Ann. Zool. Fennici 34: 217–228 ISSN 0003-455X
Helsinki 31 December 1997

Red, blue and green: Dyeing population dynamics

Veijo Kaitala, Per Lundberg, Jörgen Ripa & Janica Ylikarjula

Kaitala, V., Department of Biological and Environmental Science, University of Jyväskylä, P. O. Box 35, FIN-40351 Jyväskylä, Finland; alternative address: Integrative Ecology Unit, Division of Population Biology, P. O. Box 17, FIN-00014 University of Helsinki, Finland
Lundberg, P. & Ripa, J., Department of Theoretical Ecology, Ecology Building, Lund University, S-223 62 Lund, Sweden
Ylikarjula, J., Systems Analysis Laboratory, P. O. Box 1100, FIN-02015 Helsinki University of Technology, Finland

Received 3 October 1997, accepted 19 November 1997

Numbers or densities of a natural population typically change over time. These fluctuations result from density-dependence mechanisms in the populations or external environmental variations. According to modern ecological research, time series describing population sizes and physical environments tend to be dominated by low-frequency fluctuations, whereas, contrary to this, simple population dynamic models are mostly dominated by short-term fluctuations. We review the recent theoretical advances in this ecological research theme, referred to as the ecological colour problem. Here population dynamics are analysed in the frequency domain, and named, in analogy of the light wave length, red, white or blue. We emphasise the modern tendency of deriving population ecological insight from dynamic, non-equilibrium analyses. We first deal with deterministic and stochastic single-species population dynamics. We then study how simple communities may respond to environmental noise. We finish by raising the important problem of how the colour of the environmental noise may affect the risk of population extinction.

1. Introduction

The very notion of population dynamics implies that numbers, or density, are changing over time. These population fluctuations are the result of density-dependent feedback mechanisms and external variations in the environment. External influences may be periodic (e.g. seasonal changes) or apparently random fluctuations in the environment (‘noise’). Inevitably, inherent and external forces interact producing observed patterns in population fluctuations. Explaining population

---

Acknowledgements. We thank J. Brown, Mikko Heino, E. Ranta and A. White for discussions about the ecological colour problem. V. K. and J. Y. thank the laughing Department of Theoretical Ecology at the Lund University for the joyful working environment. This work was supported by the Academy of Finland, NorFA, the Swedish Natural Science Research Council, and the Swedish Research Council for Forestry and Agriculture.

fluctuations has become one of the most popular endeavours in population ecology. Substantial interest has been devoted to density-dependent mechanisms, whether they be intraspecific or the result of interactions with other species through competition or predation. Regular multiannual fluctuations, or 'cycles', have been of considerable interest for decades. In this paper, we will approach such problems from a different angle. Instead of focusing on population changes in the time domain (e.g. whether population time series are autocorrelated), the frequency domain of observed time series will be our topic.

Long-term data on population fluctuations and physical environments suggest that such variations are dominated by low-frequency fluctuations (Steele 1985, Lawton 1988, Pimm & Redfearn 1988, Pimm 1991, Sugihara 1995, Halley 1996). This means that if the frequency composition of the time series is analysed, longer wavelengths are more prominent than short ones. Spectral analysis is a statistical tool kit that enables us to do this decomposition of time series. In analogy with the wavelength composition of light, time series that are dominated by low-frequency variations are referred to as 'red', and those dominated by high-frequency fluctuations are called 'blue'. In a 'white' time series, there is no particular frequency that dominates.

By decomposing the time series into spectral frequencies we may ask whether populations are inherently stable, cyclical, or chaotic. We may also focus on the interplay between whatever internal dynamics the population may have, and its stochastic environment. This is fundamental not only for our understanding of the dynamics of populations in general, but also for very practical purposes — population persistence and extinction, their management and conservation. This approach also highlights a more epistemological problem. An ecological time series hides three distinguishable, albeit not mutually exclusive components; the internal dynamics, interactions with other populations, and the (stochastic) physical environment. How much can possibly be discerned given that all that is available is an ecological time series? This relates both to the classic signal-to-noise problem and whether we can reduce the dimensionality of an ecological system, and if so, how far?

In this paper, we review and summarise recent attempts to address these issues. We will start by analysing discrete-time deterministic population dynamics in the frequency domain, showing that the most elementary model hardly produce red power spectra. The dynamics of these models can be made less blue e.g. by introducing delays in the model. We proceed by examining single-species dynamics in a stochastic environment showing that, in the equilibrium range of the deterministic dynamics, environmental noise may dye population dynamics either red or blue. We then study simple communities and their response to environmental noise. We also address the important problem of how the colour of the environmental noise may enhance or reduce the risk of population extinction. Apart from discussing the spectral properties of these systems, we will also deal with the more general problem of endogenous and external factors influencing population time series.

2. Deterministic population dynamics — the role of intrinsic factors and population interactions

2.1. Single-species models

The most famous discrete-time population model is the non-linear Moran-Ricker model (Moran 1950, Ricker 1954), in which the dynamics are given as:

$$P_{t+1} = P_t \exp[r(1 - \mathrm{P}_t)], \quad (1)$$

where P_t is the population size in generation t, t = 1, 2, … , and r is the density-independent per capita growth rate of the population. The surprisingly complicated dynamics of this simple model was one of the great discoveries in population biology in the 70s (May 1974, 1976, May & Oster 1976). As the growth rate increases the population dynamics are first locally stable, then become periodic, and ultimately, through a series of period-doublings, chaotic. Ever since, the population biologists have attempted to detect chaos, and other forms of complicated dynamics in natural population dynamics (Sugihara & May 1990, Cazelles & Ferrière 1992, Stone 1993, Hastings *et al.* 1993, Cohen 1995, Kaitala & Ranta 1996)

