THE ROYAL SOCIETY

# Environmental colour affects aspects of single-species population dynamics

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Single-species populations of ciliates (*Colpidium* and *Paramecium*) experienced constant temperature or white or reddened temperature fluctuations in aquatic microcosms in order to test three hypotheses about how environmental colour influences population dynamics. (i) Models predict that the colour of population dynamics is tinged by the colour of the environmental variability. However, environmental colour had no effect on the colour of population dynamics. All population dynamics in this experiment were reddened, regardless of environmental colour. (ii) Models predict that populations will track reddened environmental variability more closely than white environmental variability and that populations with a higher intrinsic growth rate ($r$) will track environmental variability more closely than populations with a low $r$. The experimental populations behaved as predicted. (iii) Models predict that population variability is determined by interaction between $r$ and the environmental variability. The experimental populations behaved as predicted. These results show that (i) reddened population dynamics may need no special explanation, such as reddened environments, spatial subdivision or interspecific interactions, and (ii) and (iii) that population dynamics are sensitive to environmental colour, in agreement with population models. Correct specification of the colour of the environmental variability in models is required for accurate predictions. Further work is needed to study the effects of environmental colour on communities and ecosystems.

**Keywords:** temporal autocorrelation; environmental tracking; variability; temperature fluctuations

## 1. INTRODUCTION

Time-series of real environmental variables contain positive temporal autocorrelation, that is, successive values are more similar than expected by chance (often referred to as reddened variability) (Mandelbrot & Wallis 1969; Monin *et al*. 1977; Steele 1985; Williamson 1987; Cuddington & Yodzis 1999). The dynamics of natural populations are also reddened (Pimm & Redfearn 1988; Sugihara 1995; Halley 1996), prompting questions about whether this results from the intrinsic properties of populations and communities or from reddened environmental variability (Cohen 1995; Sugihara 1995, 1996; Kaitala *et al*. 1997*a*; Ripa *et al*. 1998). Recent theoretical studies have revealed the importance of reddened environmental variability for population dynamics and extinction risks (Roughgarden 1975; Steele & Henderson 1984; Goodman 1987; Lawton 1988; Pimm 1991; Arino & Pimm 1995; Sugihara 1995; Halley 1996; Ripa & Lundberg 1996; Johst & Wissel 1997; Kaitala *et al*. 1997*a*,*b*; Petchey *et al*. 1997; Cuddington & Yodzis 1999; Halley & Kunin 1999; Morales 1999), bringing assumptions of uncorrelated (white) environmental variability (e.g. Leigh 1981; Wissel & Stöcker 1991; Lande 1993) into question. These questions about reddened environmental variability and population dynamics prompted Cohen *et al*. (1998) to design a unique experiment investigating how environmental reddening affects real population dynamics. I conducted this experiment and also tested fundamental hypotheses (e.g. Roughgarden 1975; May 1976; Luckinbill & Fenton 1978; Pimm 1991) about how the intrinsic properties of populations and extrinsic factors control population dynamics.

Ciliate populations growing in aquatic microcosms were ideal for this study because they have short generation times and because their environmental conditions can be closely controlled and temperature easily manipulated. The 64 days of this experiment represented at least 64 generations of the ciliates, so the temporal scale was appropriate for answering questions about population dynamics (Connell & Sousa 1983). In addition, temperature fluctuations affect ciliate growth rates (Müller & Geler 1993; Walton *et al*. 1995) and more generally the structure of aquatic systems (Beisner *et al*. 1996; Norberg & DeAngelis 1997; Norberg 1998). I chose two ciliate species, *Colpidium striatum* and *Paramecium aurelia*, because they have high and low intrinsic growth rates, respectively. Single-species populations of each species experienced either constant, white or reddened temperature fluctuations. This design allowed me to test hypotheses about how environmental variability and intrinsic rate of increase interact to determine (i) the colour of the population dynamics, (ii) how closely the population tracks the environmental variability, and (iii) the population variability. I describe each hypothesis after a discussion about terminology.

### (a) *Temporal autocorrelation and colour*

Temporal autocorrelation is often referred to by its effect on the colour (the relation between the frequency and amplitude of fluctuations) of time-series (e.g. figure 1). Positive temporal autocorrelation results in low-frequency fluctuations with high amplitude, which by analogy to red light is often referred to as reddened variability or noise. No temporal autocorrelation results in equal amplitude for all frequencies of fluctuations, which



