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Populations embedded in trophic communities respond differently to coloured environmental noise

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Abstract

Noise in environmental variables is often described as ‘coloured’, where colour describes the exponent β of the scaling relationship between the amplitude of variability and its frequency of occurrence ($1/f^\beta$). Different environments are known to have different colours and models have shown that colour can have important impacts upon population persistence and dynamics. This study advances current knowledge about the impact of environmental colour using a trophic model (consumer–resource) experiencing environmental noise (temperature) in a biologically realistic manner—derived mechanistically from metabolic scaling theory. The model demonstrates that the variability of consumers and resources can respond differently to changing environmental colour, depending upon (i) their relative ability to track and over or undercompensate for environmental changes and (ii) the relative sensitivity of their equilibria to environmental changes. These results form the basis with which to interpret differences and facilitate comparisons of the variability of ecological communities across gradients of environmental colour.

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1. Introduction

Organisms living in the natural world constantly experience fluctuations in the environmental variables on which their lives depend. These fluctuations occur in space and time, often with a characteristic degree of autocorrelation or ‘colour’. Environmental colour can have a large influence over population-level processes such as persistence and stability, as evidenced by spatial and temporal models of population dynamics (Ripa and Lundberg, 1996; Kaitala et al., 1997; Petchey et al., 1997; Cuddington and Yodzis, 1999; Morales, 1999; Heino et al., 2000; Schwager et al., 2006) and laboratory experiments (Petchey, 2000; Laakso et al., 2003; Fontaine and Gonzalez, 2005). However, little work has extended this knowledge to communities and food webs (Caswell and Cohen, 1995; Ives, 1995; Ripa et al., 1998; Ripa and Ives, 2003; Golinski, 2006), in particular those described by non-linear dynamics

where feedback mechanisms can play an important role in determining the ultimate influence of environmental noise (Xu and Li, 2003; Brassil, 2006).

One parameter capable of describing the strength of autocorrelation in data is the spectral exponent β (e.g. Halley, 1996; Talkner and Weber, 2000; Pelletier, 2002). This parameter describes the relative contributions of different frequencies f to the variance of the data, assuming that these contributions scale as a power-law of the form $1/f^\beta$. Analogous to light, fluctuations comprised mainly of low-frequency components ($\beta > 0$) have been branded ‘red’ noise, while those comprised mainly of high-frequency components ($\beta < 0$) are known as ‘blue’ noise. The special case where $\beta = 0$ describes ‘white’ noise: where fluctuations in time (or space) lack frequency dependence. For ecologists, the discussion of noise colour tends to fall mainly in the realm of ‘red’ noises (Halley, 1996) giving rise to special designations for pink $\beta \approx 1.0$, brown $\beta \approx 2.0$, and black $\beta > 2.0$.

Interest in the ecological consequences of red noise was spurred by an early and influential study which

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demonstrated that variation in temporal biomass generally increased as a function of census length (Pimm and Redfearn, 1988). Consistent with red noise, this ‘more time means more variation’ effect (coined by Lawton, 1988) was assumed to be detrimental for persistence, given that it carried with it a greater probability of spending long periods of time at low densities (Lawton, 1988). There is an emergent consensus that population dynamics are coloured red by internal processes (Kaitala et al., 1997; Miramontes and Rohani, 1998; Balmforth et al., 1999; Petchey, 2000; Laakso et al., 2003); however, a variety of mechanisms can influence the colour of population dynamics, including time delays (Kaitala and Ranta, 1996), stochastic density dependence, long-range spatial interactions, and tracking of coloured environmental noises (Sugihara, 1995; Inchausti and Halley, 2002).

There is mounting evidence to suggest that temperature and a variety of other environmental variables are well-described as red ($\beta > 0$) $1/f^\beta$ -type noises (Steele, 1985; Halley, 1996; Koscielny-Bunde et al., 1998; Talkner and Weber, 2000; Cyr and Cyr, 2003; Pelletier, 2002; Vasseur and Yodzis, 2004; Király et al., 2006). Although there is large geographic variation in the colour of environmental noise (e.g. Király et al., 2006), some systematic trends have been described. Steele (1985) suggested that marine environments should have a redder environmental spectrum than terrestrial environments and recent comparisons of global temperature variability have supported this result (Cyr and Cyr, 2003; Vasseur and Yodzis, 2004). Perhaps due to the influence of strongly reddened marine noise, there is a weak tendency for maritime atmospheric temperatures to have redder spectra than continental localities over certain frequency ranges (Cyr and Cyr, 2003; Pelletier, 2002; Vasseur and Yodzis, 2004; cf. Koscielny-Bunde et al., 1998). Although general agreement about the exact structure of environmental noise is still lacking (e.g. Talkner and Weber, 2000; Pelletier, 2002), demonstrated geographic variation in noise colours and anticipated changes in colour arising from global climate change (Wigley et al., 1998) warrant a better understanding of how environmental colour impacts ecological systems.

Despite Lawton's (1988) prediction that red noise is inherently bad for population persistence, theoretical models have shown both negative and positive effects of environmental reddening on population persistence, depending upon the underlying dynamics of the model (Ripa and Lundberg, 1996; Petchey et al., 1997; Heino, 1998; Cuddington and Yodzis, 1999; Greenman and Benton, 2003) and on the noise model employed (Cuddington and Yodzis, 1999; Halley and Kunin, 1999; Morales, 1999). Schwager et al. (2006) recently resolved this disparity by demonstrating that populations with high sensitivity to environmental change, or those subject to extreme (catastrophic) events, were at less risk of extinction in reddened environments (while the opposite was true for those with low environmental sensitivity). A number of studies have extended these results to systems of interacting popula-

tions, where population colour and dynamics are determined by a mix of direct and indirect (those passed through interactions) environmental fluctuations (Caswell and Cohen, 1995; Ives, 1995; Ripa et al., 1998; Xu and Li, 2002, 2003; Ripa and Ives, 2003; Brassil, 2006; Golinski, 2006). Linear models have demonstrated that environmental fluctuations passed through population interactions become more reddened, leading populations further from the source of environmental noise to have redder dynamics (Ripa et al., 1998). The combined effect of direct and indirect coloured environmental noise ultimately determines the colour of population dynamics (Golinski, 2006) and can lead to changes in the variability and covariance of populations (Ripa and Ives, 2003). Using non-linear models Xu and Li (2002) confirmed the reddening effect of trophic interactions and showed that higher trophic levels tend to have redder spectra, even when direct and indirect sources of environmental noise are considered (Xu and Li, 2003). However, patterns in the variability and persistence of non-linear populations embedded in trophic systems and experiencing coloured noise have yet to be described in the literature.

