCFs along the diagonal lag line (figure 2*a-d*). Red noise was also detectable using this method for the high growth rate but the visibility was lower.

When the total population abundance was correlated with the environmental disturbance all three colours of noise were clearly visible when the growth rate was high (figure 2*e*). This is a consequence of the total population being dominated by the first age group, which is also the group that has had the noise applied to it. Correlating the noise with the total population was less successful for the low growth rate, and the noise could not be detected using this method.

The impact of the noise was visible for the low growth rate when correlating the individual age classes with the environment averaged over several time steps. Red noise was less visible with this method but was still apparent in all but the last few age classes. As expected, the length of the averaging window that yielded the highest CCFs was shorter for high frequencies than for low frequencies. Using running averages of the environment it was also possible to detect the impact of the noise in the total population abundance when the growth rate was low (figure 2*f*). This method was not successful for detecting the impacts of the noise in either individual age classes or total abundances when the growth rate was high. All of these results clearly demonstrate that using different, yet still simple, statistical methods can make the impact of the noise visible and that Kaitala and Ranta's conclusions are unduly pessimistic and must be treated with caution.

We have argued in § 2 that some of the reasons for Kaitala and Ranta's failure to detect the impacts of environmental noise are that the model with the high growth rate recovers very quickly from being perturbed and that the model with the low growth rate has extremely low resilience to noise. We briefly looked at the effects of using other growth rates on the visibility of the noise. We found that it was possible to detect the impacts of all colours of noise on the individual age classes for low growth rates using direct CCFs providing that the population fluctuated about an equilibrium. Reducing the amplitude of the

Figure 2. First differences of individual population abundances from the original iteroparous model correlated with environmental noise for: (a) blue noise and high growth rate; (b) white noise and high growth rate; (c) blue noise and low growth rate; and (d) white noise and low growth rate. Total population abundance from the original iteroparous model correlated with (e) the environmental noise when the population growth rate is high and (f) the averaged noise when the growth rate is low (solid line, blue noise; dashed line, white noise; circles, red noise). The maximum CCFs were found with window lengths of 25 for blue and white noise and 40 for red noise.

Figure 3. Individual population abundances correlated with environmental noise when Leslie density dependence is applied to fecundity only and the growth rate is high, for: (a) blue; (b) white; and (c) red noise. When density dependence is applied to the fecundity only the impacts of the noise are less blurred and easier to detect.

noise also increased the visibility of the noise at lower growth rates. Regardless of growth rate, blue and white noise could be detected by correlating the first differences of each age group with the noise. All colours of noise could be detected in the total population providing that the population abundance fluctuated around an equilibrium. When the population showed the outbreaks characteristic of a very low growth rate the noise could be detected by correlating the individual age classes with the environment averaged over several time steps. These results are not

analysed in depth but serve to illustrate further that Kaitala and Ranta's results are partly dependent upon the model's parameters and are not general, a point that they do acknowledge in passing. Stenseth *et al.* (2003, see electronic Appendix A) have drawn attention to some potential problems with Kaitala and Ranta's method of truncating the noise term, particularly regarding distortion of the correlation patterns. Consequently Stenseth *et al.* (2003) warn that Kaitala and Ranta's findings should be interpreted cautiously.

How a population responds to environmental forcing is strongly dependent on the formulation of density dependence. The models used by Kaitala and Ranta include only one formulation: Leslie density dependence applied to both fecundity and survival rates. The effect of using different formulations of density dependence can be illustrated by looking at the iteroparous model but with the density dependence affecting only the fecundity of each age class. The same vital rates for high and low growth rate were used. As before, the CCFs of the input noise and the population abundances of each age class were calculated with lags of 0 to -10 years. The visibility of the impacts of the noise was considerably higher than in the original formulation. When the growth rate was high the maximum CCFs were close to 1 for all age classes (with decreasing time-lag) regardless of the colour of the perturbations (figure 3). When the growth rate was low the visibility of the noise was much lower. However, blue and white noise were detectable when the first differences of individual age-class abundances were correlated with the environment. Red noise could be detected by correlating individual age-class abundances with the environment averaged over several time steps. This demonstrates that the pattern of density dependence can affect how a population responds to environmental perturbations and can subsequently affect the visibility of the impacts.

