

no doubt be more widely substituted for the disappearing commercial caviar species. At present, these commercial species are not included in the appendices of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), the only international agreement on endangered species trade. CITES will consider placing all sturgeon species in the appendices at a meeting (23–27 September 1996) in Pruhonice, Czech Republic. The enforcement of such a listing depends largely on the ability to diagnose these species accurately. Our method will give wholesalers an alternative to the crude identification methods they use now and give consumer groups a weapon to ensure accurate labelling.

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Red/blue chaotic power spectra

SIR — Cohen¹ has reported that the time series of chaotic, single-species ecological models have blue power spectra rather than the reddened ones associated with natural populations². In other words, the dynamic behaviour of real populations is apparently dominated by longer-term trends, but population models, of one common type at least, fail to capture this crucial characteristic, being dominated instead by shorter-term responses. This calls into question both the usefulness of the models and the applicability of chaotic dynamics to natural systems. However, equivalent analyses (see Fig. 1) of chaotic metapopulation time series from explicitly spatial models (comprising coupled-map-lattices of $n \times n$ identical patches, describing host–parasitoid³ or host–pathogen⁴ dynamics, with the eight nearest-neighbouring patches linked by dispersal) give rise to distinctly reddened spectra — like the natural population data, but quite unlike the simpler models.

Note that the two-dimensional models within patches are dominated by short-term responses to population density (governed by 'biotic' mechanisms). This tends to undermine any suggestion^{1,2} that the important contrast is necessarily between systems dominated by biotic

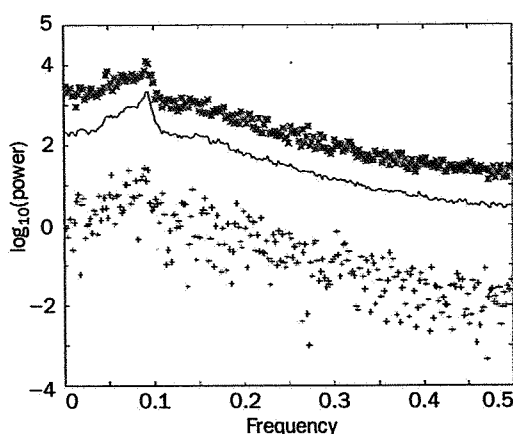


FIG. 1 Power spectral densities of the metapopulation of hosts in a spatially explicit host–parasitoid model³ (similar portraits are observed for the host–pathogen model⁴). Parameter values, taken from ref. 4, are $r = 2$, $\sigma_1 = 0$, $\sigma_2 = 1$, $\lambda = 1$, $\nu = 1$, $\mu_X = 0.2$, $\mu_W = 0.89$ and $n = 30$; similar results are obtained for larger values of n . In common with natural populations, the spectra are reddened, with greater power at low frequencies. (Scale on axes was chosen to allow comparison with ref. 1.)

factors (blue) and external, 'climatic' factors (red). Moreover, similar spectral analyses of chaotic but non-spatial two-dimensional models^{5,6} still give rise to blue spectra. Thus, we judge that including the spatial dimension is crucial in reddening our power spectra, and that those of natural populations may still be explained (at least partly) by chaotic dynamics.

We can also deduce why, biologically, space can produce reddened spectra. In the spatially explicit lattice, subpopulations respond quickly only to the density in their immediate neighbourhood. Hence, the concerted response of the whole metapopulation to its own total density can occur only on much longer timescales that allow initially local effects to spread and to influence the whole. This echoes, and puts flesh on, the complaints of empiricists that population density may be uninformative because individuals experience only local crowding.

Chaotic population dynamics, when generated by spatially explicit systems, may be important in explaining the reddened spectra seen in natural populations.

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SIR — We wish to add to the debate about colour in the power spectra of the complex dynamics of natural populations^{1,2,7,8}. Power spectra of population trajectories are observed to be white (no dominating frequency) or red (dominance of low-frequency fluctuations^{2,9}). Thus, low frequencies might be expected to dominate in population models producing chaos-like

oscillations. But Cohen showed in various nonlinear models that high frequencies dominate in their chaotic fluctuations¹, making the power spectra blue. Here we report that adding delayed density dependence^{10–12} to these population models reduces the dominance of high-frequency oscillations and either whitens or reddens their power spectra.

In a non-delayed density-dependent system, the population size P_t at time t defines the population size at time $t+1$ with a given growth rate r . We analysed the power spectra of chaotic trajectories of six of the eight models discussed by Cohen¹ by incorporating delayed density dependence into their dynamics. As an example, the Moran–Ricker discrete-time nonlinear dynamics^{13,14}, $P_{t+1} = P_t \exp [r(1 - P_t)]$, modifies into $P_{t+1} = P_t \exp [r(1 - (P_t + cP_{t-1}))]$. Of the models analysed by Cohen, we omitted the Verhulst model, known to produce white noise¹, and the Malthus–Condorcet–Mill model, in which delayed density dependence creates typically isolated spikes in spectra.

It is generally expected that the addition of time delays in population models will lower the stability of the dynamics. However, the consequences of delayed density dependence for the colour of the power spectra of chaotic population dynamics are not known. Adding delayed density dependence in the models can remove the dominance of high-frequency oscillations and can whiten or redden their power spectra (see Fig. 2), which brings them better into line with data from natural populations⁹.

Simple population models have drawn attention to the possibility of complex dynamics in natural populations^{7,8}, but they may be of limited use in explaining the rich phenomena observed in dynamics of natural populations. Chaos in models of natural populations can be obtained in several ways, including periodic doubling (used in simple models¹), quasiperiodicity and intermittency^{15,16}. Depending on the way in which chaos is obtained, there may be fundamental differences in the power spectra of the population trajectories. For example, the quasiperiodic route, which strongly affects the power spectra of the population trajectory, occurs often in the context of species or population interactions, or in age-class interactions in a single population. Delayed density dependence may also produce the quasiperiodic route to chaos. Thus, when adding delayed density dependence to population models, we not only altered the assumptions on the density dependence, but also increased the dimension of the dynamics and moved to