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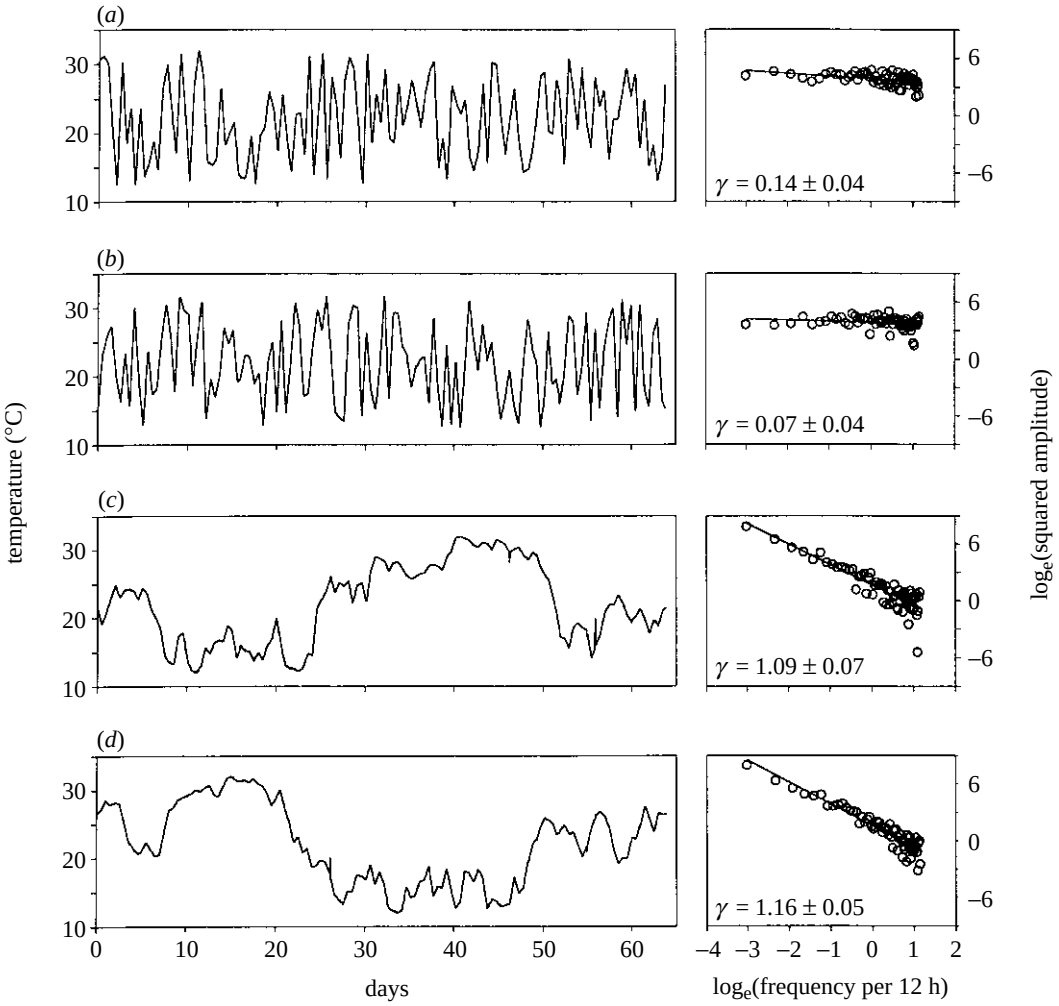


Figure 1. Example white and reddened time-series which were the actual temperatures recorded from the incubators (plotted here every *ca.* 90 min, but recorded by computer every 10 min). (*a*) White A, (*b*) white B, (*c*) red A and (*d*) red B. Expected temperatures were inserted into a short period (days 48.3–51.9) when the PC failed to record temperatures. Plots of the relation between $\log_e$(squared amplitude) and $\log_e$(frequency) show the colour of the actual 12-hourly temperature fluctuations. All frequencies had similar amplitude in the white treatments ($\gamma \approx 0$, where $\gamma = -b/2$), whereas lower frequency fluctuations had greater amplitude than high-frequency fluctuations in the reddened treatments ($\gamma \approx 1$) ($\gamma \pm 1$ s.e.).

by analogy to white light is referred to as white variability or noise (see Halley (1996) for a review). (Negative autocorrelation is not part of most theoretical studies or this empirical study and is not discussed.) I use the terms white and reddened to describe time-series (of either environmental variables or population dynamics) which contain no temporal autocorrelation or positive temporal autocorrelation, respectively, both for brevity and because the colour analogy has been used by previous authors. I use the terms environmental colour and population colour when discussing the pattern of temporal autocorrelation in environmental variables and population dynamics, respectively, for the same reasons.