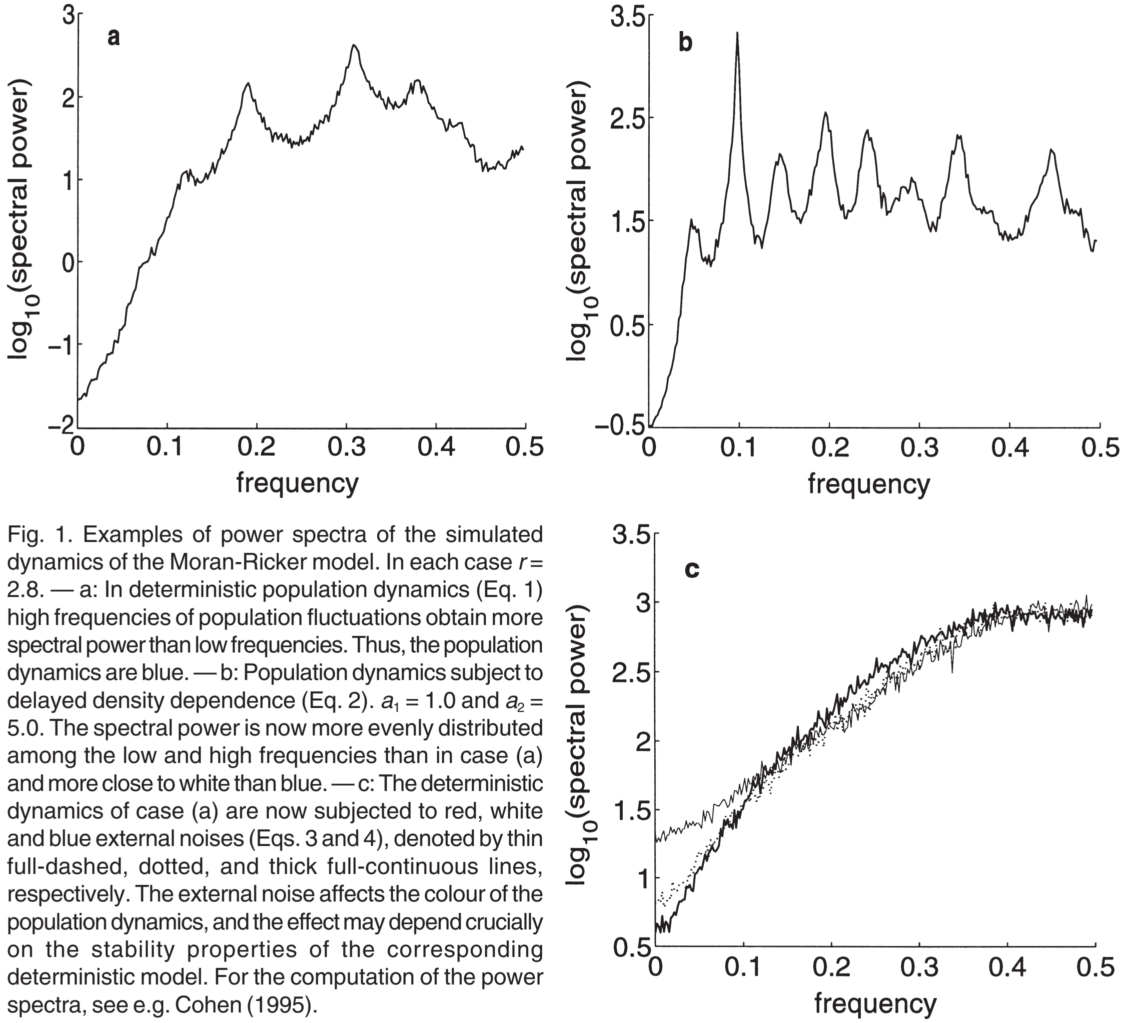

Fig. 1. Examples of power spectra of the simulated dynamics of the Moran-Ricker model. In each case $r = 2.8$. — a: In deterministic population dynamics (Eq. 1) high frequencies of population fluctuations obtain more spectral power than low frequencies. Thus, the population dynamics are blue. — b: Population dynamics subject to delayed density dependence (Eq. 2). $a_1 = 1.0$ and $a_2 = 5.0$. The spectral power is now more evenly distributed among the low and high frequencies than in case (a) and more close to white than blue. — c: The deterministic dynamics of case (a) are now subjected to red, white and blue external noises (Eqs. 3 and 4), denoted by thin full-dashed, dotted, and thick full-continuous lines, respectively. The external noise affects the colour of the population dynamics, and the effect may depend crucially on the stability properties of the corresponding deterministic model. For the computation of the power spectra, see e.g. Cohen (1995).

without any major success. However, a possible breakthrough may be in sight. R. F. Costantino and his co-workers have recently been able to verify experimentally different types of population dynamics and bifurcation diagrams predicted by the nonlinear age-structured model of the flour beetles of the genus *Tribolium* (Costantino *et al.* 1995, 1997, Dennis *et al.* 1995, Desharnais *et al.* 1997).

Stability properties and the types of the ultimate dynamics, that is, attractors, are only one part of the classification of the population dynamics. A more detailed study of time series in the frequency domain reveals that there are qualitatively different types of dynamics even within the classes of periodic or chaotic dynamics. This problem of the colour of the population dynamics has recently given rise to a number of theoretical population dynamics studies. Cohen (1995), when analysing chaotic dynamics of simple nonlinear population models, observed that chaotic time series produced by these models are without exception dominated by high frequencies, that is, the population dynamics are blue. This was argued to be in contradiction with the empirical observations that ecological time series tend to be red. Thus, a puzzle was born.