Most studies describing the impact of environmental colour on population dynamics incorporate an additive and linear stochastic (environment) element in a single model parameter such as the population carrying capacity (e.g. Petchey et al., 1997; Heino, 1998; Cuddington and Yodzis, 1999), growth rate (Heino, 1998) or as demographic stochasticity (e.g. Ripa and Ives, 2003; Xu and Li, 2003; Golinski, 2006). Environmental noise will most likely influence all, if not the majority of population growth and interaction parameters in a non-linear fashion (Laakso et al., 2001; Vasseur and McCann, 2005), which provides a great potential to complicate previous findings (e.g. Brassil, 2006). This study builds upon previous findings by employing: (i) a mechanistic framework, derived from metabolic theory for the non-linear translation of environmental variability (temperature) into the units appropriate for the model (biomass); and (ii) a non-linear two-population model (consumer–resource) where the influence of environmental variability enters directly into multiple model parameters. These two aspects increase the biological plausibility of the model, and the reliability of the predictions for the impact of coloured environmental variability on simple food webs. By comparing the results with previously published estimates of the environmental colours in different geographic areas, this study highlights important patterns in population variability, which may occur predictably along gradients of environmental colour.

2. Consumer–resource and environmental noise models

2.1. Consumer–resource equations

Consumer–resource dynamics are modelled using an energetically-based version of the MacArthur–Rosenzweig

equations (Yodzis and Innes, 1992):

$$\begin{aligned}\frac{dR}{dt} &= rR \left(1 - \frac{R}{K}\right) - JC \left(\frac{R}{R + R_0}\right), \\ \frac{dC}{dt} &= C \left[-M + (1 - \delta)J \left(\frac{R}{R + R_0}\right)\right],\end{aligned}\quad (1)$$

where R and C are the biomass densities of resources and consumers respectively. Resource growth is logistic and is governed by the intrinsic rate of resource production r and the carrying capacity K . Consumers ingest resources according to a saturating Monod function (Holling type II) where R_0 is the half-saturation density, J is the asymptotic threshold for ingestion (maximum ingestion rate), and δ is the fraction of energy that is lost during ingestion and digestion. The consumer population loses biomass to metabolic processes at the rate M .

Yodzis and Innes (1992) provide an allometric framework for the model (1) that can be used to scale the mass normalized biological rates r , J and M to the $-1/4$ power of body size for resources m_R and consumers m_C (see West et al., 1997). This framework was recently extended by Vasseur and McCann (2005) to include the impact of temperature on biological rates using predictions from metabolic theory (see Brown et al., 2004). Incorporating size and temperature dependence, the scaling relationships for the biological rates r , J and M are:

$$\begin{aligned}r &= a_r(T_0)m_R^{-0.25}e^{E_r(T-T_0)/kTT_0}, \\ (1 - \delta)J &= a_J(T_0)m_C^{-0.25}e^{E_J(T-T_0)/kTT_0}, \\ M &= a_M(T_0)m_C^{-0.25}e^{E_M(T-T_0)/kTT_0},\end{aligned}\quad (2)$$

where the coefficients a_i are the intercepts of the allometric relationships at the temperature T_0 , the E_i are activation

energies, k is Boltzmann's constant, and T is temperature in Kelvin. Vasseur and McCann (2005) provide a comprehensive description of the equilibrium dynamics of this system, and some of the aspects needed to interpret the non-equilibrium dynamics are reiterated here. The two-species equilibrium

$$\begin{aligned}R_e &= \frac{R_0}{(1 - \delta)J/M - 1} \\ C_e &= \left(1 - \frac{R_e}{K}\right) \left(\frac{(1 - \delta)}{M/r}\right) R_e\end{aligned}\quad (3)$$

can be stable or unstable (in which case the dynamics may be cyclic) depending on parameter values. For most plausible parameter sets the equilibrium densities of resources and consumers tend to decline with increasing temperature and the equilibrium may, in some cases, transition from a stable to an unstable state. Vasseur and McCann (2005) analysed the equilibrium dynamics of a parameter set representing the interaction between photosynthetic algae and herbivorous zooplankton, for which both resource and consumer equilibrium density decline with increasing temperature. This study employs the same parameter set and fixes the free parameters of the model so that the equilibrium remains stable over the entire range of temperatures generated by the noise model (see below). Table 1 provides a summary of the model parameters and their values used in this study.

2.2. 1/f noise model

To generate time-series of temperature a two step procedure is used; noise with a desired $1/f^\beta$ power spectrum is generated using spectral synthesis (Saupe, 1988; Voss, 1988; Cuddington and Yodzis, 1999) and standardized

Table 1
Model parameter descriptions and values

Parameter	Description	Value (units)	Source
<i>Consumer resource model</i>			
R_0	Half saturation density	60 kg area ⁻¹	Yodzis and Innes (1992)
K	Carrying capacity	10 kg area ⁻¹	
δ	Fraction of energy lost during ingestion and digestion	0.55	
<i>Scaling function parameters</i>			
a_r	Allometric intercept	0.386 kg (kg year) ⁻¹ kg ^{0.25}	Yodzis and Innes (1992) in Vasseur and McCann (2005)
a_J	Allometric intercept	9.7 kg (kg year) ⁻¹ kg ^{0.25}	
a_M	Allometric intercept	0.51 kg (kg year) ⁻¹ kg ^{0.25}	
E_r	Activation energy for resource growth	0.467 eV	Eppley (1972) in Vasseur and McCann (2005)
E_J	Activation energy for consumer ingestion	0.772 eV	Hansen et al. (1997) in Vasseur and McCann (2005)
E_M	Activation energy for consumer metabolism	0.652 eV	
m_R	Resource body mass	1.0e ⁻¹² kg	
m_C	Consumer body mass	1.0e ⁻⁷ kg	
k	Boltzmann's constant	8.618e ⁻⁵ eV K ⁻¹	
T	Temperature	K	
<i>Noise model parameters</i>			
β_{ENV}	Environment spectral exponent	0–2.0	
μ_T	Mean temperature	293 K	
σ_T	Standard deviation of temperature	5 K	

using spectral mimicry (Cohen et al., 1999) to ensure that the mean, variance, and range of temperature is conserved across different values of β .

