Explaining the colour of power spectra in chaotic ecological models

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SUMMARY

Power spectrum analysis is often used to determine whether population time series are dominated by particular frequencies. Results for chaotic time series are often reported in terms of the colour of the spectra whereby red spectra indicate a dominance of low frequency (long-term) fluctuations, white spectra indicate that all frequencies are equally dominant and blue spectra indicate a dominance of high frequency (short-term) fluctuations. Several studies have employed such analysis and much discussion has been provoked by an apparent conflict between the fact that the time series of natural populations produce reddened power spectra whereas chaotic, single species ecological models can produce blue, white or red spectra. Here, we resolve the question of which parameter values give rise to particular colour spectra by analysing simple models in terms of 'universal' parameters allowing direct comparisons between models to be drawn. This suggests that some models are not capable of producing reddened spectra, which would question their usefulness in describing ecological systems. The population behaviour associated with each colour spectrum is described and compared with models that incorporate simple modifications to represent delayed density dependence, spatial structure and environmental effects.

1. INTRODUCTION

There has long been a desire to interpret and explain empirical population dynamics data by the use of theoretical population models. Although approaching an exact correspondence between models and natural systems is fraught with difficulties, there is a hope that model systems embody the fundamental features of the dynamics exhibited by their natural counterparts. It is commonly perceived that one such fundamental feature is that patterns in the dynamics of natural populations are dominated by low frequency fluctuations (Ma 1958; Diamond & May 1977; Pimm & Redfearn 1988; Sugihara 1995; Halley 1996). Power spectrum analysis can be used to determine whether population dynamics are dominated by particular frequencies, with the results often reported in terms of spectral colour. Here, spectra can be red, indicating a dominance of low frequency (long-term) fluctuations, white, indicating no overall frequency dominance, or blue, indicating a dominance of high frequency (short-term) fluctuations (for examples of these spectra see figure 2a(i), b(i) and c(i)). Thus, it has been suggested that the spectral analysis of the time series of natural populations would produce reddened spectra (Sugihara 1995; Halley 1996). However, Cohen (1995) reported that the time series of a number of chaotic, single-species ecological models have blue power spectra. In other words, the dynamics of real populations are 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.

Cohen's (1995) paper, highlighting this apparent red–blue power spectra conflict in ecological time series, stimulated a number of responses. Blarer & Doebeli (1996) showed that for different choices of parameter values, some of the models in Cohen's (1995) study can exhibit reddened or white spectra in addition to the blue spectra which Cohen reported. They remarked that the question posed by these results is to understand when and why some parameter values give rise to blue spectra and others red. Other studies have shown how reddened spectra may be expected in the case of explicitly spatial models (White *et al.* 1996a), as here, the response of the whole metapopulation to its own total density may occur on much longer timescales that allow initially local effects to spread and to influence the whole. Kaitala & Ranta (1996) analysed the same single-species models as Cohen (1995) for the same parameter values but added delayed density dependence. This converted the power spectra of the time series from blue to white. They raised the question of whether the colour of the spectrum was related to the route by which chaos was

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obtained (period doubling, quasiperiodicity or inter-mittency). Finally, Sugihara (1995, 1996) suggested that although biotic models (such as those described above) can produce reddened spectra, it is equally likely that external forcing by the climate or other factors could be the main cause of high dominance at low frequencies in the natural spectra. All these studies suggest that chaotic population dynamics may still be important in explaining the red spectra seen in natural populations, but exemplify the difficulty of the debate over whether natural population fluctuations represent regulation by biological mechanisms (Blarer & Doebeli 1996; Kaitala & Ranta 1996; White *et al.* 1996a) or whether they are mostly the result of environmental forcing (Ma 1958; Cohen 1995; Sugihara 1995).

2. APPROACH AND METHODS

We consider here the models examined by Cohen (1995) and undertake parameter space investigations aimed at characterizing the 'colour' of the spectra obtained at each point. First, though, we describe how the power spectra were generated and a method by which we can quantify the different colour types.

To produce power spectra for the models, 100 sample paths of 512 time steps were generated for each model (after 10000 time steps were eliminated to remove transients) from an initial population size P_0 distributed randomly and uniformly. Spectra produced from longer time series vary only minimally in shape and will not alter the results reported here. Hence, for consistency with Cohen (1995) and subsequent responses, 512 steps are used. The average of the power spectra over the 100 simulations was then computed at the appropriate frequencies between 0 and 0.5 (per time step). Because the power varied widely over frequencies we choose to work with $\log_{10}$ (power). For a more detailed explanation of the technique used to calculate power spectra see Cohen (1995).