Cohen (1995) showed in particular that the power spectra densities of the Moran-Ricker model, as well as of the seven other models, are predominantly blue with greater power at high frequencies (Fig. 1a). The results are summarised so that the power spectra of each of the population fluctuations studied was on average at least two orders of magnitude higher at high frequencies than the power at low frequencies. Blarer and Doebeli (1996) and White *et al.* (1996b) commented on these results showing that in the eight basic models analysed by Cohen (1995), the colour of chaotic dynamics may change for different parameter values, and furthermore, the type of the density dependence may crucially affect the colour of the population dynamics.

2.2. Delayed-density dependence

Kaitala and Ranta (1996) re-analysed the power spectra of chaotic trajectories of six deterministic autonomous non-linear population models by using a modification incorporating delayed-density dependence into the model dynamics. For example, model (1) is now replaced by:

$$P_{t+1} = P_t \exp[r(1 - a_1Pt - a_2P_{t-1})], \qquad (2)$$

where a_1 and a_2 are parameters.

The results by Kaitala and Ranta (1996) showed that adding delayed-density dependence in the population models may remove the dominance of the high-frequency oscillations and may whiten or redden the frequency distribution of the population dynamics (Fig. 1b). It should be noted that a single population model including delayed-density dependence can also be used to describe interactions between different species or different cohorts of the same species (Turchin & Taylor 1992).

Kaitala and Ranta (1996) drew our attention to the route to chaos in explaining their results. They argued that the simplest population dynamic models, having their own merits, may be of limited use in explaining the fluctuations of natural populations. Among the several routes to chaos (period-doubling route, quasiperiodic route, and intermittency, May 1974, 1976, Hastings *et al.* 1993) the simple population dynamics models generate the period-doubling route, and sometimes intermittency, but never the quasiperiodic route. Nevertheless, the route to chaos may be connected to fundamental differences in the power spectra of the chaotic solutions. For example, the quasiperiodic route to chaos often occurs in the context of species or population interactions (Kaitala & Heino 1996), or in age-class interactions in a single population (e.g. Costantino *et al.* 1995). Delayed-density dependence may also produce the quasiperiodic route to chaos, which may produce more red power spectra than the period-doubling route.

3. Spatial dimension of the population dynamics

Populations seldom live in one spot but are spatially distributed. Introducing spatial dimension into population dynamics, e.g. through dispersal, has been observed to result in a variety of heterogeneous temporal and spatial patterns. The patterns, identified so far by the theoretical models, include different kinds of waves, lattices and spatial synchrony patterns (Bascompte & Solé 1995, Ranta *et al.* 1995, Ranta & Kaitala 1997, Ranta *et al.* 1997abc).

The implications of spatial structure to the colour of the population dynamics was studied by White *et al.* (1996a) who showed that spatial population structure may give rise to reddened spectra. Their spatial model included also host–parasite interactions, although White *et al.* (1996b) tend to overlook this aspect in favour of spatial structure in explaining the reddened population dynamics. Thus, convincing studies on the role of space on the colour of population dynamics seem to be missing.

4. The interaction between population dynamics and environmental noise

During the debate following Cohen's results (recall section 2.1) Sugihara (1995) suggested that environmental fluctuations possibly need to be incorporated. Indeed, the colour of environmental noise affects the colour of the power spectrum of the population time series. This dependence was studied by Kaitala *et al.* (1997) who showed that adding white noise to stable population dynamics will make the population dynamics either red or blue, depending on the value of the population growth rate or the type of density dependence. Population dynamics that are subjected to red and blue environmental noise show respectively more red or blue power spectra than those subjected to white noise.

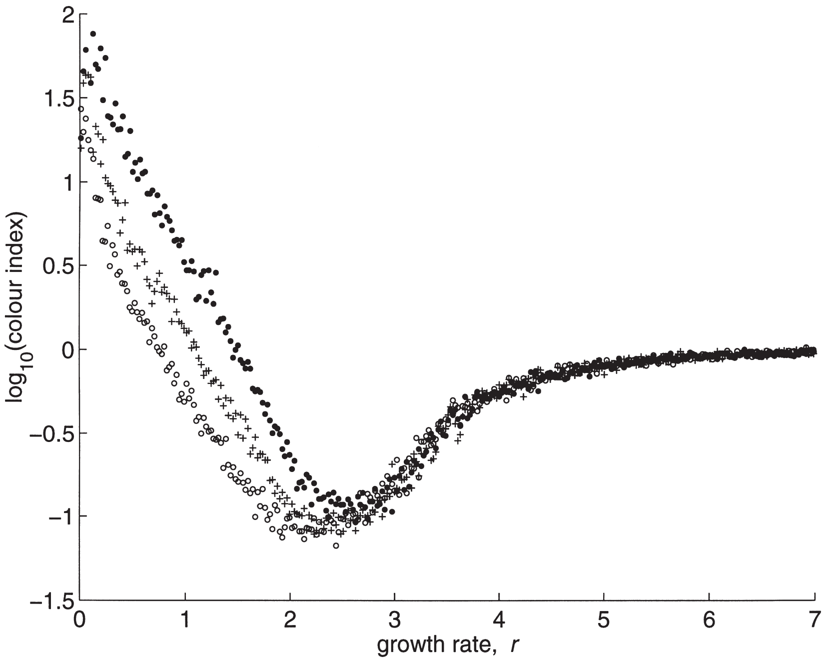

Fig. 2. The logarithms of the colour indices as a function of the intrinsic growth rate *r* in the Moran-Ricker model. Notations ‘o’, ‘+’ and ‘•’ correspond to blue, white, and red environmental noises, respectively. Positive and negative colour indices indicate red and blue population dynamics, respectively. The different effects of red, white and blue noises are most distinctive in the stable area ($r < 2$) of the deterministic population dynamics.