Spectral synthesis uses an inverse Fourier transform to generate a time-series from a manufactured power spectrum with the desired $1/f^\beta$ scaling property. Unlike first-order autoregressive models [AR(1)], which are commonly invoked to generate autocorrelated (coloured) noise, spectral synthesis produces time series whose variance increases over time (Halley, 1996). Although the question of exactly which model best portrays environmental noise is still open (Vasseur and Yodzis, 2004), spectral synthesis is used here because it provides better control than an AR(1) model over the independent variable of interest, the scaling exponent β .

For each value of β ($0 \leq \beta \leq 2.0$), N normally distributed uncorrelated random numbers $\varepsilon_f = (\varepsilon_1, \dots, \varepsilon_N)$ with zero mean and unit variance and N random uncorrelated phases $\theta_f = (\theta_1, \dots, \theta_N)$ uniformly distributed over the interval $[0, 2\pi]$ were generated. To create a frequency series with the desired scaling attributes, the random numbers ε_f were multiplied by $1/f^{\beta/2}$ to form the amplitudes $\alpha_f = (\alpha_1, \dots, \alpha_N)$. The inverse Fourier transformation of the complex coefficients

$$\alpha_f e^{i\theta_f} \equiv \alpha_f \cos \theta_f + i \alpha_f \sin \theta_f \quad (4)$$

was then taken and the real part of the result was used to form the time-series $\tau = (\tau_1, \dots, \tau_N)$. Since spectral synthesis generates time-series whose variance increases to $N/2$, only the first $N/2$ points were consequently used.

Ensuring that the variance of environmental noise is conserved across different environmental colours is a particularly important and challenging issue (Heino et al., 2000; Wichmann et al., 2005). For both AR(1) and $1/f^\beta$ generated noises, variance depends upon the autocorrelation/colour of the process, and one must decide what time-scale is appropriate for measuring and rescaling the variance of differently coloured noises. While short temporal windows are valid for estimating the true variance of white, or near-white noises, strongly coloured noises require much longer windows (Wichmann et al., 2005). Many authors opt to rescale the variance to the length of their simulations (e.g. Cuddington and Yodzis, 1999; Heino et al., 2000) or to the asymptotic variance of the process (e.g. Ripa and Lundberg, 1996; Petchey et al., 1997; Cuddington and Yodzis, 1999) by multiplying the noise vector by a constant factor. However, this alters the frequency distribution of the values and can influence the effect of noise colour on dynamics by altering the frequency of extreme events (e.g. Fig. 1 in Schwager et al., 2006). I employ a method known as ‘spectral mimicry’ (Cohen et al., 1999) which does not rely on rescaling and

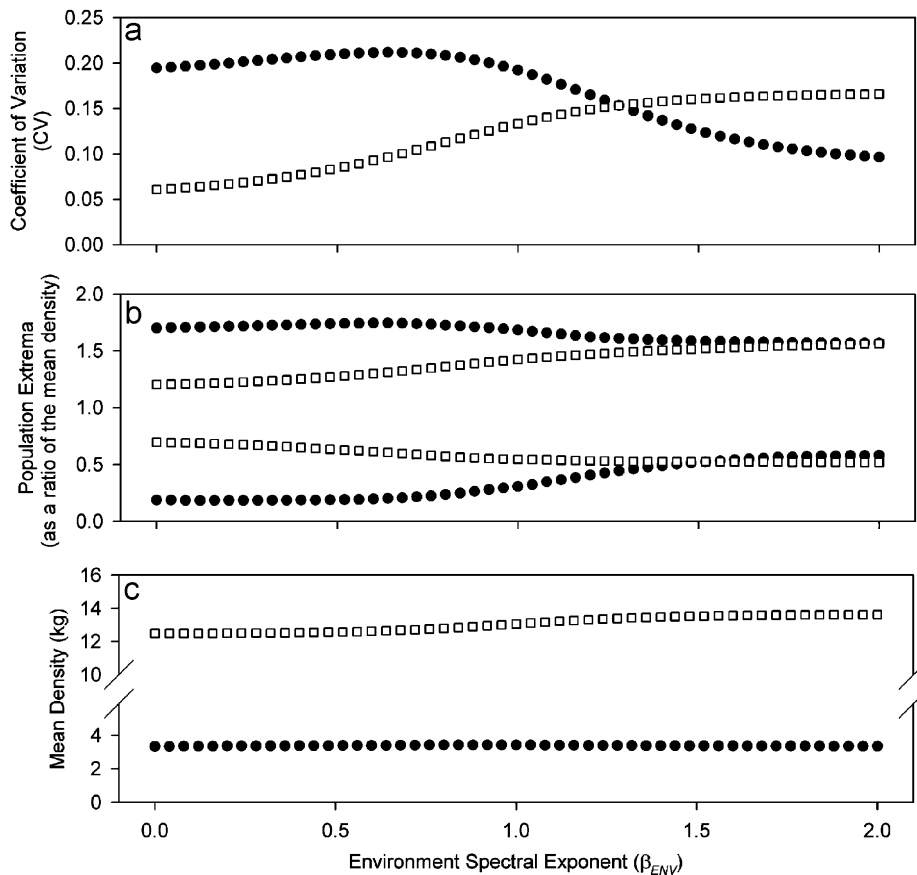


Fig. 1. (a) The coefficient of variation (CV), (b) extremes of density, and (c) mean densities for the resource population (solid circles) and consumer population (open squares) as a function of the environmental spectral exponent β_{ENV} (for the parameters listed in Table 1).

therefore is capable of conserving all moments of the noise distribution as colour is varied (i.e. the mean, variance, and frequency distribution).