To characterize the colour of the power spectra, we propose an index, I_d, for each spectrum as follows:

$$I_d = \begin{pmatrix} \text{area under spectrum for} \\ \text{frequencies } 0\text{--}0.25 \end{pmatrix} - \begin{pmatrix} \text{area under spectrum for} \\ \text{frequencies } 0.25\text{--}0.5 \end{pmatrix}.$$

The lower boundary, above which the area is calculated, must be at most the minimum power value across all the frequencies for each spectrum.

For the purposes of this study, white spectra have an index in the region of zero ($-0.05 < I_d < 0.05$), blue spectra have a more negative index ($I_d < -0.05$) which decreases as the 'blueness' increases and red spectra a more positive index ($I_d > 0.05$) which increases as the 'redness' increases. This index is preferred to the one outlined by Blarer & Doebeli (1996), which uses the ratio of the respective areas, because in their index the dominance of low to high frequencies is relative (to $\log_{10}(1)$) and sensitive to scale. For instance, altering the size of a parameter which only alters the scale of the dynamics alters their ratio index. The difference index, however, is not sensitive to scale, giving the absolute dominance of low versus high frequencies, and hence allowing a quantitative comparison of indexes for different parameter values and between different models. However, I_d is a heuristic measure of spectral colour and should be used in conjunction with the spectrum portrait to avoid errors. For example, a bell shaped spectrum portrait, centred at 0.25, would have an index of zero but is clearly not white.

3. ANALYSIS OF THE MAYNARD SMITH MODEL

Using the above method we present a thorough parameter space analysis of the chaotic region of one of Cohen's (1995) models, that of Maynard Smith (1974). This model is sufficiently versatile to exhibit red, white and blue spectra and it transpires that the results and descriptions generalize to explain the behaviour in other models. The Maynard Smith model is

$$P_{t+1} = \frac{rP_t}{1 + (aP_t)^b} = f(P_t). \tag{1}$$

Here P_t denotes the population size at generation t, and the dynamics are determined by the intrinsic growth rate r and by the parameter b, describing the type and 'strength' of competition. Here, 'strength' is used in the sense of describing the fact that for any P_{t+1} above P^* (the carrying capacity, where $P_{t+1} = P_t$), and with all other parameters fixed, a higher value of b will force the population to crash to lower levels over the next time step. The parameter a does not influence the qualitative dynamics but scales the densities and in particular the carrying capacity, P^*. The $r-b$ parameter space analysis, for the chaotic region of the model, is portrayed in figure 1 in terms of contour lines for I_d, the difference index, with regions shaded to indicate where the different colour spectra are found. The behaviour of the population causes a discontinuity at the chaos boundary (where 'bell' shaped spectra centred at 0.25 are observed) and parameter values that produce periodic solutions within the chaotic region are ignored.

The dynamical behaviour of the population itself varies with the colour of spectrum observed. A general description of this behaviour will also prove informative when results are extended to include model comparisons.
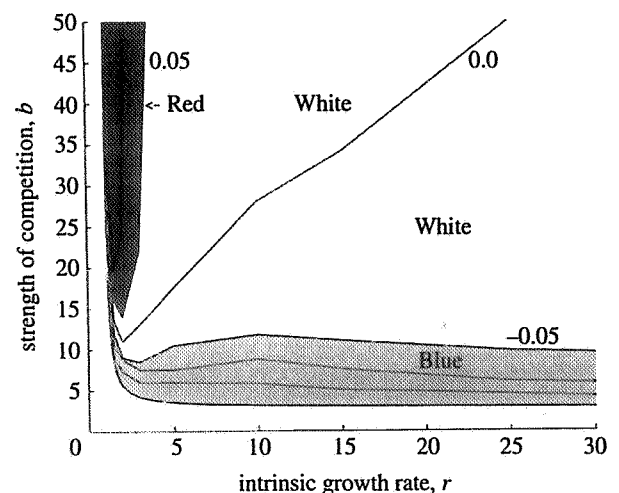

Figure 1. The $r-b$ parameter space portrait for the Maynard Smith model ($a = 0.5$), where the shaded regions are labelled to indicate where the different spectral colours are found. The contour lines for I_d, reading clockwise are 0.1, 0.05, 0.0, -0.05, -0.1, -0.2 respectively and the $r-b$ portrait is bordered below by the boundary of the chaotic region.