(i) *Population colour*

Models generally predict that the colour of environmental variability tinges the colour of population dynamics, raising the possibility that the dynamics of natural populations are reddened because environmental variability is reddened (Pimm & Redfearn 1988; Sugihara 1995, 1996; Halley 1996; Kaitala *et al.* 1997*a*). Other studies have emphasized the importance of the intrinsic properties of populations (Cohen 1995; Blarer & Doebeli 1996; Kaitala & Ranta 1996; White *et al.* 1996*a*), interspecific interactions (Ripa *et al.* 1998) or population subdivision (White *et al.* 1996*b*) for reddened population dynamics. Population dynamics should be redder in reddened environments than in white environments if environmental colour does influence population colour (Roughgarden 1975; Kaitala *et al.* 1997*a*).

(ii) *Environmental tracking*

How well the population density tracks the environmental variability should be affected by environmental colour (Roughgarden 1975). Model population dynamics track the environmental variability closely if environmental fluctuations occur slowly compared to the population intrinsic growth rate and average over fluctuations if they occur quickly relative to the intrinsic growth rate ($r$) (Hubbell 1973; May 1976; Pimm 1991). Therefore, populations should track reddened environments more closely than white environments because reddened environments

contain strong, long-term fluctuations, and populations with a high $r$ (*Colpidium*) should track variable environments more closely than populations with a low $r$ (*Paramecium*).

(iii) *Population variability*

In a constant environment a high $r$ should lead to lower population variability because the population density is tightly regulated around its equilibrium compared to when $r$ is low (May 1973). In a variable environment, a higher $r$ should lead to a more variable population, because the population is able to track the environmental variability better than a population with a low $r$. This theory predicts a statistical interaction between $r$ (species identity) and the pattern of environmental variability (Pimm 1991). Specifically, *Colpidium* (high $r$) population variability should increase from constant to white to reddened environments more than *Paramecium* (low $r$) population variability.

## 2. MATERIAL AND METHODS

### (a) *Protist microcosms*

The culture methods closely followed those of Lawler & Morin (1993). The microcosms were 240 ml covered glass bottles placed in dark incubators. Each bottle contained 100 ml of nutrient medium (0.55 g of Carolina Biological Supply protozoan pellet per litre of well water) and three sterile wheat seeds to provide additional nutrients. Sterile nutrient medium was first inoculated with bacteria (*Bacillus cereus*, *Bacillus subtilus* and *Serratia marcescens*) and then with bacterivorous ciliates after waiting two days for the bacteria to grow to high densities. The bacterivores were introduced into the microcosms by adding five pipette drops of either *C. striatum* (Ehrenberg) or *P. aurelia* (Ehrenberg) stock culture medium (originally obtained from Carolina Biological Supply, Burlington, NC, USA). *Colpidium* ($r \approx 1.5$ day$^{-1}$) and *Paramecium* ($r \approx 0.3$ day$^{-1}$) were used because they have very different intrinsic growth rates at room temperature (*ca.* 22 °C). After seven days the populations had increased to high density but there were large differences between replicates. All microcosms of a species were poured into large sterile flasks, mixed and returned to the replicate jars to remove this variation. Four replicates of each of the ten treatment combinations made a total of 40 microcosms. The experiment lasted 64 days during which 10 ml of media were removed and replaced with fresh media each week.

### (b) *Experimental design*

Species identity (*Colpidium* or *Paramecium*) and temperature regime were two factors in a fully factorial design. The temperature regime was either constant temperature (22 °C), one of two white temperature regimes (white A or white B) or one of two reddened temperature regimes (red A or red B). Two temperature regimes with each colour were used to separate the effects of colour from the possible effects of particular series of temperature fluctuations and also so that the environmental colour was not completely confounded by incubator identity. Each of the fluctuating temperature regimes contained the same 128 temperatures ($12 + 20x/127$ °C with $x = 0$–127 in unit steps), two for each day of the experiment, but differed by shuffling the order of these 128 temperatures. Randomly shuffling the 128 temperatures produced white temperature regimes. Shuffling so that consecutive temperatures were more similar than by chance produced reddened temperature regimes. The 128 temperatures were shuffled four times to produce two white and two reddened series of temperatures. A procedure called spectral mimicry (Cohen *et al*. 1999) used template white and reddened time-series to shuffle the 128 temperatures. Spectral mimicry ensured that the means (22 °C), minimums (12 °C), maximums (32 °C) and variances (34.1 °C) of the 12-hourly temperatures were identical for the white and reddened temperature regimes. Temperatures of 12–32 °C are sublethal for both species.