Spectral mimicry (Cohen et al., 1999) is a permutation method which applies a desired colour to a reference time series, whose statistical moments remain unchanged after permutation. For this, a new time series $X = (X_1, \dots, X_{N/2})$ of random normal, uncorrelated (white noise) deviates was generated with mean $\mu = 293$ and standard deviation $\sigma = 5$. This ‘reference’ series (X) was subsequently permuted by the ‘coloured’ series τ to create the temperature time series $T = (T_1, \dots, T_{N/2})$ which consisted of the values from X , permuted by the ordered-ranks of τ . For example, if the largest element in τ was the third observation in time (τ_3), the largest element of X was placed as the third element in the new time-series T . This process was iterated until T was filled.

Fifty independent replicates of the reference series (X) were each permuted by 200 different ‘coloured’ time-series (τ) with spectra ranging from 0 to 2.0. This process ensured that within each replicate the temperature time series were identical with respect to mean, variance, and frequency

distribution, but had different spectral exponents (Cohen et al., 1999). In practice, the realized spectral exponents of the temperature series were slightly less than the values of β used for their construction; this effect has been previously attributed to the spectral synthesis method (Cuddington and Yodzis, 1999).

2.3. Model simulation

The model was integrated using the 5th and 6th order Runge–Kutta method (supplied by the IMSL subroutine ‘IVPRK’) for $N/2 = 16384$ time-steps, where each step was equal to 1 day. At each time t (day), the temperature was set to T_t ; thus temperature was constant within each day, but changed discretely from one day to the next. On day 1 the densities of resources and consumers were initialized at their equilibrium values (which in turn depended upon the temperature on day 1). The range of temperatures encountered in the simulations did not vary within replicates and the average minimum and maximum temperatures encountered across replicates were 0.18 and 39.92 °C, respectively. Temperatures in this range did not

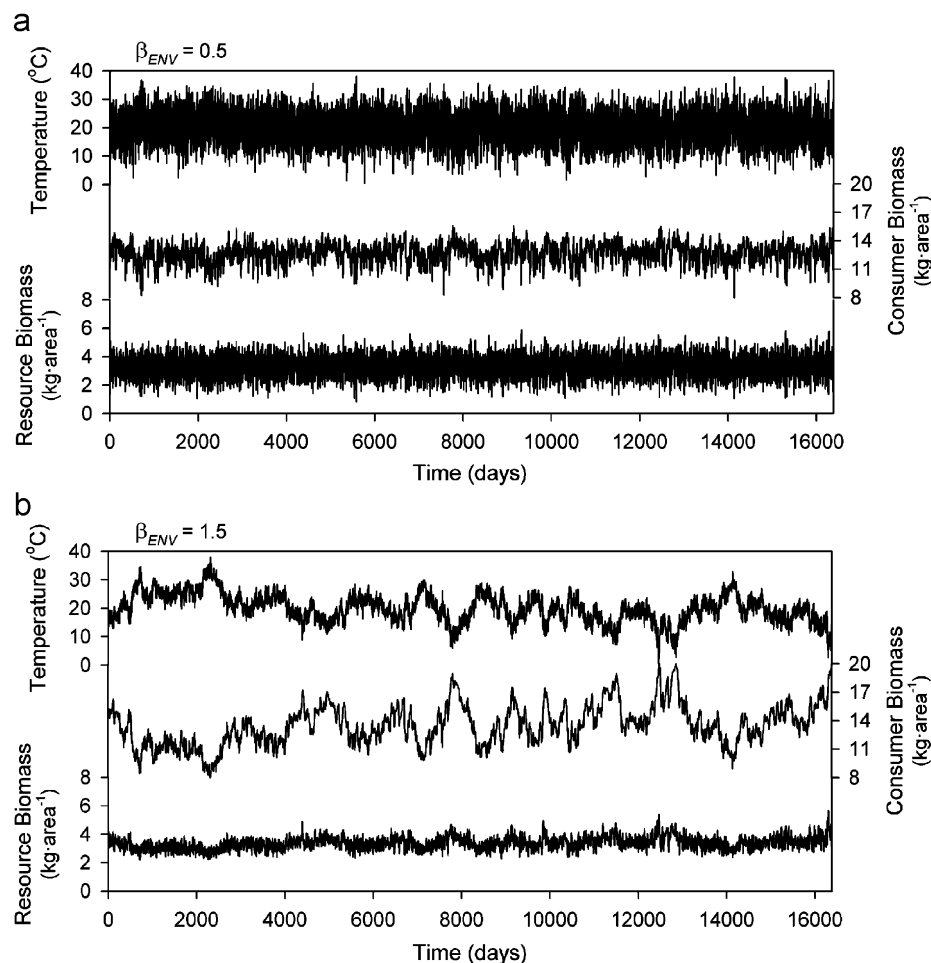


Fig. 2. The temporal model dynamics of resources and consumers and the time-series of temperature to which they were subjected for (a) $\beta_{ENV} = 0.5$ and (b) $\beta_{ENV} = 1.5$. The two panels represent dynamics from the same model replicate and thus the two time-series of temperature were constructed from the same set of values (e.g. they have identical mean, variance and range).

introduce qualitative changes to the equilibrium stability of the model (Hopf or transcritical bifurcations were not encountered; see Vasseur and McCann, 2005) and thus extinctions were neither expected nor observed in the simulations. For each value of β , the fifty independent replicates were used to determine the ensemble average for the mean density, extrema, and coefficient of variation (CV) for resources and consumers.

In the following sections of the paper the spectral exponent describing the environment (temperature) is labelled β_{ENV} and the following assignment of colours is adopted: environmental reddening progresses from white $\beta_{ENV} \approx 0$, to pink $\beta_{ENV} \approx 1.0$, to brown $\beta_{ENV} \approx 2.0$. Although the model requires temperature in Kelvin, temperature is transformed into degrees Celsius for ease of interpretation by the reader.