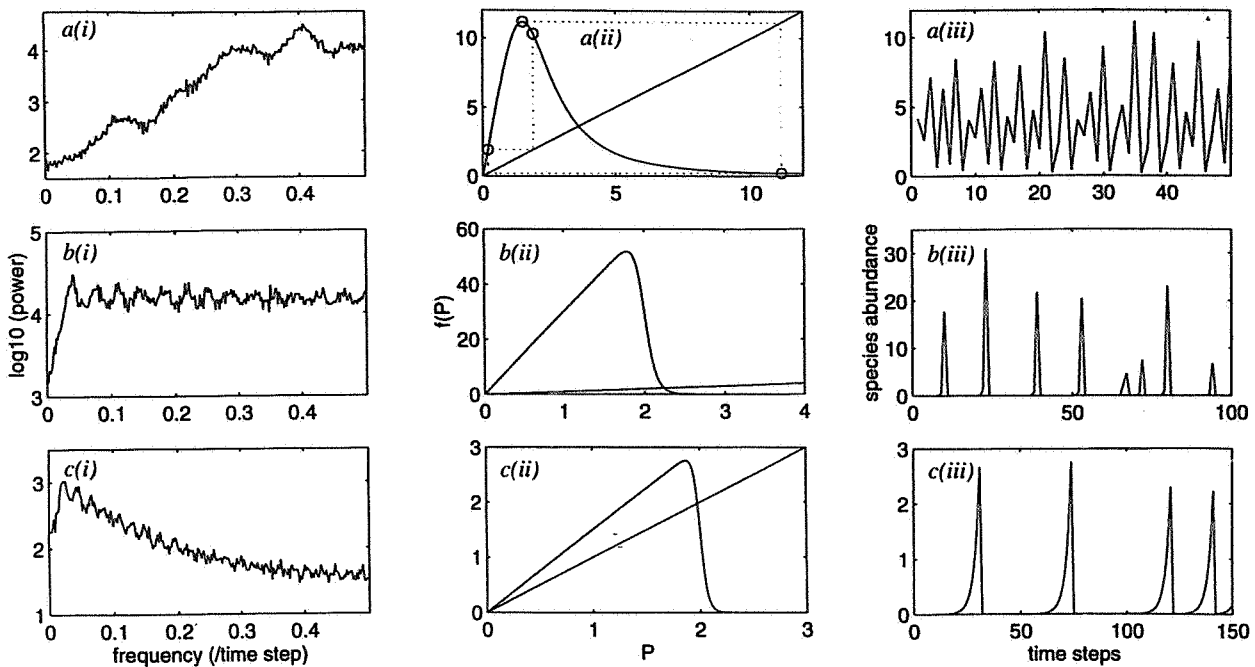Figure 2. Portraits for the Maynard Smith model for: (*a*) blue spectra ($a = 0.5$, $b = 3.7$, $r = 10$): (*b*) white spectra ($a = 0.5$, $b = 30$, $r = 30$): and (*c*) red spectra ($a = 0.5$, $b = 60$, $r = 1.5$) indicating the typical (i) power spectra patterns, (ii) maps profiles of P plotted against $f(P)$, and (iii) population behaviour.

(*a*) *Blue spectra*

Blue spectra (higher power at high frequencies) indicate that the population dynamics are dominated by short-term trends (figure 2*a*(i)). They occur for all values of r but typically require low strength competition (low b for this model). Figure 2*a*(ii) depicts a typical plot of $P_{t+1} = f(P_t)$ against P_t for parameters that produce blue spectra. By using this plot we can calculate the maximum length of the 'quasi-cycle' obtainable for these parameter combinations.

Here, a quasi-cycle is a description of the gross level dynamics in terms of symbolic dynamics (often used to describe chaotic systems (Ott 1993)). We represent the population time series at each iteration by a 1 if $P_{t+1} > P_t$ or a 0 if $P_{t+1} < P_t$. The dynamics are 'symbolic' in the sense of describing only whether the population is increasing or decreasing. Starting at 0 (population decrease), the quasi-cycle is defined as the number of iterations until the next 0. For the maximum quasi-cycle (after transients) we must iterate forwards from $\hat{P} = \max f(P)$, as the next time step will incur the largest possible crash (note, crashes for blue spectra are never too severe, figure 2*a*(iii)). In this case a quasi-cycle of 'period' 3 is the maximum ('011' – follow the dotted line in figure 2*a*(ii)). Note, one dimensional maps of this kind will always have growth following a crash (i.e. '00' is not possible). The only other possible quasi-cycle is of period 2 ('01') and so here, all dynamics are constructed from quasi-cycles of period 2 or 3. This domination of short period (high frequency) fluctuations gives rise to the blue spectra.