The template white and reddened times-series used in the spectral mimicry procedure each contained $n/2$ summed sine waves such that

$$\text{temperature}(t) = \sum_{f=1}^{n/2} \frac{1}{f^{\gamma}} \sin\left(\frac{2\pi f t}{n} + \theta_f\right), \qquad (1)$$

where $n$ is the length of the series, $f$ is the frequency (units of cycles per 12 h), $t$ is the time (units of 12 h), $\gamma$ determines the relation between amplitude and frequency and $\theta_f$ is a uniform deviate $[0, 2\pi]$ which adds random phase to each sine wave. The two white template series were two independent realizations of this model both with $\gamma = 0$ (each sine wave had equal amplitude) and the two reddened template series were two independent realizations both with $\gamma = 1$ (lower frequency sine waves had larger amplitude than higher frequency sine waves). $1/f$ models of environmental variability, such as equation (1), are probably better representations of real environmental variability than, for example, first- or second-order autoregressive models (Halley 1996; Cuddington & Yodzis 1999).

Four incubators (Percival I-36VL with 982 microprocessors; Percival Scientific, Inc., Iowa, USA) were used to vary the temperature according to the white and reddened temperature regimes. The temperature regimes were uploaded to the incubator microprocessors using PACES software (Percival Scientific Inc.) installed on a standard PC. Each incubator was assigned a temperature regime and started at the first temperature of the regime. The temperature changed linearly (ramped) to the next temperature in the regime over the next 12 h and each of the following 127 12-h periods. The constant temperature regime was maintained in a fifth incubator.

The PC recorded the temperature in each incubator every 10 min except during 3.6 days (days 48.3–51.9) when the PC failed to record temperatures. The temperature in each incubator was controlled by the incubator microprocessors so the PC failure did not affect the temperature control. During the vast majority of the experiment, when the actual temperature was recorded by the PC, the temperature control was accurate ($\pm 0.1$ °C) and closely followed the required patterns of temperature fluctuations. Therefore, I inserted the expected temperatures into the 3.6-day period to complete the recorded temperature series (figure 1). Spectral analysis (Chatfield 1984) of the actual 12-hourly temperatures showed that the temperature fluctuations in the incubators were approximately white or strongly reddened according to the treatments (figure 1). The colour of the temperature fluctuations in the white A treatment was significantly different from zero ($\gamma = 0.14 \pm 0.04$ (1 s.e.) and $p < 0.001$). However, the low value of $\gamma$ in the white A treatment indicates different frequency fluctuations with very similar amplitude (white) compared to the strongly reddened fluctuations in the reddened treatments. Ramping between 12-hourly temperatures added short-term (< 12 h) autocorrelation to the actual temperature series, but spectral analysis of the mean temperature over the previous 12 h showed that the white and

reddened treatments still differed strongly (O. L. Petchey, unpublished analysis).

### (c) *Population monitoring*

I estimated the population densities of the two ciliate species every two days by withdrawing a sample of known weight (*ca.* 0.35 ml) from each microcosm and counting the number of protists under a dissecting microscope (Nikon SMZ-U). The samples were diluted if their densities were too high to count. The counts were transformed to $\log_{10}(\text{density ml}^{-1} + 1)$ to correct for heteroscedasticity.

### (d) *Data analysis*

(i) *Population colour*

I used spectral analysis (Chatfield 1984) to measure the colour of the population dynamics in each of the three environments and analysis of covariance (ANCOVA) to test for the effects of species identity and environmental colour (either white or reddened) on population colour. Spectral analysis decomposes the observed population dynamics into sine waves, but does not assume that summation of sine waves is the process responsible for population dynamics. The data from the constant temperature treatments were excluded from the ANCOVA because the theoretical predictions are about variable environments only. Spectral analysis (by fast Fourier transform) and subsequent transformations provided the relation between $\log_e$(squared amplitude) and $\log_e$(frequency) (the complete manipulation is well described in Cohen (1995)). The regression coefficient (slope $b$) of the relation between $\log_e$(squared amplitude) and $\log_e$(frequency) was estimated as $-2\gamma$ (recall from equation (1) that $\gamma = 0$ for white dynamics and $\gamma > 0$ for reddened dynamics). $\text{Log}_e$(frequency) was the continuous explanatory variable in the ANCOVA and environmental colour (white A and B treatments were grouped into white, and red A and B treatments were grouped into red, in this and all other analyses) and species identity were the categorical explanatory variables. $\text{Log}_e$(squared amplitude) was the response variable. The theoretical predictions are about how environmental colour and species identity affect population colour (where the population colour is measured by the slope of $\log_e$(squared amplitude) regressed on $\log_e$(frequency)), so the predictions are about the interaction terms of the ANCOVA which include $\log_e$(frequency). A statistically significant interaction between the environmental colour (or species identity) and $\log_e$(frequency) indicates differences in slope which imply a significant effect of the environmental colour (or species identity) on population colour. (Alternate statistical analysis, including testing for the effects of environmental colour and species identity on the relative power of low- and high-frequency portions of the spectra (e.g. Blarer & Doebeli 1996; White *et al.* 1996*a*), led to the same conclusions as the ANCOVA presented here.)