Kaitala *et al.* (1997) studied the colour problem using two discrete time models, a simple Moran-Ricker (Moran 1950, Ricker 1954) and a more sophisticated Maynard Smith (Maynard Smith 1974) model. In both cases, the coloured noise was added to the population size by using a multiplicative form. The colour index (Blarer & Doebeli 1996), i.e. the ratio between the area under the spectrum ranging from 0 to 0.25 to the area ranging from 0.25 to 0.5, was used to explore the effects of the coloured noise on the population dynamics. If the logarithm of the colour index is positive, the power spectrum is red, and if it is negative the spectrum is blue.

4.1. Moran-Ricker model

In their simulations, Kaitala *et al.* (1997) subjected the population dynamics to environmental noise of different colours, and assumed a multiplicative effect of the noise yielding the following population dynamics:

$$P_{t+1} = P_t f(P_t)(1 + d_t), \tag{3}$$

where $f(P_t) = \exp[r(1 - P_t)]$ is the per capita growth rate, and d_t is a coloured environmental noise generated by:

$$d_{t+1} = cd_t + \mathrm{w}_t, \tag{4}$$

where w_t is a random variable (i.i.d., uniformly distributed on the interval $(-0.5, 0.5)$). This process yields power spectra of the coloured noise as red, white, and blue for $c >, =,$ and < 0, respectively.

In the stable region of the deterministic dynamics ($r < 2$) the colour of the environmental noise strongly affects the colour of the population dynamics (Fig. 2). For low values of the intrinsic growth rate ($r < 0.8$), the dynamics are red, turning to blue with increasing growth rate. Red population dynamics are observed for low values of r even for white and blue environmental noises, and blue population dynamics are discovered for higher values of r ($1.5 < r < 2$) even for white and red environmental noises. The colour of population dynamics subjected to environmental noise could be determined by the different approaches to equilibrium. For $0 < r < 1$ the approach to equilibrium is exponential and non-oscillatory. This means that the time series are positively autocorrelated and therefore the dominance of the long-term trends and reddened spectra are expected. The oscillatory approach for $1 < r < 2$, however, implies negative autocorrelations and, thus, blue spectra.

In the stable region for each value of r, the colour of the population dynamics is affected by the colour of the environmental noise: red and blue environmental noises cause, respectively, more red and blue spectra of the population dynamics, as compared with the colour under white noise. Thus, stable population dynamics are sensitive to the colour of the environmental noise (Kaitala *et al.* 1997). Especially for $r \approx 1$ the colour of the environmental noise determines the colour of the population dynamics.

When the coloured noise is superimposed on the population dynamics, the power spectra remain blue for the whole interval of the period-doubling cascade ($2.0 < r < 2.6924$). However, for $2.0 < r < 2.4$, the difference of the environmental colour can be discovered but this sensitivity to the differences in the environmental colours vanishes as the dynamics approach the chaotic region with increasing r.

For $r > 2.6924$ the deterministic population dynamics turn to chaos. In this range the difference between the different coloured environmental noises seems to be minor, as compared with the differences observed for the stable and periodic regions of the population dynamics. Nevertheless, the colour of the environmental noise still maintains its ability to affect the colour of the population dynamics (Fig. 1c). Furthermore, with increasing growth rate the colour of the power spectrum approaches that of white, irrespective of the colour of the environmental noise.

4.2. Maynard Smith model

To check the robustness of the results produced by the Moran-Ricker model, Kaitala *et al.* (1997) repeated the analysis, also applying the Maynard Smith model in Eq. 3 so that $f(P_t) = r/(1 + (aP_t)^b)$, where a and b are parameters. The findings reported above were discovered also with this model for high growth rates when the strength of density dependence b was varied. However, for low growth rates the power spectra of the population dynamics with noise are red in stable, periodic and aperiodic ranges irrespective of the noise colour. Chaotic population fluctuations may show blue spectra in the deterministic case, and thus, blue deterministic chaos may become red under any colour of the noise. However, Kaitala *et al.* (1997) did not observe the opposite — red dynamics turning blue.

Analysis of the Maynard Smith model shows that the stability properties of the model do not alone determine the colour of the dynamics under environmental noise — different combinations of growth rate and density dependence may produce qualitatively different results. This was observed in the stable region of the model by maintaining the derivative at the equilibrium constant but changing the values of r and b. The results show that although the equilibrium population size of the undisturbed model remains equally stable, the disturbed dynamics may be blue or red.

5. Food chains and sensitivity to environmental noise

The obvious restriction in previous models has been the predominant use of single-species models. It is true that much of the multidimensional reality can be reduced by built-in time-lags in single-species models (Turchin 1990, Royama 1992, Kaitala *et al.* 1997), but it is inevitable that an analysis of entire food webs will reveal new features of stochastic processes in natural populations. Considering larger systems of interacting species also enables us to ask questions about how disturbances of one or more parts in a system are transferred to other parts or how such disturbances might become absorbed. Also, the question is whether different trophic levels or different types of community components (e.g., omnivores, squeezed-in competitors) respond to, and transfer external noise differently. As in all ecological modeling, increased dimensionality decreases tractability, especially if we are interested in stochastic processes.

When we move onto multispecies systems, we generally have to make a number of critical assumptions about the exact nature of the species interactions. This is not a trivial task, and the choice of competitive terms and the functional response of predators, among other things, may tremendously influence the outcome of the analysis. In the first serious attempt to understand the general effects of external noise on simple food webs, Ripa *et al.* (1998) solved that problem by letting the type of interaction in the web be unspecified and expressed in very general terms.

Their results also turned out to be perfectly general. We will here summarize those results and point out directions for future studies of this important topic.