(*b*) *White spectra*

White spectra indicate that there is an equal dominance of (attainable) frequencies (figure 2*b*(i)).

Again, they can occur for all values of r, but, for given r, require competition to be stronger than for blue spectra. The typical behaviour involves the (1 step) population crash to very low levels (after P^* is breached) followed by many steps of population growth ('0111...'), which occurs effectively at the intrinsic growth rate. Because the population drops to such low levels, the abundance is low for many generations of population growth, and moderate or high abundance is observed for only two or three steps per quasi-cycle (figure 2*b*(iii)). The maximum quasi-cycle here is 28. However, sometimes a crash to only moderate levels occurs, followed by relatively few steps of growth before the next crash. Hence, considerably more frequencies within the spectrum are attainable: the period between these population outbreaks (i.e. the period of the quasi-cycle) varies considerably from two up to 28 generations, resulting in approximately equal power spectrum values for frequencies between $1/28 (\approx 0.04)$ and $1/2$, and explaining the drop in power for frequencies smaller than 0.04.

(*c*) *Red spectra*

Red spectra indicate that the population dynamics are dominated by long-term (low frequency) trends (figure 2*c*(i)). They occur where competition is strong, but, for given strength of competition require r to be lower than for white spectra. The typical population behaviour has similarities to that associated with white spectra, in that there is a crash to low population levels followed by an increase over many generations (maximum quasi cycle 47 generations for figure 2*c*). The behaviour differs however, in that short quasi-cycles are uncommon, and as a result of the lower intrinsic growth rate, abundance can be observed at

significant levels for 10–15 steps before the 1 step crash (figure 2c(iii)).

4. COMPARING MODELS: A UNIVERSAL PICTURE

To compare the behaviour of different models, we must be able to analyse each model in terms of an equivalent set of parameters. This can be achieved by analysing the models in terms of the 'boom' and 'bust' of the population dynamics. The boom parameter is the maximum growth rate of the population (it is equivalent to the per capita rate of increase at low densities for many of the models), and the bust parameter is a measure of the 'strength' of the density dependence, i.e. the ability of the dynamics to force the population back to low levels after the carrying
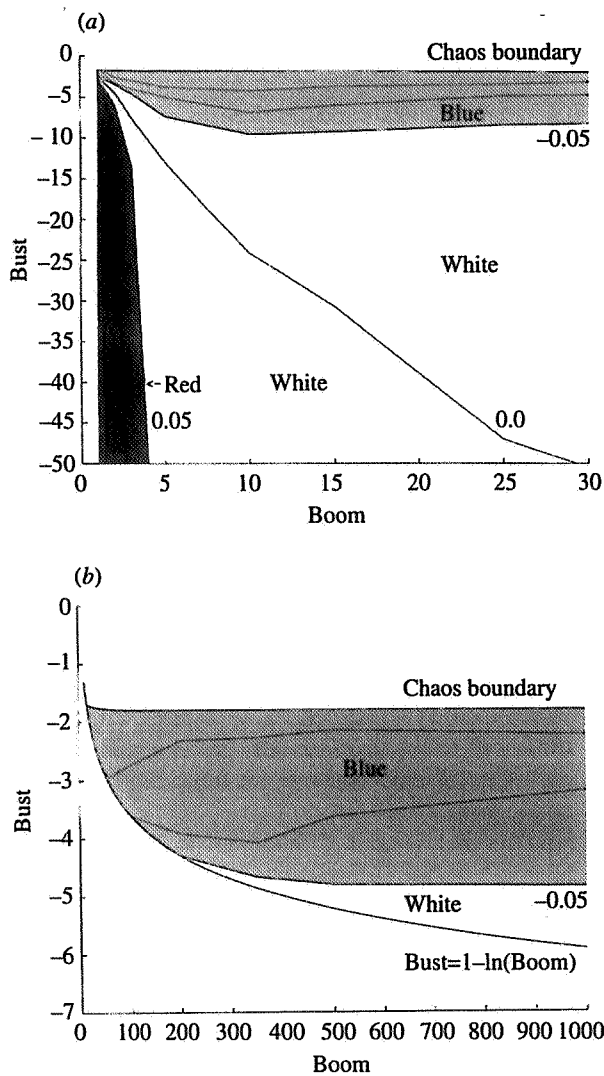

(a)

(b)