3. Results

An important descriptor of the response of resource and consumer populations to the colour of environmental noise is the change in their temporal variability. In white environments ($\beta_{ENV} = 0$) the CV of the resource population is nearly 4 times that of the consumer population and resource density ranges from 19% to 170% of their mean value while consumers range from 70% to 121% of their mean value (Fig. 1). As β_{ENV} increases there is a reversal of this relationship; at approximately $\beta_{ENV} = 1.28$ the CV of resource density becomes less than that of consumer density. There is a similar change in the ranges of resource and consumer densities; the range of resource density narrows with increased redness while that of consumers increases in breadth. It is interesting to note that despite the increase in consumer variability in redder environments, the range of the population remains well-bounded from low densities. Mean densities of consumers and resources vary little as the environmental colour is altered (Fig. 1c) substantiating that the trends in CVs are a consequence of altered variability. The changes to the temporal variability and range of consumer and resource densities are visible from their temporal dynamics when comparing them at low and high values of β_{ENV} (Fig. 2).

To better understand how the results are generated by the interaction between environmental noise and the model's intrinsic dynamics, Fig. 3 shows three exemplary trajectories in the consumer–resource phase plane. In this figure each trajectory begins on the equilibrium at 10 °C. The trajectories demonstrate the response of the system to a linear 20 °C temperature increase over a period of 10, 20 or 100 days (trajectories A, B, and C, respectively). Trajectory A is an analogy of temperature change in environments with slightly reddened (white/pink) spectra, where large shifts in environmental conditions can occur rapidly. Trajectory C is an analogy of environments with strongly reddened (pink/brown) spectra where large shifts in environmental conditions take much longer to develop. While the equilibrium densities of both consumers and

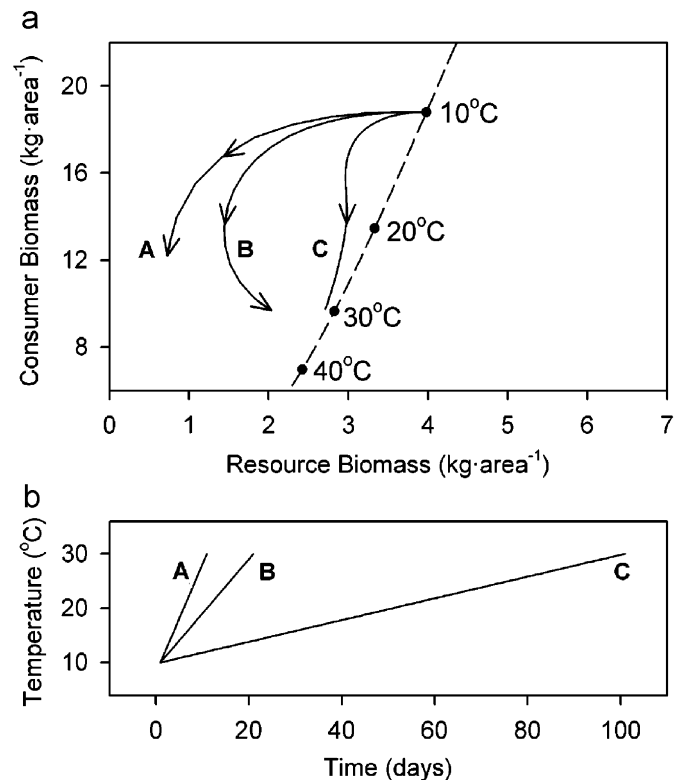


Fig. 3. (a) The phase plane of resource and consumer density showing their equilibrium response to temperature (dotted line) and three exemplary trajectories for a linear 20 °C increase in temperature over (A) 10 days, (B) 20 days, and (C) 100 days (panel b).

resources decline with warming (Fig. 3 dashed line), the short-term response to warming is initially greater (lesser) than that projected by the equilibrium change in resources (consumers). The ‘overcompensation’ occurring in the resource population is less prevalent as the period of environmental change lengthens (cf. A, B and C), because the daily temperature changes become less abrupt. This translates into a reduction in resource variability as β_{ENV} increases from white to brown (see Fig. 1).

Consumer population density responds to temperature in an opposing manner; consumer densities lag behind the equilibrium density as temperature is varied (Fig. 3). This behaviour leads to the expression of low consumer variability when temperature noise is white, since long runs of autocorrelated temperatures (which are rare in white noise) are required to lead the consumer population toward a new equilibrium density. Alternatively, when temperature noise is brown, long runs of autocorrelated temperatures are common and consumers track their equilibrium density more closely. Since consumer equilibrium density is more sensitive to temperature change than resource equilibrium density (Vasseur and McCann, 2005), consumers exhibit increasing variability as β_{ENV} transitions from white to brown (see Fig. 1).

Although linear changes in temperature provide a useful metaphor for understanding the impact of temperature

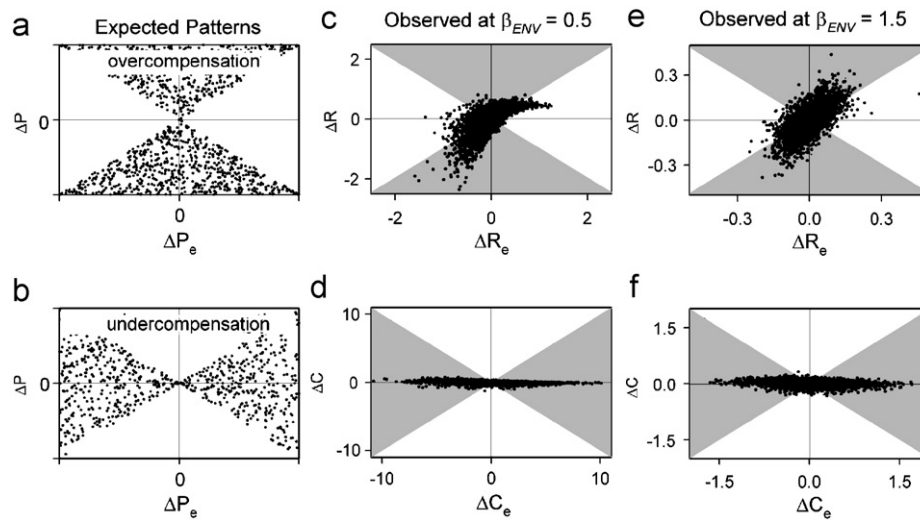


Fig. 4. The expected relationship between realized population change (ΔP) and equilibrium population change (ΔP_e) for (a) overcompensatory populations and (b) undercompensatory populations. Panels (c) and (d) show the relationship between realized and equilibrium change for resources and consumers, respectively, at $\beta_{ENV} = 0.5$ and at $\beta_{ENV} = 1.5$ (panels e and f). Each point represents the observed change and equilibrium change from time t to $t + 1$ from one model iteration. Note the change in scale from panels (c)/(d) to (e)/(f).