Ripa *et al.* (1998) chose to start analysing the problem with the simplest possible food web; a two-species system, $N_1(t)$ and $N_2(t)$ (the densities of the two populations at time t), with a single noise factor:

$$\begin{cases} N_1(t+1) = f_1\big(N_1(t), N_2(t), z(t)\big) \\ N_2(t+1) = f_2\big(N_1(t), N_2(t), z(t)\big) \end{cases}, \tag{5}$$

where f_i denotes the density-dependent recruitment function for species i. The factor $z(t)$ is any kind of stochastic element in the model, it could be a stochastic model parameter or an additive or multiplicative noise factor, possibly density-dependent, to account for different kinds of demographic or environmental stochasticity (see also Ripa & Lundberg 1996 for how noise can be included in the model). Now suppose that an equilibrium point exists for this system, taken at the average value of the stochastic factor, $E(z(t)) = z^*$. The stability of the equilibrium is determined by the Jacobian matrix:

$$J = \begin{bmatrix} J_{11} & J_{12} \\ J_{21} & J_{22} \end{bmatrix} = \begin{bmatrix} \dfrac{\partial f_1\big(N_1^*, N_2^*, z^*\big)}{\partial N_1} & \dfrac{\partial f_1\big(N_1^*, N_2^*, z^*\big)}{\partial N_2} \\ \dfrac{\partial f_2\big(N_1^*, N_2^*, z^*\big)}{\partial N_1} & \dfrac{\partial f_2\big(N_1^*, N_2^*, z^*\big)}{\partial N_2} \end{bmatrix}$$

where Ni^* denotes the equilibrium density of the respective population. The Jacobian helps us to determine the stability properties of the system. Let us suppose that the equilibrium point is stable and that we, as a thought-experiment, displace the system a small part away from the equilibrium. If the equilibrium is stable, and the stochastic disturbances are small, the system will stay in the neighbourhood of the equilibrium, and it is justified to use a linearised version of it. With all higher order terms eliminated, the system then takes the form:

$$\begin{cases} x_1(t+1) = J_{11}\,x_1(t) + J_{12}\,x_2(t) + \dfrac{\partial f_1}{\partial z}\big(N_1^*, N_2^*, z^*\big) \times \zeta(t) \\ x_2(t+1) = J_{21}\,x_1(t) + J_{22}\,x_2(t) + \dfrac{\partial f_2}{\partial z}\big(N_1^*, N_2^*, z^*\big) \times \zeta(t) \end{cases}, \tag{6}$$

where $x_i(t) = N_i(t) - N_i^*$, and $\zeta(t) = z(t) - z^*$, or, in a vector form:

$$\boldsymbol{x}(t+1) = \boldsymbol{J}\boldsymbol{x}(t) + \boldsymbol{g}^*\zeta z(t),\ \boldsymbol{g}^* = \begin{bmatrix} \dfrac{\partial f_1\big(N_1^*, N_2^*, z^*\big)}{\partial z} \\ \dfrac{\partial f_2\big(N_1^*, N_2^*, z^*\big)}{\partial z} \end{bmatrix} \tag{7}$$

This is the system that is the subject for further analysis.

5.1. Frequency analysis

Ripa *et al.* (1998) proceeded their analysis of the influence of noise on the simple food web by first noting that the vector $\boldsymbol{g}^*$ contains the standard deviations of the external noise at each trophic level, i.e., the strength of the disturbance at each level. An element equal to zero means that this specific population is not directly influenced by the noise. Second, they performed a frequency analysis of the linear system (6), giving the explicit power spectra of the populations:

$$\boldsymbol{P}_x(f) = |(\mathrm{e}^{i2\pi f}\boldsymbol{I} - J)^{-1}\boldsymbol{g}^*|^2 P_z(f), \tag{8}$$

where I is the identity matrix, $|\ldots|^2$ denotes element-wise squared magnitude, $\boldsymbol{P}_x(f)$ is a vector of power spectra for each population and $P_z(f)$ is the power spectrum of the external noise $z(t)$, which all are functions of f, frequency. An attractive feature of this somewhat cumbersome expression is that J, the Jacobian of the system under study, enters nicely. In fact, Eq. 8 on its own, yields the whole predicted power spectra of the populations in the food web. It is general and independent of food web size and structure. The only assumption so far is that the system can be linearised around its equilibrium. This is a very profound result; if we know the properties (i.e., the power spectrum) of the noise and the Jacobian (i.e., the direction and magnitudes of intra- and interspecific-density dependencies), the resulting power spectra of all the populations in the food web are known!

Now we return to the two-species case, where further predictions emerge. Suppose only species 1 is subject to external noise ($g_2 = 0$). Then the ratio of the power spectra of the two populations can be shown to be (Ripa *et al.* 1998).

$$\frac{P_1(f)}{P_2(f)} = \frac{1 + J_{22}^2 - 2J_{22}\cos(2\pi f)}{J_{21}^2} \tag{9}$$