Figure 3. A parameter space portrait in terms of the universal parameters boom and bust where the shaded regions are labelled to indicate where the different spectral colours are found. Here, the boom–bust portrait represents: (a) the Maynard Smith model ($a = 0.5$), the contour lines for I_d reading clockwise are -0.2, -0.1, -0.05, 0.0, 0.05, 0.1, 0.2; and (b) the Hassall model with contour lines -0.2, -0.1, -0.05. In the Hassall model the limiting magnitude of the bust parameter, for fixed levels of boom, is finite (it is constrained by the relation Bust $= 1 - \ln(\text{Boom})$), meaning red spectra cannot be produced.

capacity is breached. A suitable choice for the bust parameter is the slope of the map, $df(P)/dP = f'(P)$ at P^*, the carrying capacity. As the severity of the density dependence increases, $f'(P^*)$ will become more negative. We choose P^* as the evaluation point as it has neat analytical properties.

The equivalent portrait to figure 1 for the Maynard Smith model, but in terms of 'boom' plotted against 'bust', is displayed in figure 3a. Note that the chaos boundary line has been transformed into a straight line at $f'(P) \approx 1.7$ and that $r > 1$ to ensure that population values are biologically realistic (i.e. to ensure positive populations). In terms of the new 'universal' parameters, blue spectra require low density-dependent pressures (low bust) but occur for any boom (although there is clearly a threshold effect for fixed bust), whereas red spectra require low boom but occur for any bust (with a similar threshold effect). It is important to note that in the Maynard Smith model, boom and bust values can be set quite independently and, in particular, the density dependent strength (bust) can be increased to any severity (i.e. the slope of the curve at P^* will be vertical for high enough b). To see this note that

$$f'(P^*) = 1 - b(r-1)/r \quad \text{and} \quad f'(P^*) \to -\infty$$

as $b \to \infty$.

This means that when boom is low the bust component can still be made arbitrarily large, thereby producing red spectra. Crucially, this is not a feature of all single species models.

For example, the behaviour of the Hassall (1974) model, described as,

$$P_{t+1} = \frac{rP_t}{(1 + aP_t)^b}, \tag{2}$$

in terms of boom plotted against bust is portrayed in figure 3b. While blue and white spectra are possible, this model cannot produce dynamics with reddened spectra, because for any fixed level of the boom, the bust parameter is constrained to a finite limit. In particular, at low boom, the strength of the bust parameter cannot be increased to levels where red spectra would be observed. To see this for the Hassell model note that:

$$f'(P^*) = 1 - b + b/\sqrt[b]{r} \quad \text{and} \quad f'(P^*) \to 1 - \ln(r)$$

as $b \to \infty$.

Models that cannot produce red spectra typically have the property that the strength of density dependence is constrained to a finite limit. The models studied by Cohen (1995) are characterized in terms of the boom–bust parameters in table 1.

The table is partitioned into models that cannot produce red spectra (bust is confined to a relatively low limit for fixed boom) and those which can produce red spectra (limit of $-\infty$). Note, here, the models which depend on one parameter only (Moran-Ricker, Verhulst) will be curves in parameter space that do not pass through the red region and that bust $\to -\infty$ indicates red spectra but is not a strict requirement.

Table 1. *Nonlinear population models from Cohen (1995) partitioned into those which cannot produce red spectra (top) and those which can (bottom)*

(The results here apply only to the chaotic regions of the models. For models references see Cohen (1995)).

	$f(P)$	boom ($= \max f'(P)$)	bust ($= f'(P^*)$)	limit of bust for fixed boom
Moran-Ricker	$P\exp(r(1-P))$	$\exp(r)$	$1-r$	$1-\ln(\text{boom})$
Verhulst	$P(1+r(1-P))$	$1+r$	$1-r$	$2-\text{boom}$
Hassell	$rP/(1+aP)^b$	r	$1-b+b/\sqrt[b]{r}$	$1-\ln(\text{boom})$
Maynard Smith	$rP/(1+(aP)^b)$	r	$1-b(r-1)/r$	$-\infty$
Pennycuick	$rP/(1+\exp(-b(1-P/a)))$	$r/(1+\exp(-b))$	$1-(1-1/r)(b+\ln(r-1))$	$-\infty$
Varley	$P_{t+1}=rP_t$ if $P_t \leqslant C$ or rP^{1-b} if $P_t > C$	r	$(1-b)$	$-\infty$

5. DISCUSSION

The results here, for chaotic single-species ecological models, resolve the open question posed by Blarer & Doebeli (1996) of 'why some parameter values give rise blue spectra and other red spectra'. The answer explained in terms of universal parameters, boom and bust, clearly shows why some models are incapable of producing the full range of spectral colours. Thus, if red spectra are a feature of natural systems, this provides a criteria for selecting more appropriate models.