(ii) *Environmental tracking*

The correlation coefficients of the relation between population density and average temperature over the previous two days measured how closely each replicate population tracked temperature fluctuations. The average temperature over the previous two days was used because, by definition, populations have no time to respond to instantaneous temperature changes. The two-day average is otherwise arbitrary, but the results were qualitatively the same when the average temperature was calculated over the previous one, two, three, four or five days. Two-way ANOVA tested for significant effects of the temperature regime and species identity on the correlation coefficients.

(iii) *Population variability*

The coefficient of variation of untransformed density measured the population variability over the total length of the experiment (McArdle *et al.* 1990) and two-way ANOVA tested for the effects of temperature regime and species identity. SAS was used for all the statistical analyses.

## 3. RESULTS

### (a) *Population colour*

The population dynamics of both species (figure 2) were significantly reddened in all environments (table 1 and figure 3). The *Colpidium* population dynamics were significantly redder than the *Paramecium* population dynamics, but the colour of the environmental variability had no effect on the population colour (table 1 and figure 3).

### (b) *Environmental tracking*

Although tracking was generally poor, species identity and environmental colour affected population tracking exactly as theory predicts. Both species tracked reddened environments more closely than white environments and *Colpidium*, with its higher intrinsic growth rate, tracked temperature fluctuations more closely than *Paramecium* (figure 4) (two-way ANOVA: species identity $F_{1,28} = 6.6$ and $p = 0.02$, environment $F_{1,28} = 17.3$ and $p = 0.0003$, and species × environment $F_{1,28} = 0.4$ and $p = 0.52$).

The *Colpidium* populations in both of the white environments decreased to low density early in the experiment independently of temperature (during days 6–18) (figure 2). The *Colpidium* populations in both the reddened environments decreased to low density at different times during the experiment, depending on when a series of hot temperatures ($> 29\,^{\circ}\text{C}$) occurred (days 42–50 in red 1 and days 10–20 in red 2) (figure 2). This appears to be the reason that *Colpidium* tracked the reddened environments more closely than the white environments. Sensitivity and acclimation to relatively high rates of temperature change (average rate of change ±1 s.e. in white environments $= 6.9 \pm 0.3\,^{\circ}\text{C}\ 12\,\text{h}^{-1}$ and in red environments $= 1.4 \pm 0.1\,^{\circ}\text{C}\ 12\,\text{h}^{-1}$) could have caused the early decrease in the *Colpidium* population density in white environments. The *Paramecium* populations did not show as large and obvious responses to the temperature fluctuations as *Colpidium* (figure 2).

### (c) *Population variability*

The population variability was affected by a significant interaction between species identity and temperature regime as predicted by the theory (figure 5) (two-way ANOVA: species identity $F_{1,34} = 13.3$ and $p = 0.001$, temperature regime $F_{2,34} = 2.6$ and $p = 0.09$, and species × temperature regime $F_{2,34} = 3.4$ and $p = 0.046$). The *Colpidium* population variability was lowest in constant environments, intermediate in white environments and highest in reddened environments, in contrast to *Paramecium*'s idiosyncratic changes in population variability between environments (figure 5). The