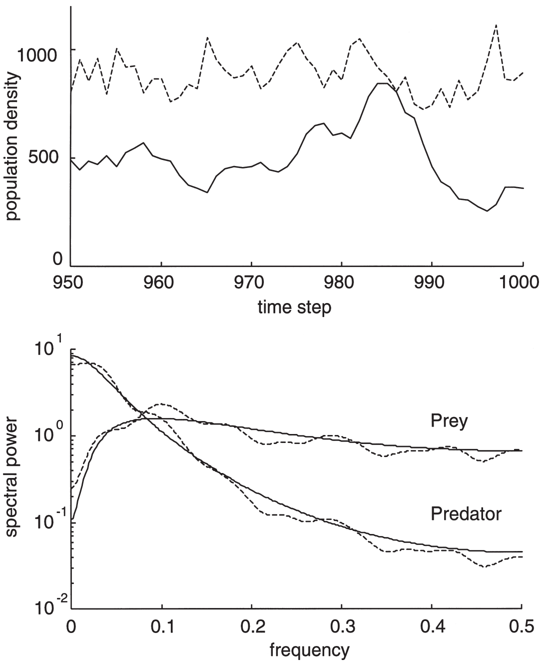

Fig. 3. The last 50 years of the simulated time series of predators (time 50; solid line) and prey (dashed line) according to Eq. 9 with white external noise with zero mean and variance equal to 0.12 affecting the prey population. Lower panel shows the corresponding power spectra (dashed lines) for the two populations along with the predicted spectra (solid lines) according to the linearized version of Eq. 9. The parameter values in Eq. 9 were r = 1.0, K = 1 000, a = 0.012, c = 0.1. The equilibrium densities were 883 and 9.7 for prey and predator, respectively.

Note that this ratio is independent of the noise spectrum. This is an *increasing* function in the appropriate frequency interval ($0 \leq f \leq 0.5$) if and only if J_{22} is positive. If the ratio (9) is increasing, the spectrum of population 1 will be more dominated by high frequencies than population 2's spectrum. Population 1 will therefore have a bluer spectrum than population 2. A negative J_{22} gives a decreasing function, and the opposite relationship between the colours of the two power spectra. Of course, the numbering of the species is arbitrary. Ripa *et al.* (1998) thus reach the following conclusion regarding the resulting spectra of a two-species food web: If population 1 is subject to external noise, the sign of one single element of the Jacobian matrix, J_{22}, determines the relative noise response by the populations. Whenever J_{22} is positive (negative), population 1 will be more blue (red) than population 2.

Let us illustrate this fundamental result with a simple example. This is the well-known Beddington *et al.* (1975) predator–prey model with multiplicative noise at the prey level:

$$\begin{cases} N(t+1) = N(t)e^{r\left(1-\frac{N(t)}{K}\right)}e^{-aP(t)}\left(1+z(t)\right) \\ \qquad P(t+1) = cN\left(t-e^{-aP(t)}\right) \end{cases}, \quad z(t) \in N\left(0, s^2\right), \tag{10}$$

where K is the carrying capacity, c is the average number of predator progeny produced per prey attacked, and s^2 is the variance of the noise term. Fig. 3 shows the power spectra of the two populations resulting from a simulation of this system with white noise. First, note the good correspondence between the predicted power spectra (Eq. 6) and the power spectra calculated from the simulated time series, although the disturbing noise has a quite large amplitude and the populations often move far away from the equilibrium densities. Secondly, it is readily shown that J_{22} of the Jacobian matrix of model (Eq. 10) is always positive. Hence, the principle of relative spectrum colour predicts that the prey spectrum will be more blue, i.e. more dominated by high frequencies, than the predator spectrum (Fig. 3).

Apart from the very simple rule determining the relative frequency response by interacting species, our results also have some important ramifications for how we interpret the colour of real ecological time series. It has been suggested that the red-shifted population time series we often observe in natural systems is a direct result of the colour of the environmental fluctuations (Pimm 1991, Powell & Steele 1995) or other properties of the environment, e.g. spatial structure (White *et al.* 1996a). Alternatively, most populations are inherently 'red' and the power spectrum we are able to detect is by and large unaffected by environmental stochasticity. This would be true if, for example, the population is governed by sufficiently strong time-delayed density dependence (which tends to redden the spectrum) that override the external noise signal (Ranta *et al.* 1995, Kaitala & Ranta 1996, Kaitala *et al.* 1997). We know, however, that the interplay between internal dynamics and external noise may produce a wide variety of frequency responses in the time series so that the observed spectrum may say very little about the relative contribution of the internal and external determination of its properties

(Cohen 1995, Blarer & Doebeli 1996, Kaitala *et al*. 1997). Our results further emphasize this problem. If a population is embedded in a food web, which all populations are, the interactions themselves may significantly modify the expected frequency response, and differently so for different components of the web. We therefore propose that all interpretations of ecological time series in the frequency domain must be accompanied by at least rudimentary knowledge about: (1) the nature of the external noise, (2) the basic properties of the internal dynamics, and (3) the basic food web structure in which the focal population is embedded.

Although this requires a whole lot of detailed ecological knowledge, we nevertheless feel that our results hint at an interesting way of gaining some insight into this problem. Determining food web structure is not a trivial issue, either from a philosophical or practical point of view. We note, however, that in our simple system, only the sign of one of the elements in the community matrix (the Jacobian) is of importance. It is not an impossible task to determine this in real systems, provided that we safely can reduce the dimensionality of the web. We therefore call for a cautious interpretation of frequency analyses of ecological time series unless food web structure is taken into account. The basic problem of the lack of long time series remains, of course, but without properly accounting for food web structure the enigmas of fluctuating population dynamics will remain.

6. Noise colour and extinction risk

A recurrent problem in ecology and conservation biology is to estimate the risk of population extinction. Extinction probabilities are not only imperative for conservation and management, but may also elucidate basic mechanisms of the regulation of natural populations (Pimm 1991, Burgman *et al*. 1993). One of the crucial steps in risk calculations is the formulation of the stochastic parts of the model. The usual way of modeling stochastic influence on population dynamics has been to assume that the external noise is uncorrelated, or white. As it has been pointed out by several authors (Steele 1985, Ariño & Pimm 1995, Caswell & Cohen 1995, Halley 1996, and others), this might not be the best choice. Abiotic factors tend to have reddened spectra, hence they are autocorrelated. What implications does this observation give us in the context of extinction risk assessments? Does an autocorrelated environment increase or decrease the risk of population extinction? What kind of autocorrelation is appropriate?