What then can be said of the other responses to Cohen's (1995) original study? Kaitala & Ranta (1996) reported that adding delayed density dependence to the single species models would reduce the dominance of high frequency oscillations and either whiten or redden the power spectra (by using our index, I_d, their results would be categorized as white). The effect of delayed density dependence, for any set of parameter values, is similar to that of increasing the strength of competition in the simpler models. To observe this we will examine the Pennycuick (1968) model with delayed density dependence:

$$P_{t+1} = \frac{rP_t}{1+\exp(-b(1-(P_t+cP_{t-1})/a))}. \tag{3}$$

Here, the dynamics are determined by the scaled

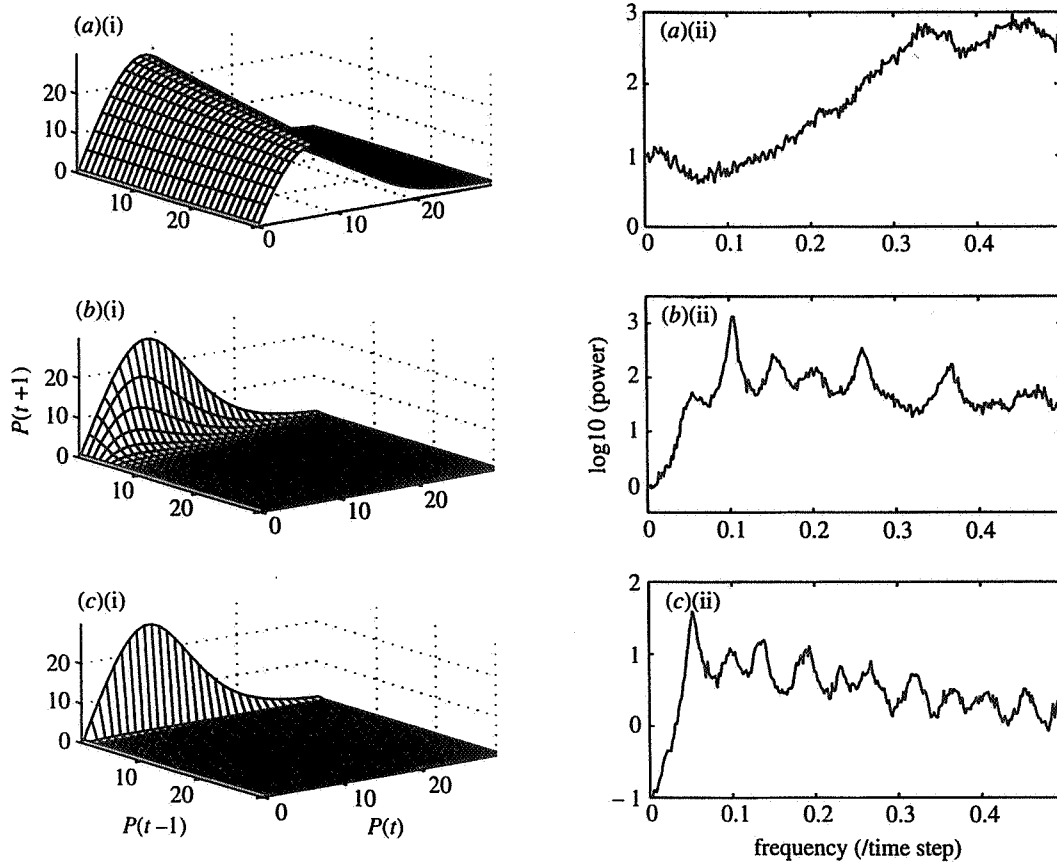
Figure 4. Portraits for the Pennycuick model of: (i) the three dimensional map profile, the three dimensions being P_t, P_{t-1}, and $f(P_t,P_{t-1})$; and (ii) the power spectrum. The parameters $r = 5$, $b = 3$, $a = 10$ and (a) $c = 0.1$ producing blue spectra ($I_d = 0.36$); (b) $c = 3$ producing white spectra ($I_d = 0.005$); and (c) $c = 20$ producing red spectra ($I_d = 0.063$).