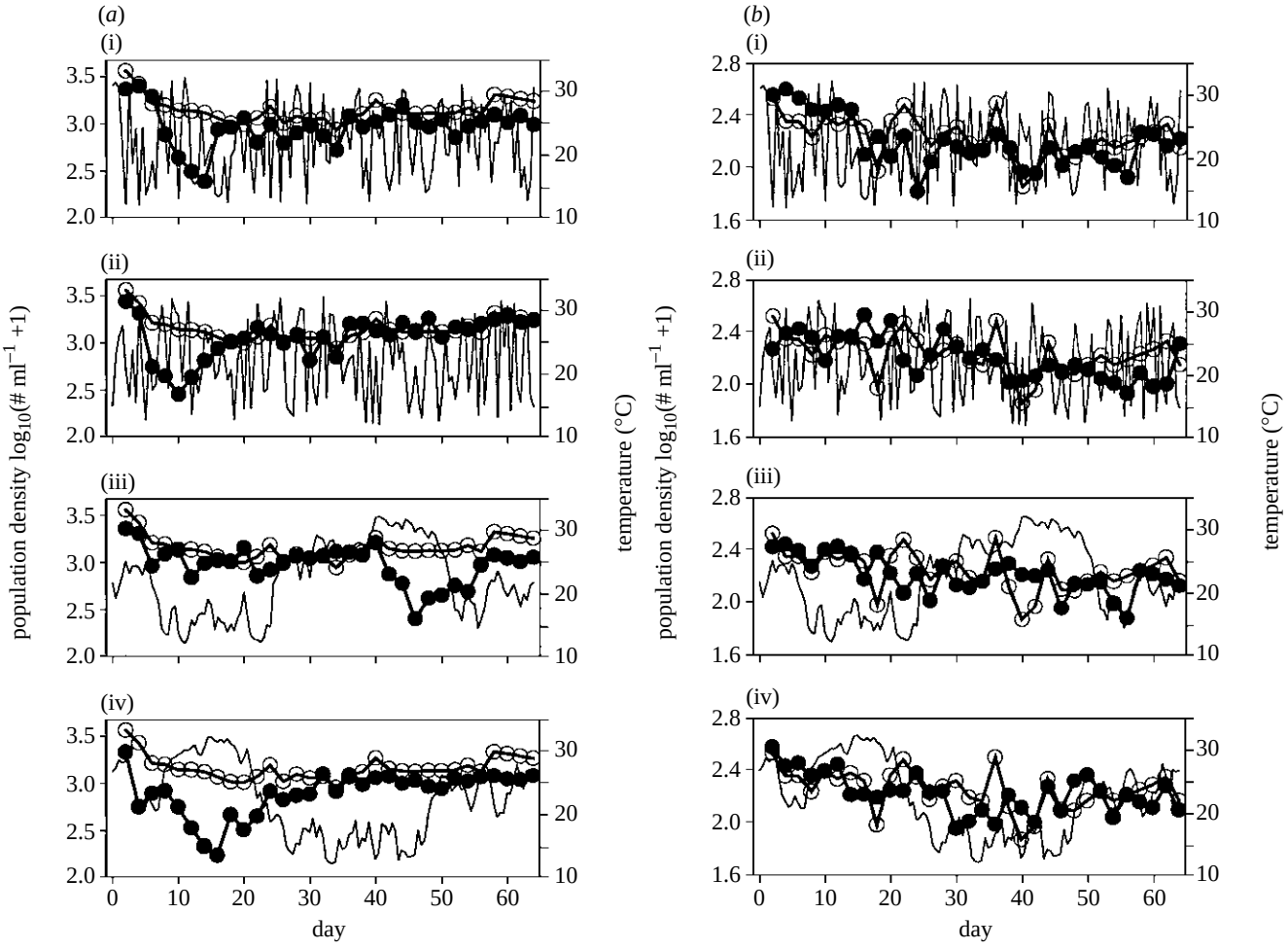


Figure 2. Example population dynamics of the two ciliate species in the variable environments (filled circles; one representative replicate). (*a*) *Colpidium* was sensitive to white (white A and white B) and reddened (red A and red B) environments, whereas (*b*) *Paramecium* seemed insensitive (white A, white B, red A and red B). The population dynamics in a constant temperature environment replicate (open circles) and temperatures (lines without symbols) are shown for reference. (i) White A, (ii) white B, (iii) red A, and (iv) red B.

*Colpidium* population variability was generally higher than the *Paramecium* population variability, even in the constant environment where theory predicts lower *Colpidium* population variability.

## 4. DISCUSSION

The results from this experiment about how single species track a variable environment and how populations vary through time show encouraging agreement with simple models (May 1973; Pimm 1991) and a previous empirical investigation (Luckinbill & Fenton 1978) of how the intrinsic properties of populations and environmental variability determine population dynamics. The results agree with many theoretical studies which have indicated important differences between the effects of white and reddened environments on population dynamics (Mode & Jacobson 1987; Lawton 1988; Foley 1994; Halley 1996; Ripa & Lundberg 1996; Johst & Brandl 1997; Johst & Wissel 1997; Kaitala *et al*. 1997*b*; Petchey *et al*. 1997; Cuddington & Yodzis 1999; Morales 1999; Halley & Kunin 1999). These differences suggest that predictions about real populations (e.g. minimum viable size or extinction risk) will be inaccurate and could lead to incorrect policy decisions if we continue to assume white environmental variability falsely, when the real environmental variability is actually reddened (Mandelbrot & Wallis 1969; Monin *et al*. 1977; Steele 1985; Williamson 1987; Cuddington & Yodzis 1999).

### (a) *Population colour*

Recent discussions have queried whether natural populations are reddened as a result of intrinsic or extrinsic (environmental variability, interspecific interactions or immigration–emigration) factors (Pimm & Redfearn 1988; Sugihara 1995, 1996; Halley 1996; White *et al*. 1996*b*; Kaitala *et al*. 1997*a*). All populations in this study, regardless of intrinsic (species identity) or extrinsic (colour of the environment or the presence of any variability at all) factors, were reddened (figure 3), suggesting that population dynamics are, by default, reddened. This contention is sensible for undercompensatory populations (e.g. the ciliate populations in this study) (O. L. Petchey, unpublished data) because positive temporal autocorrelation between densities of successive generations leads to reddened dynamics. These results therefore suggest that we should not necessarily be surprised to see natural populations with reddened dynamics or need to explain the reddened dynamics with extrinsic influences.