Strebel (1985) carried out a preliminary analysis of the topic. He analyzed a continuous time logistic model with variations in the carrying capacity K. In Strebel's model, fluctuations with a characteristic 'correlation time', depending on the intrinsic growth rate r, were severe to the population, whereas faster or slower fluctuations were not as dangerous. Johst and Wissel (1997) observed that extinction risk increases with correlation time if the strength of the noise is large enough.

Mode and Jacobson (1987ab) used an AR(2) environment process that, transformed, controlled mortality and nativity in an age-structured, density-independent population model. They found that the extinction risk greatly depended on the characteristics of the environmental process, such as its autocorrelation function or its variance. For instance, a more positively autocorrelated environment increased the extinction risk, even if the variation of the environment was kept constant. Not surprisingly, a largely fluctuating environment was more hazardous to a population than a relatively constant environment.

Ripa and Lundberg (1996) investigated the well known Moran-Ricker equation and its sensitivity to autocorrelated noise in the form of an AR(1) process. Their results were much the same as Mode and Jacobson (1987ab), only they found that increased autocorrelation seemed to decrease, not increase, the risk of extinction. These results were more thoroughly investigated by M. Heino and V. Kaitala (unpubl.) and M. Heino (unpubl.). By investigating different model structures related to age, space and noise scaling they showed that the question whether increased autocorrelation in the environmental fluctuations increased or decreased the extinction risk of a population did not have a straightforward answer.

It remains as a general result, though, that the attributes of the environmental fluctuations in a population dynamic model are of paramount importance for the estimated risk of extinction. This calls for very careful modeling of stochastic population dynamic systems and points to the need for more knowledge of the way in which abiotic factors influence biological systems, how they are connected and on what time scale the influence is taking place.

7. Concluding remarks

The study of the interplay between external noise and ecological system has just begun. The first attempts to add an arbitrary noise signal to an arbitrary ecological model were obviously incomplete, although the very idea of including the inevitably noisy component of the world into models of natural populations certainly is welcome. Science always has the delicate task of finding the adequate balance between simplicity and realism and one may argue that the wonderful simplicity of purely deterministic population models is to be preferred. It all depends, of course, on what kind of problem we are addressing. We will not, however, be able to avoid uncertainty, i.e., random events that we cannot control or predict. This is perhaps most obvious in population management (including harvesting) and in conservation biology. If we do not understand what estimation errors or a noisy environment can do to harvested or otherwise vulnerable populations, we will never be able to minimize extinction risks and maintain natural biological diversity.

We have learned that one of the most prominent properties of ecological time series in the frequency domain, i.e. the red-shift, does not necessarily say anything about either the nature of the environmental noise, or the systems affected by it. Instead of asking whether there is a single cause for most time series to share this common property, we should perhaps ask what makes an ecological system (population, food web) robust to external environmental noise. Also, can such noise signals do other things to the populations so that we may be fooled about the true nature of the dynamics by just scrutinizing the time series as such? The interplay between internal dynamics and external variability is apparently rich in possible net results. To understand more about this interplay also helps us understand how to disentangle the two players. If the noise is out of influences' reach, the deterministic components of the vital rates of the population may not be. Thus, knowing what kind of systems are sensitive to what kind of noise (and how) may help us not only to understand very fundamental population processes, but also how to moderate potentially detrimental affects from stochastic fluctuations in the environment. Therefore, the study of larger food webs and environmental stochasticity should be high up on the agenda.

Demographic noise is one source of stochasticity that we have not dealt with here. This is not because we think that it is unimportant, on the contrary, but we feel that it is such a built-in part of the internal dynamics. The interplay between demographic and environmental stochasticity is in itself an intriguing issue and we have dealt with it elsewhere (P. Lundberg & J. Ripa unpubl.). We also have omitted a more detailed analysis of systems in continuous time. Again, it is not because that approach is irrelevant or unimportant. Stochastic continuous time models are, however, considerably more complicated, and we hope to have sacrificed completeness to simplicity, although not all not-so-mathematically inclined readers may agree.

Analysing population dynamics in the frequency domain certainly adds new tools to the analytical toolbox for studies of changes of population number and distribution. We must not forget, however, that this approach, just as any other, must build on reasonable assumption about the biological mechanisms behind changes in vital rates (births and deaths). New statistical methods for time series analysis, as well as better model representations of biological populations are both wanted and badly needed for understanding successfully both the remarkable stability of some populations and the dramatic changes in abundance over time in others. Let us go and look for them!

References

Ariño, A. & Pimm, S. L. 1995: On the nature of population extremes. — Evol. Ecol. 9: 429–443.

Bascompte, J. & Sol, R.V. 1995: Rethinking complexity: modelling spatiotemporal dynamics in ecology. — Trends Ecol. Evol. 10: 361–366.

Beddington, J. R., Free, C. A. & Lawton, J. H. 1975: Dynamic complexity in predator–prey models framed in difference equations. — Nature 255: 58–60.

Blarer, A. & Doebeli, M. 1996: In the red zone. — Nature 380: 589–590.

Burgman, M. A., Ferson, S. & Akçakaya, H. R. 1993: Risk assessment in conservation biology — Chapman & Hall, London.

Caswell, H. & Cohen, J. E. 1995: Red, white and blue: environmental variance spectra and coexistence in metapopulations. — J. Theor. Biol. 186: 301–316.

Cazelles, B. & Ferrire, R. H. 1992: How predictable is chaos. — Nature 355: 25–26.

Cohen, J. E. 1995: Unexpected dominance of high frequencies in chaotic nonlinear population models. — Nature 378: 610–612.