change on consumer–resource dynamics (Fig. 3), such idealized environmental fluctuations are absent from the simulations employed in this study and from real systems. To determine the prevalence of over and under compensation that occurs in the model simulations, the change in equilibrium density from one time point to the next is compared to the realized change in density for each population (Fig. 4). Overcompensation is characterized by a realized change in population density (ΔP), which is greater than the change in its equilibrium density ($\Delta P > \Delta P_e$) while undercompensation occurs when the realized change is smaller than the equilibrium change ($\Delta P < \Delta P_e$). By plotting ΔP_e and ΔP (i.e. equilibrium and realized density change) as coordinate pairs one can infer from the location of points in Cartesian space if the dynamics are predominantly over or undercompensatory (Fig. 4a,b). Resource dynamics are predominantly overcompensatory (Fig. 4c,e); strong overcompensation occurs when the resource equilibrium change is negative (caused by a temperature increase) yet resource dynamics can in some instances be undercompensatory when equilibrium change is positive (caused by a temperature decrease). This asymmetry may arise from the relative increase in the resilience or “attractiveness” of the model’s equilibrium at high temperatures (see Vasseur and McCann, 2005). Consumers exhibit strong undercompensation regardless of the direction of change of the consumer equilibrium (Fig. 4d,f). The result of these patterns of over and undercompensation can be seen in the scatter of points in Fig. 5, where plots show the densities of consumer and resource populations encountered during simulations at (a) $\beta_{ENV} = 0.5$ and (b) $\beta_{ENV} = 1.5$. Overcompensatory dynamics in the resource population generates a wider scatter on the resource axis in panel (a), while the improved ability of the system to better track its equilibrium under red noise

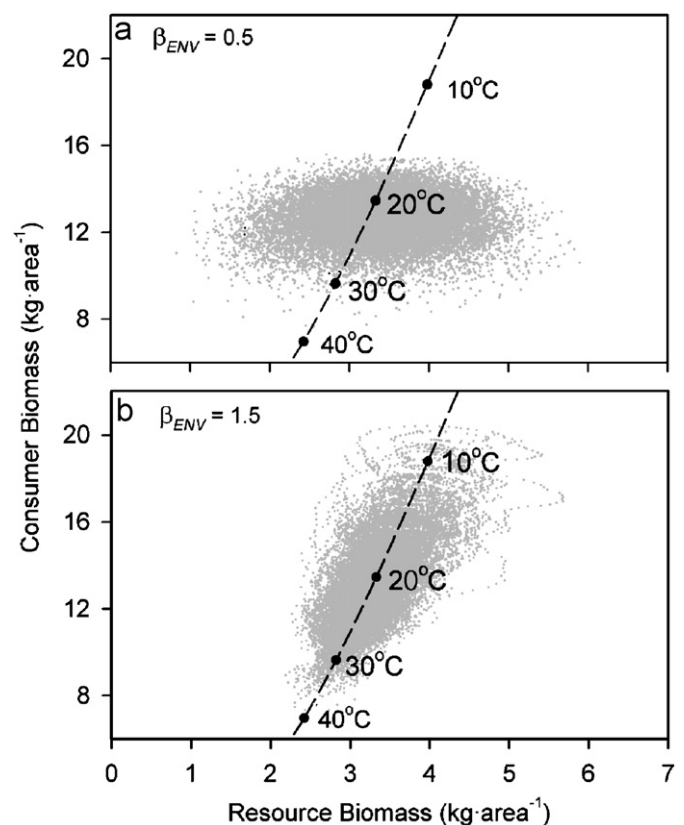


Fig. 5. The phase plane of resource and consumer density showing their equilibrium response to temperature (dotted line) at (a) $\beta_{ENV} = 0.5$ and (b) $\beta_{ENV} = 1.5$. Each point represents the observed resource and consumer density at some time t from a single model run.

drives a wider scatter on the consumer axis in panel (b). The change in population variability (both resources and consumers) along the gradient of β_{ENV} in Fig. 1 is evident

from the difference in relative scatter along the resource and consumer axes between Figs. 5a and b.

4. Discussion

The results show that the temporal variability of consumer and resource populations can be strongly influenced by the autocorrelation structure of environmental noise. As the spectral exponent increases, describing a progression of environmental noise from white to brown, the model system demonstrates a decrease in resource variability, and an increase in consumer variability; in white environments resources are more variable than consumers, while in brown environments the trend is reversed.

An important determinant of the patterns demonstrated in this study arises from the ability of the two populations to ‘track’ their environment. How well a population tracks its environment is linked to its intrinsic growth rate (Hubbell, 1973; May, 1973); all else being equal, populations with high growth rates tend to be more variable, reflecting their closer association with environmental conditions. Reddened environments improve environmental tracking since high serial correlations allow even slow growing populations to respond to changing conditions (Roughgarden, 1975). In this study, both resource and consumer densities track environmental fluctuations better in reddened environments (Fig. 5—shown by a closer association with the equilibrium contour at $\beta = 1.5$), consistent with Roughgarden’s (1975) predictions. However, resources, which are faster-growing than consumers (due to their smaller body size—see Eq. (2)) tend to overcompensate for environmentally induced changes in their equilibrium—a property not predicted by the population models of Hubbell (1973), May (1973) and Roughgarden (1975).