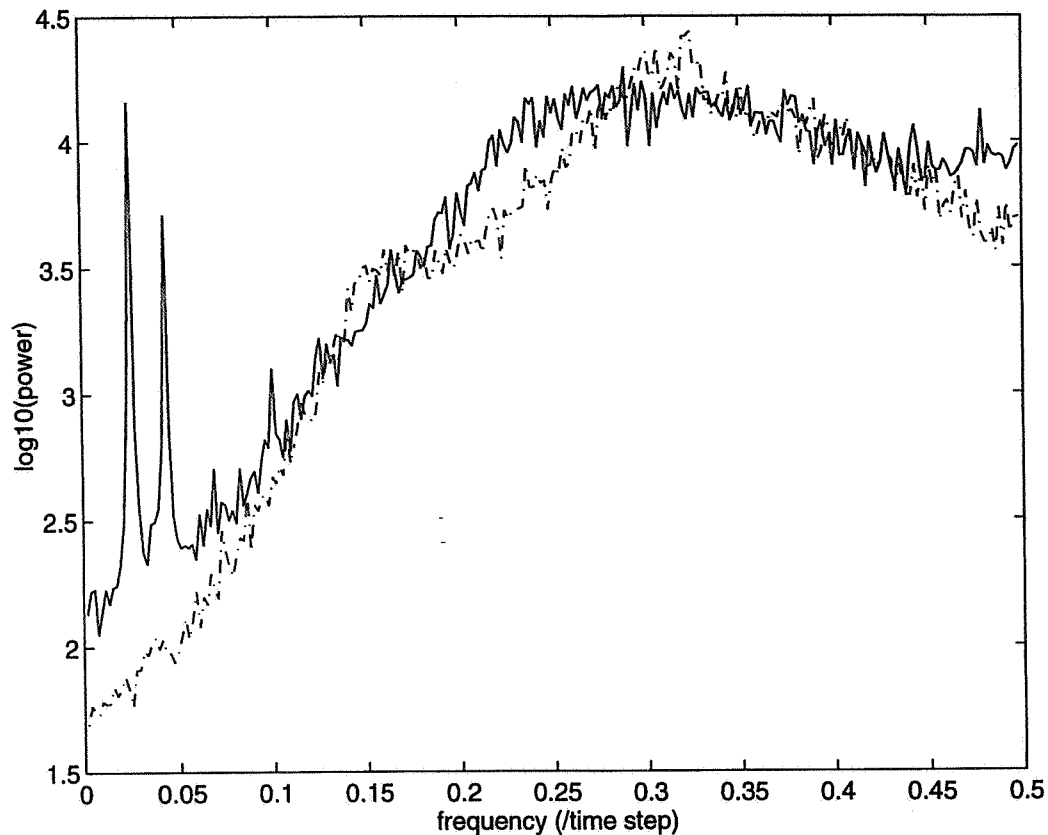
Figure 5. A power spectra portrait for the Maynard Smith model ($a = 0.5$, $b = 4.8$, $r = 10$) where birth is coupled to a $1/f$ environmental effect. The solid line represents the power spectrum when the environmental effect is included; and the broken line represents the spectrum without environmental coupling. The $1/f$ effect is modelled as $e(t) = 1 + A(\omega_1^{-1} \sin 2\pi\omega_1 t + \omega_2^{-1} \sin 2\pi\omega_2 t + \omega_3^{-1} \sin 2\pi\omega_3 t)$ where $\omega_1 = 1/40$, $\omega_2 = 1/23$, $\omega_3 = 1/10$ and $A = 0.5/(\omega_1^{-1} + \omega_2^{-1} + \omega_3^{-1})$. So, $e(t)$ is the sum of three sine waves, where the wave of the lowest frequency $(2\pi\omega_1)$ is given the greatest amplitude (A/ω_1), where here, A acts as a normalizing parameter to confine $e(t)$ to varying between 0.5 and 1.5 only. Thus, r becomes $re(t)$ which can vary between $r/2$ and $3r/2$ and has a mean of r. The shape of $e(t)$ resembles a sine wave of frequency $2\pi\omega_1$ with sine waves of smaller amplitude $(A/\omega_2, A/\omega_3)$ and frequencies $2\pi\omega_2$ and $2\pi\omega_3$ superimposed on top.