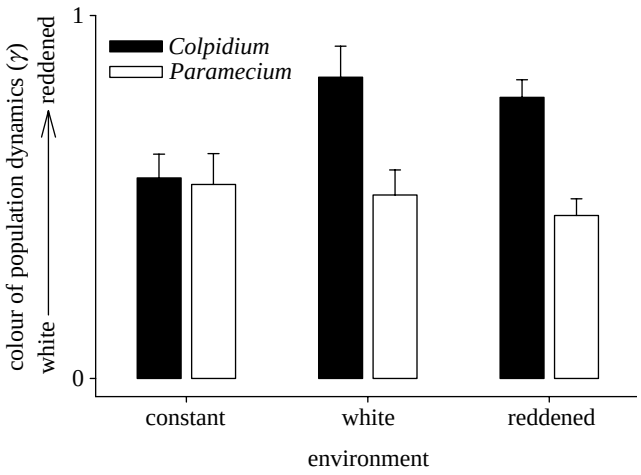


Figure 3. Mean colour ($\gamma$) of the population dynamics across replicates for each of the treatment combinations. The dynamics were significantly reddened in all treatments ($\gamma > 0$) and the extent of reddening was affected only by species identity (table 1). The error bars are $\pm 1$ s.e.

Why were the population dynamics not coloured by the environment as predicted by theory (Kaitala *et al.* 1997*a*)? Theoretical studies have often modelled environmental fluctuations by changing the carrying capacity of a population (Ripa & Lundberg 1996; Petchey *et al.* 1997; Cuddington & Yodzis 1999) or by multiplicative effects on the population density (Kaitala *et al.* 1997*a*). The temperature fluctuations probably had weak effects on the carrying capacity in this experiment (see § 4(b)), making any effects of environmental colour too weak to detect.

### (b) *Environmental tracking*

The apparent mechanism by which the *Colpidium* populations tracked the reddened environments more closely than the white environments was long runs of temperatures above *ca.* 29 °C which resulted in sustained periods of low birth rate and/or high mortality during which $r < 0$. Presumably $r < 0$ during the short periods of high temperatures in the white environments, but had a small effect on population density which was quickly recovered from once the temperature decreased. However, none of the populations tracked any of the environments very closely (correlation coefficients of less than 0.5); the temperature fluctuations appeared to have little obvious effect on the *Colpidium* density over the range of 12–29 °C or the *Paramecium* density over the entire temperature range, even in reddened environments. Another experiment (Petchey 1998) showed that increasing temperature increases the *r* of *Paramecium tetraurelia*, but has little effect on its carrying capacity over the range of 15–30 °C. This probably occurs because the increased respiration by the bacterivores at higher temperature is almost completely compensated for by increased productivity (also respiration) by the bacteria. Weak effects of temperature on the carrying capacity (apart from *Colpidium* at $> 29$ °C) could explain the generally poor environmental tracking by both species. Similar experiments with photosynthetic primary producers (algae) and herbivores would be very interesting, because their rates of photosynthesis (less sensitive) and respiration (more sensitive) respond differently to temperature changes (Norberg & DeAngelis 1997; Norberg 1998).

In models, environmental tracking is largely determined by the relation between the characteristic response time ($T_R$) of single-species populations (where $T_R = 1/r$) and the period of environmental fluctuations (May 1973). Populations track environmental fluctuations when $T_R$ is short relative to the period ($\tau$) of environmental fluctuations ($T_R \ll \tau$) and average over fluctuations when $T_R \gg \tau$. A transition between averaging over fluctuations and tracking fluctuations occurs when $T_R \approx \tau$. This implies that environmental reddening at periods shorter (frequencies higher) than populations can respond to is irrelevant to the populations; the

Table 1. *ANCOVA of the effects of environmental colour (only white or reddened treatments) and species identity on population colour*

(The interaction terms of colour × frequency, species × frequency and colour × species × frequency (indicated by a superscript 'a') indicate whether environmental colour, species identity and the colour × species identity interaction, respectively, affect population colour. The environment, species and environment × species effects are about the intercepts of the ANCOVA and are not interesting in this context.)

| source | d.f. | *F* | *p* |
|---|---|---|---|
| $\log_e$(frequency) | 1 | 241.70 | < 0.0001 |
| environmental colour | 2 | 0.17 | 0.68 |
| species | 1 | 46.00 | < 0.0001 |
| environmental colour × species | 2 | 5.00 | 0.03 |
| environmental colour × $\log_e$(frequency)[a] | 2 | 0.46 | 0.50 |
| species × $\log_e$(frequency)[a] | 1 | 15.60 | 0.0001 |
| environmental colour × species × $\log_e$(frequency)[a] | 2 | 0.00 | 0.97 |
| error | 639 | 1193.00 | — |
| total | 640 | — | — |