6. DISCUSSION

We have shown that the formulation of density dependence strongly affects how a population responds to environmental perturbations and the visibility of the impacts of the noise. Density dependence acting on all age classes of a population can 'blur' the environmental perturbations over several time steps making their effects harder to detect. If density dependence is applied only to the fecundities and the population fluctuates about the equilibrium, the impacts of the noise become clearly visible using the standard CCFs. Although we did not pursue this in detail, we have also shown that different growth rates and levels of noise can affect the visibility of the noise. These results show that Kaitala & Ranta's (2001) results are a consequence of the details of the way that their model has been constructed. They do not indicate a general conclusion about the visibility of the impacts of noise.

Our results have also shown that correlating the noise directly with the individual abundances is not always the best way of detecting the impacts of the noise. By examining the population time-series it is possible to decide which other methods may be more useful. If the growth rate is very low and the population does not fluctuate about the equilibrium, it may still be possible to detect the noise by correlating the individual abundances with averaged environmental conditions. The length of the averaging window that yields the highest CCFs can indicate the dominant frequencies of the noise. For low and high growth rates it is also possible to detect blue and white noise by correlating the first differences of the individual age classes with the noise. For higher growth rates correlating noise with the total population abundance can also be useful and is more realistic from a data-collecting perspective.

The results are applicable only to iteroparous models. When the model cannot be considered to be linear, like the semelparous model, analysing the fate of environmental perturbations becomes more complicated. However, there are many examples of nonlinear methods being successfully used in these contexts (Lek *et al.* 1996; Dixon *et al.* 1999; Pascual & Ellner 2000; Pascual *et al.* 2000).

If they hold generally, Kaitala and Ranta's results would have very strong implications for understanding the population ecology of field populations. However, the impacts of the noise can be more visible for other population models. In addition, alternative statistical methods can detect impacts of noise when CCFs fail to do so, meaning that their results are unduly pessimistic.

There is a large body of literature on how systems respond to external forcing. A non-equilibrium system will have a relatively unpredictable response and is often difficult to analyse. The responses of an equilibrium system that can be considered to be linear for small perturbations can vary widely. It has not been the intention of this paper to explore these issues. In a future paper we will be presenting work on how a system's responsiveness to external forcing can be characterized by the stability of the system and the importance of the perturbed vital rate.

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REFERENCES

- Bendat, J. & Persol, A. 1980 *Engineering applications of correlation and spectral analysis*. New York: Wiley.
- Caswell, H. 2001 *Matrix population models: construction, analysis and interpretation*. Sunderland, MA: Sinauer.
- Dixon, P. A., Milicich, M. J. & Sugihara, G. 1999 Episodic fluctuations in larval supply. *Science* **283**, 1528–1530.
- Kaitala, V. & Ranta, E. 2001 Is the impact of environmental noise visible in the dynamics of age-structured populations? *Proc. R. Soc. Lond. B* **268**, 1769–1774. (DOI 10.1098/rspb.2001.1718.)
- Lek, S., Delacoste, M., Baran, P., Dimopoulos, I., Lauga, J. & Aulagnier, S. 1996 Application of neural networks to modelling nonlinear relationships in ecology. *Ecol. Model.* **90**, 39–52.
- Lundberg, P., Ripa, J., Kaitala, V. & Ranta, E. 2002 Visibility of demography-modulating noise in population dynamics. *Oikos* **96**, 379–382.
- Nisbet, R. M. & Gurney, W. S. C. 1982 *Modelling fluctuating populations*. Chichester: Wiley.
- Pascual, M. & Ellner, S. P. 2000 Linking ecological patterns to environmental forcing via nonlinear time series models. *Ecology* **81**, 2767–2780.
- Pascual, M., Rodo, X., Ellner, S. P., Colwell, R. & Bouma, M. J. 2000 Cholera dynamics and El Niño-Southern Oscillation. *Science* **289**, 1766–1769.
- Stenseth, N. C., Ottersen, G., Hurrell, J. W., Mysterud, A., Lima, M., Chan, K. S., Yoccoz, N. G. & Adlandsvik, B. 2003 Studying climate effects on ecology through the use of climate indices: the North Atlantic Oscillation, El Niño Southern Oscillation and beyond. *Proc. R. Soc. Lond. B* **270**, 2087–2096. (DOI 10.1098/rspb.2003.2415.)
- Sugihara, G. 1996 Red/blue chaotic power spectra. *Nature* **381**, 198–199.
- Turchin, P. & Ellner, S. P. 2000 Living on the edge of chaos: population dynamics of Fennoscandian voles. *Ecology* **81**, 3099–3116.