Previous studies have shown how the degree of over or undercompensation exhibited by a population influences its persistence in coloured environments. Using an AR(1) model of environmental noise Petchey et al. (1997) found that populations exhibiting overcompensatory dynamics persisted longer in pink ($\beta \approx 1$) than in white environments, whereas the opposite trend occurred for populations exhibiting undercompensatory dynamics. These results were later extended to include larger values of β using a $1/f^\beta$ model of environmental noise (Cuddington and Yodzis, 1999); although extinction risk peaked in pink environments due to large variability in persistence times, the mean persistence time of both over and undercompensatory populations converged to a high value as β increased, suggesting that compensation patterns, like growth rates, are of reduced importance in reddened environments. Conclusions arising from both of these studies necessarily assume that catastrophic extinctions cannot occur (Heino et al., 2000; Schwager et al., 2006). This assumption is easily extended to continuous time models where the approach to an ‘extinct’ state is

asymptotic and therefore reasonably slow to ensure long-term persistence. Given that mean persistence time should vary inversely with population variance, the results presented here are consistent with previous findings; overcompensatory (undercompensatory) populations are less (more) variable in reddened than in white environments. However, rather than the convergence of variability in reddened environments demonstrated in previous studies (Petchey et al., 1997; Cuddington and Yodzis, 1999) this study shows a reversal in the relative variability of over and undercompensatory populations (respectively resources and consumers) that arises from differential sensitivities of their equilibrium densities to environmental conditions. Since the consumer’s equilibrium density is more sensitive than the resource’s equilibrium density, consumers demonstrate relatively more variability in reddened environments. Thus in order to understand how a trophic community is influenced by the colour of its environment, we must understand both the nature of over and undercompensatory dynamics occurring in the community, and the sensitivity of each community member’s equilibrium density to environmental change.

In this study, the temperature scaling relationships (Eq. (2)) are fixed to represent a population of zooplankton feeding upon algae (see Table 1), leaving the body sizes m_R and m_C , and the temperature-independent parameters R_0 and K free to vary (cf. Savage et al., 2004 who argue for temperature dependence in K). These ‘free’ parameters influence the model’s equilibrium densities and the pattern of compensation demonstrated by the two populations. The paragraphs below detail the impact of a change in these free parameters on the model dynamics in white ($\beta_{ENV} \approx 0$) and brown ($\beta_{ENV} \approx 2.0$) environments as a means to generalize the results depicted here to a wider class of consumer–resource systems.

Resources grow at a rate determined by the intrinsic rate of growth r , which in this model is governed by body size and temperature. Resource body size is inversely related to the intrinsic rate of growth according to the power law $r \propto m_R^{-0.25}$ (see Eq. (2)). Since growth rate and variability should be positively correlated (Hubbell 1973; May 1973), an increase in resource body mass should lead to a reduction in variability in environments where environmental tracking is of less consequence (Roughgarden 1975). Figure A1 in supplementary Appendix A demonstrates the influence of a change in resource body size on the relationships shown in Fig. 1. As expected, an increase in resource body mass reduces its variability, but the effect is limited to lesser values of β where environmental tracking is less important. Theory demonstrates that changes in consumer body size will have a similar effect (Appendix A).

The ratio of the free parameters R_0/K in part determines the strength of the interaction coupling the two populations (Yodzis and Innes, 1992; Vasseur and McCann, 2005). Lessening the value of R_0/K increases the flow of energy from the resource to the consumer, in turn

increasing the propensity of the resource population to overcompensate for environmentally induced changes in the equilibrium density (Fig. 6). Alternatively, increasing the value of R_0/K reduces the flow of energy and the propensity of the resource population to overcompensate (Fig. 6). This study employs a moderate value of this ratio ($R_0/K = 6$) to avoid the complication encountered when the system becomes unstable ($R_0/K < 1$) or non-persistent ($R_0/K > 12.4$) inside the range of temperatures examined here (approximately 0–40 °C). Lower (large) values of this ratio lead to increased (decreased) resource variability in white environments where the compensatory patterns are most important.

The parameters defining the body-size/temperature scaling functions ultimately determine whether resources and consumers decline or increase in response to changing temperature and at what rate they do so. The behaviour depicted in Fig. 1 requires that the consumer equilibrium be more sensitive to temperature change than the resource equilibrium. There is accumulating evidence that species occupying higher trophic levels are indeed more sensitive to long-term warming (Allen et al., 2002; Voigt et al., 2003); however, it is worthwhile to investigate the range of conditions which uphold this behaviour in the model. In Supplementary Appendix A, expressions for the relative sensitivity of the consumer and resource equilibrium densities are derived (Eq. (A5)). These expressions demonstrate that body sizes have no impact upon the sensitivity of the equilibrium densities to temperature. In addition, only the consumer's sensitivity is influenced by the free parameters R_0 and K ; increasing the ratio R_0/K brings the system nearer to the boundary for consumer persistence and reduces the sensitivity of the consumer's equilibrium density to temperature; decreasing the ratio R_0/K produces the opposite effect.

The strong dependence of consumer and resource variability on the colour of environmental noise demon-

strated here and elsewhere highlights the importance of understanding exactly which colours describe variability in which environments. The colour of temperature fluctuations have been shown to vary widely with geography (Király et al., 2006). Steele (1985) was first to generalize that terrestrial environments are well described by white noise and marine environments by red noise. Using monthly sampled data, Cyr and Cyr (2003) provide the most detailed description of spectral exponents on an environmental gradient for temperature from air ($\beta = 0.16$), rivers ($\beta = 0.24$), lakes ($\beta = 0.61$); great lakes ($\beta = 0.88$) and oceans ($\beta = 1.16$). These, and the results from Vasseur and Yodzis (2004; also using monthly data) for atmospheric ($\beta = 0.588$) and ocean temperature ($\beta = 1.564$), corroborate Steele's (1985) early findings. Pelletier (2002) and Koscielny-Bunde et al. (1998) both suggest similar spectral exponents for atmospheric temperature at continental and maritime localities ($\beta \approx 0.5$ – 0.7); however, the use of daily data revealed a shift to larger spectral exponents at continental locations for frequencies above 1/month. In contrast, Vasseur and Yodzis (2004) showed larger spectral exponents at maritime than continental localities using monthly data. A mild increase in spectral exponents of temperature extrema at higher elevations has also been noted (for frequencies > 1 /month; Talkner and Weber, 2000). These studies show that the range of spectral exponents along natural environmental gradients has enough breadth to produce noticeable changes in the variability patterns of natural populations. The model studied here predicts that zooplankton communities should be less variable in lakes and rivers than in oceans, whereas algal communities should be more variable in lakes and rivers than in oceans. Although these predictions are easily testable in laboratory microcosm experiments, their validation in natural systems is confounded by an array of complicating factors. Most notably, other important environmental variables may not demonstrate the same change of colours along environmental gradients as exhibited by temperature and the two-trophic level system modelled here lacks the food-web complexity that is ubiquitous in natural systems.