Costantino, R. F., Cushing, J. M., Dennis, B. & Desharnais, R. A. 1995: Experimentally induced transitions in the dynamic behavior of insect populations. — Nature 375: 227–230.

Costantino, R. F., Desharnais, R. A., Cushing, J. M., & Dennis, B. 1997: Chaotic dynamics in an insect population. — Science 275: 389–391.

Dennis, B., Desharnais, R. A., Cushing, J. M. & Costantino, R. F. 1995: Nonlinear demographic dynamics: mathematical models, statistical methods, and biological experiments. — Ecological Monographs 65: 261–281.

Desharnais, R. A., Costantino, R. F., Cushing, J. M. & Dennis, B. 1997: Estimating chaos in an insect population. Reply to Perry et al. — Science 276: 1881–1882.

Halley, J. M. 1996: Ecology, evolution and 1/f noise. — Trends Ecol. Evol. 11: 33–38.

Hastings, A., Holm, C. L., Ellner, S., Turchin, P. & Godfray, H. C. J. 1993: Chaos in ecology: is mother nature a strange attractor. — Ann. Rev. Ecol. Syst. 24: 1–33.

Johst, K. & Wissel, C. 1997: Extinction risk in a temporally correlated fluctuating environment. — Theor. Pop. Biol. 52: 19–100.

Kaitala, V. & Heino, M. 1996: Complex nonuniqueness in ecological interactions. — Proc. R. Soc. Lond. B 263: 1011–1013.

Kaitala, V. & Ranta, E. 1996: Red/blue chaotic power spectra. — Nature 381: 198–199.

Kaitala, V., Ylikarjula, J., Ranta, E. & Lundberg, P. 1997: Population dynamics and the colour of the environmental noise. — Proc. R. Soc. Lond. B 264: 943–948.

Lawton, J. H. 1988: More times means more variation. — Nature 334: 563.

May, R. M. 1974: Biological populations with non-overlapping generations: stable points, stable cycles and chaos. — Science 186: 645–647.

May, R. M. 1976: Simple mathematical models with very complicated dynamics. — Nature 261: 459–467.

May, R. M. & Oster, G. F. 1976: Bifurcations and dynamic complexity in simple ecological models. — Am. Nat. 110: 573–590.

Maynard Smith, J. 1974: Models is ecology. — Cambridge University Press, Cambridge.

Mode, C. J. & Jacobson, M. E. 1987a: A study of the impact of environmental stochasticity on extinction probabilities by Monte Carlo integration. — Math. Biosci. 83: 105–125.

Mode, C. J. & Jacobson, M. E. 1987b: On estimating critical population size for an endangered species in the presence of environmental stochasticity. — Math. Biosci. 85: 185–209.

Moran, P. A. P. 1950: Some remarks on animal population dynamics. — Biometrics 6: 250–258.

Pimm, S. L. 1991: The balance of nature. — Univ. Chicago Press, Chicago.

Pimm, S. L. & Redfearn, A. 1988: The variability of population densities. — Nature 334: 613–614.

Powell, T. M. & Steele, J. H. 1995: Ecological time series. — Chapman & Hall, New York.

Ranta, E. & Kaitala, V. 1997: Travelling waves in vole population dynamics. — Nature 390. (In press.)

Ranta, E., Kaitala, V. & Lindström, J. 1997a: Spatial dynamics of populations. Modelling spatiotemporal dynamics in ecology. — In: Bascompte, J. & Solé, R.V. (eds.), Modelling spatiotemporal dynamics in ecology. R.G. Landes Company, Austin, USA. (In press.)

Ranta, E., Kaitala, V. & Lundberg, P. 1997b: Population variability in space and time: the dynamics of synchronous population fluctuations. — Science (28 Nov. 97). (In press.)

Ranta, E., Kaitala, V., Lindström, J. & Lindén, H. 1995: Synchrony in population dynamics. — Proc. R. Soc. Lond. B 262: 113–118.

Ranta, E., Lindström, J., Kaitala, V., Kokko, H., Lindén, H. & Helle, E. 1997c: Solar activity and hare dynamics – a cross-continental comparison. — Am. Nat. 149: 765–775.

Ricker, W. E. 1954: Stock and recruitment. — J. Fish. Res. Bd. Can. 11: 559–623.

Ripa, J. & Lundberg, P. 1996: Noise colour and the risk of population extinctions. — Proc. R. Soc. Lond. B 263: 1751–1753.

Ripa, J., Lundberg, P. & Kaitala, V. 1998: A general theory of environmental noise in ecological food webs. — Am. Nat. 151. (In press.)

Royama, T. 1992: Analytical population dynamics. — Chapman & Hall, London.

Steele, J. H. 1985: A comparison of terrestrial and marine ecological systems. — Nature 313: 355–358.

Stone, L. 1993: Period-doubling reversal and chaos in simple ecological models. — Nature 365: 617–620.

Strebel, D. E. 1985: Environmental fluctuations and extinction – single species. — Theoretical Population Biology 27: 1–26.

Sugihara, G. & May, R. M. 1990: Nonlinear forecasting as a way of distinguishing chaos from measurement error in time series. — Nature 344: 734–741.

Sugihara, G. 1995: From out of the blue. — Nature 378: 559–560.

Turchin, P. 1990: Rarity of density dependence or population regulation with lags? — Nature 344: 660–663.

Turchin, P. & Taylor, A. D. 1992: Complex dynamics in ecological time series. — Ecology 73: 289–305.

White, A., Bowers, R. G. & Begon, M. 1996a: Red/blue chaotic power spectra. — Nature 381: 198.

White, A., Begon, M. & Bowers, R. G. 1996b: Explaining the colour of power spectra in chaotic ecological models. — Proc. R. Soc. Lond. B 263: 1731–1737.