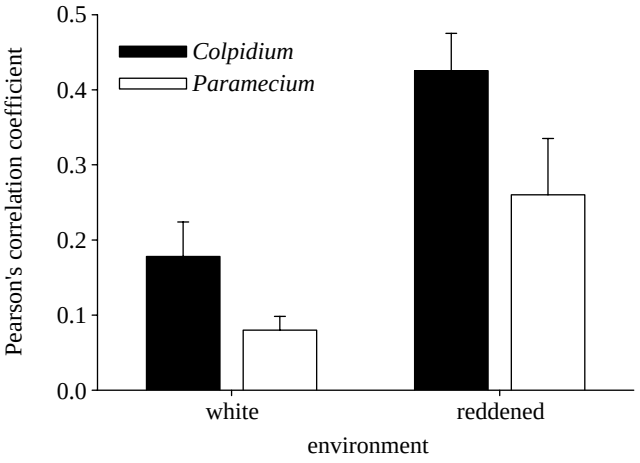


Figure 4. Mean correlation coefficients for the relation between population density and average temperature over the previous two days. Populations tracked reddened environments more closely than white environments and *Colpidium* tracked temperature fluctuations more closely than *Paramecium*. The error bars are $\pm 1$ s.e.

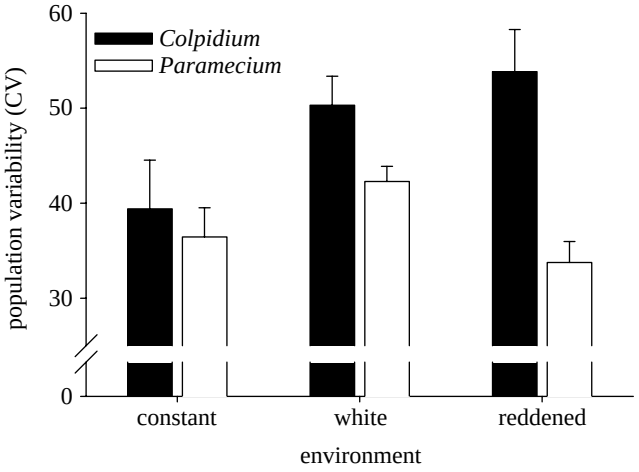


Figure 5. Mean population variability (CV) over the entire experiment. The error bars are ± 1 s.e.

population averages over this reddened variation. Thus, whether environmental variation is reddened or not depends somewhat on the population in question and general statements about reddened environmental variability should be accompanied by a frequency range over which observations were made (e.g. Steele 1985; Cuddington & Yodzis 1999).

There is a caveat to my between-species analyses. I assumed that the differences between the *Colpidium* and *Paramecium* population dynamics resulted from differences between their intrinsic rates of increase, *r*. However, *Colpidium* and *Paramecium* differ in other ways, apparently, for example, in their sensitivity to temperatures above 29 °C. Any such differences potentially confound differences between *r*. Additional interspecific differences provide a potential explanation for why the *Colpidium* population variability was not lower than the *Paramecium* population variability in the constant environment (figure 5). Further experiments are needed to confirm that the population dynamics differences result from differences in *r*.

### (c) *Population variability*

My results show that population variability is determined by an interaction between the intrinsic rate of increase (which equates to the resilience of a single-species population) and the extent (and colour) of environmental variability (the same result as Luckinbill & Fenton (1978)). Because of the interaction between the intrinsic rate of increase and environmental variability we cannot make general inferences about population variability from resilience, or resilience from population variability, without understanding the effect of environmental variability (Pimm 1991; Horwood 1993). Both population variability and resilience are measures of stability. The choice of which of these two (or other) measures of stability we use should be determined by our particular question about stability, but is often constrained for practical reasons (measuring population variability is easier than measuring resilience). However, if environmental variability is not monitored or controlled, it will be difficult to make inferences about resilience by measuring population density or vice versa.

### (d) *Final thoughts*

A recent study has suggested that global environmental change includes changes in the autocorrelation structure (colour) of the environment (Wigley *et al*. 1998), and another that possible reddening of an environmental variable (the number of dry days in runs of more than five days has increased in a Costa Rican cloud forest) caused the extinction of several species (Pounds *et al*. 1999). These studies, the results presented in this paper and many theoretical studies indicate that explanations and predictions of population and community (Caswell & Cohen 1995; Ripa *et al*. 1998) patterns will benefit from understanding the effects of environmental colour.

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