Most studies analysing the response of interacting populations to environmental colour have focused upon the resultant colour of population dynamics. Using a tri-trophic model where each population experienced coloured [AR(1)] environmental noise in its growth rate, Xu and Li (2003) found that top predators had strongly reddened spectra regardless of the environmental colour, whereas the colour of consumer and resource populations ranged from strongly reddened to blue ($\beta < 0$) depending on the amplitude of environmental noise. While the indirect effect of environmental noise passed through trophic interactions has been shown to strongly redden population dynamics (Ripa et al., 1998; Xu and Li, 2002), the white and blue population dynamics found by Xu and Li (2003) demonstrate the importance of food web structure on population colour. The population spectral exponents

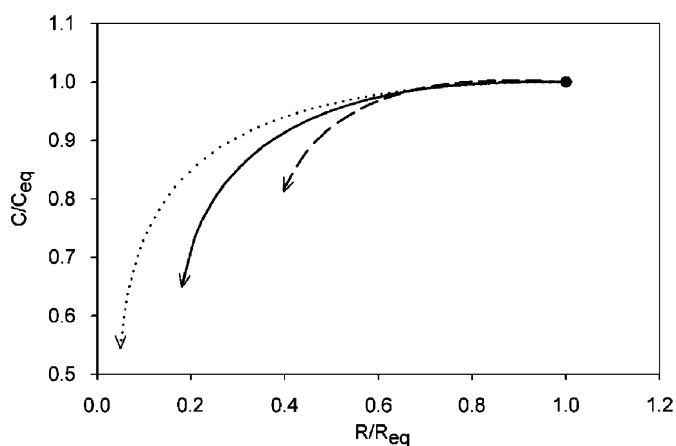


Fig. 6. Three exemplary trajectories for the consumer–resource system when temperature is increased linearly from 10 to 30 °C over a 10-day period. The three trajectories correspond to (solid) $R_0/K = 6$, (dotted) $R_0/K = 3$, and (dashed) $R_0/K = 9$. The solutions are normalized by their equilibrium values at 10 °C to allow comparison among the relative responses.

found in the present study ranged from pink to brown ($1 < \beta < 2$) for resources and from brown to black for consumers ($2 < \beta < 3$; unpublished data)—differing from those in Xu and Li (2003) potentially due to the varied implementation of environmental noise and the trophic-structural differences between the two models. For example, the dynamics in this study are influenced by ‘top–down control’ of resources by consumers; surplus or deficit production is ultimately absorbed by the consumer population, which makes their equilibrium more sensitive to environmental variation and their dynamics increasingly variable in red environments. However, the addition of a top predator would result in a trophic cascade; ‘top–down control’ would be exerted by the predator (Oksanen et al., 1981), altering the equilibrium sensitivities and variability of the consumer and resource. Further research is warranted to determine to what extent the predictions made here, and in other trophic/environment models are upheld in natural communities and in theoretical food webs with more complicated trophic structure.

The impact of environmental colour on the variability of consumers and resources has been previously described only for linear [multiple first-order autoregressive—MAR(1)] models (Ripa and Ives, 2003). Under a regime of demographic AR(1) noise (rather than parametric $1/f$ —as used herein) they found that the amplitude of consumer–resource oscillations varied with environmental colour; provided that the oscillation period met a certain threshold, oscillations had the largest amplitude in moderately reddened (approximately pink noise) environments. Ripa and Ives’ used demographic noise to show that altered environmental colour caused the population dynamics to organize along different eigenvectors in the phase space, allowing them to clearly attribute changes in variance to noise colour. Although such linear approximations can be very useful for interpreting the dynamics of non-linear systems, the model analysed herein has eigenvalues and eigenvectors which fluctuate as a consequence of environmental conditions, thus requiring a different approach to assess changes in population variability. Despite vast differences between the model used in Ripa and Ives, (2003) and that used herein, moderately reddened environments increase the variability of resources and consumers in both, suggesting this may be a conserved property of basic consumer–resource interactions. Further research into the effects of noise modulation (e.g. demographic vs. parametric noise) using non-linear models will help to identify if predictions from linear models extend to their non-linear counterparts.

To date, there are no experiments that concurrently determine the responses of consumer and resource variability to changes in the colour of temperature fluctuations; the majority of research has focused upon single populations, or multiple populations at a single trophic level. Petchey (2000) determined the change in temporal variability of two bacterivorous ciliates, *Colpidium* and *Paramecium*, to thermal fluctuations with white ($\beta = 0$) and

pink ($\beta = 1$) spectra. He found that fast-growing *Colpidium* were more variable in pink environments but that the opposite was evident for the slower-growing *Paramecium*. In a similar experiment, Laakso et al. (2003) found that pink environments increased the biomass variability of both slow and fast growing *Tetrahymena*. In the closest experimental analogue to this study, the influence of coloured temperature fluctuations on the variability of the rotifer *Brachionus* and its algal prey have been determined in reference to a constant temperature regime (Gonzalez and Descamps-Julien, 2004). Here the rotifer was 30% more variable in a pink ($\beta = 1$) environment and the algae were, on average, 19% less variable than in the constant environment. Although the reference environment differs between their study and the results presented here, the demographic noise experienced by populations in a constant environment may be most closely matched by white noise in theoretical experiments. Further experimental research is required to determine the extent to which the predictions of this study are upheld in natural systems.

This model builds on previous investigations of the impact of noise colour on population dynamics by incorporating a mechanistic framework to describe the interface between the environment (temperature) and the model equations. The novel predictions regarding the variability of resources and consumers in environments of differing colour warrant further experimental research into how the colour of temperature fluctuations influences the variability of populations. In addition to trophic structure there remains much to be learned about how population behaviour and life history influences the variability of populations in coloured environments. Given that different environments are known to have different colours and that global environmental change will likely include changes in the correlation structure (colour) of the environment (Wigley et al., 1998), it is particularly important that we better our understanding of how environmental variability is incorporated into population dynamics.

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Appendix A. Supplementary materials

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.tpb.2007.06.002.

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