growth rate r, the parameter b and the delay parameter c which describe the type and 'strength' of competition, and by a which does not influence the dynamics but scales the densities. We can see the effect increasing the delay parameter c has on the dynamics directly, from the equation, or visually, by examining a three dimensional profile of the map (namely P_t, P_{t-1}, and $P_{t+1} = f(P_t, P_{t-1})$, figure 4). We choose the parameters such that when $c = 0$ (delayed density dependence is absent) the power spectra of the dynamics would be blue, then increase c to establish its effect on behaviour. When c is small the dynamics are not significantly altered and the spectrum remains blue (figure 4a(ii)). To see the effect on the three dimensional profile we note that whatever value P_{t+1} attains, P_{t-1} will take that value two time steps later. Now, small c does not significantly alter the profile for fixed P_{t-1} (figure 4a(i)) and so the behaviour will be very similar to that of the system without the delay dimension. However, when c is increased to moderate levels the profile changes dramatically. It becomes 'skewed' such that $f(P_t, P_{t-1})$ remains near previous levels (for $c = 0$) only as $P_{t-1} \to 0$, and $f(P_t, P_{t-1})$ rapidly tends towards zero as P_{t-1} increases above zero (figure 4b(i)). Thus, if P_{t+1} becomes 'high' then two time steps later P_{t-1} takes that value and the population will crash to very low levels.

This is followed by many steps of population growth before the next crash occurs. This behaviour is similar to that for white spectra in the simple models and the population dynamics of the delay system does produce white spectra (figure 4b(ii)). If c is increased further, the profile becomes more skewed (figure 4c) and red spectra can be observed (as for the simpler models this additionally requires that growth levels are low enough).

Kaitala & Ranta (1996) suggest that the change in spectral colour occurs because delayed density dependence changes the route to chaos. The results for the simple models, with no delayed density dependence, indicate that a change in the route to chaos is not a necessary condition for changing the colour of the spectra.

The white and red spectra observed for the simple models of Cohen (1995) and their delay counterparts require the population dynamics to experience a crash to a very low level and to remain low for many generations. Such pronounced fluctuations are unlikely to be common in natural population. In explicitly spatial models however (Rhodes & Anderson 1996; White *et al.* 1996a) reddened spectra are produced without populations dropping to low abundance. Here, space is modelled as a lattice of $n \times n$ patches with each

patch linked locally to its nearest neighbours. In this way the effect of local population crashes are counter-balanced by increases in other patches, preventing the metapopulation from becoming unreasonably low. Because only local dispersal is possible, the timescale on which local effects can spread and influence the whole metapopulation is increased, which may explain the increased dominance at lower frequencies. Hence, the chaotic population dynamics generated by spatially explicit systems may more realistically explain the reddened spectra associated with natural populations. Here, the trajectories are classified as chaotic by using algorithmic complexity measures (White *et al.* 1996*b*) and phase plane portraits, but conclusive proof of chaos is very difficult in such high dimensional systems. We also acknowledge that the systems examined in the studies of Rhodes & Anderson (1996) and White *et al.* (1996*a*) are not simple extensions of one dimensional models and thus the result may be reliant on space interacting with other factors.

As an aside, it is worth noting that in spatial models, the power spectra would be the same colour regardless of whether the time series represented readings for the whole metapopulation, the population in just one patch or the sum from any combination of patches, as the fourier transforms that define power spectra are linear operations.

Finally, we return to the issue of whether external forcing by the climate or other factors could be responsible for producing reddened spectra (Sugihara 1995, 1996). Adding realistic environmental effects into the simple ecological models is difficult. One approach would be to couple the environmental effect directly to a model parameter, thereby producing model variability which is proportional to environmental change. Halley (1996) reported how $1/f$ noise might be the best method by which to model the effects of environmental fluctuations and this can be approximated by summing sine waves whose amplitude decreases as their frequency increases (see figure 5). A $1/f$ approximation of the environmental effect implies low frequency fluctuations are given higher dominance. Hence, we are intrinsically modelling an environment in which long-term trends are dominant. Anderson & May (1981) used a similar strategy to model effects which represent annual periodicity of the environment by coupling the reproductive rate to a sine wave distribution. Figure 5 shows how the $1/f$ effect acting on the growth rate r in the Maynard Smith model produces isolated spikes of power at frequencies which correspond to those producing the environmental effect, without significantly altering the underlying shape of the spectra and thus, in particular, without reddening them. This is also observed for the other simple models and if the $1/f$ effect is coupled to density dependence rather than growth. So, modelling the effect of environmental fluctuations on single species models in this manner does not redden the underlying spectra.

The results here indicate that there are models in which parameter values can be chosen to generate dynamics which produce reddened spectra, although importantly, some models cannot produce red spectra regardless of the parameter combination chosen. Thus, if red spectra are a feature of natural populations there is a basis on which some simple models may be deemed inappropriate. However, in all non-spatial models examined here, large population fluctuations, where population abundance reached very low levels, are required to produce red and white spectra. Spatial models produced reddened spectra without such dramatic fluctuations, indicating that a more rigorous study of the effects of the spatial dimension (in combination with other factors) may prove useful.

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