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A novel experimental apparatus to study the impact of white noise and 1/*f* noise on animal populations

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This paper reports on the design and construction of a novel apparatus that allows a set of aquatic microcosms to experience complex temporal environmental fluctuations. Replicate microcosms were maintained in 18 water baths with independent environmental controls. We give results from a preliminary experiment designed to look at the effects of varying temperatures with different variance spectra (i.e. white noise or 1/*f* noise) on single species population dynamics. Matching time series (with identical elements, differently ordered) of environmental temperatures with different Fourier spectra were created for use as input to the apparatus using a novel spectral mimicry method. The apparatus functioned well during the course of the experiment making this an extremely useful research tool. This apparatus now provides ecologists with a means of studying how environmental variability, and directional trends in this variability, are filtered and translated by real populations and micro-ecosystems.

Keywords: environmental variation, reddened noise, microcosm, experiment, protists

1. INTRODUCTION

Population biologists have traditionally undertaken studies on the dynamics of species in the laboratory to escape the uncertain nature of a fluctuating environment. A controlled laboratory environment remains a valuable simplification of the real world (Lawton 1995; Morin & Lawler 1996). However, the predictive power of population dynamic theory will remain uncertain until the effects of stochastic environments are understood (Roughgarden 1975; Halley 1996).

The effects of different levels of variability (variance) in the environment on population dynamics are well researched (Leigh 1981; Goodman 1987; Pimm 1991; Lande 1993). Indeed, models used to predict minimum viable population size, maximum harvesting levels or reserve size (to give but three examples) incorporate various levels of environmental variance. Traditionally, 'white noise' has been chosen to model this variability (May 1973; Halley 1996); white noise assumes no correlation, and constant variance over time. Real marine and terrestrial physical variables show increasing variance through time and temporal autocorrelations on a multitude of scales. For example, the variance of temperature (and other variables) increases through time (Monin *et al.* 1977; Steele 1985; Williamson 1987; Pimm 1991). That is, environmental variation is better described as '1/*f* noise' (Halley 1996). In the 1/*f* model, the power or amplitude of fluctuations is proportional to the reciprocal of their frequency. Daily, high-frequency events have low amplitude; yearly or decadal low-frequency events have higher amplitude; and very rare events (ice ages, for instance) have enormous amplitude. Unlike 'white noise', 1/*f* noise has a reddened spectrum in which long wavelengths predominate. This model has the important feature of increasing variance through time, closely approximating the temporal correlation observed in real environments (Mandelbrot & Wallis 1969).

The importance of the distinction between 1/*f* noise and white noise becomes apparent when one considers the effect of the uncertain nature of the environment on the persistence of plant and animal populations. To the extent that population densities are driven by environmental fluctuations (Pimm & Redfearn 1988; Ariño & Pimm 1995), the continued use of white noise in population models ignores the very real problem that populations will encounter unfavourable events with increasing probability the longer they persist (Lawton 1988). Incorporation of white noise instead of 1/*f* noise will hence tend to underestimate the population size required for persistence in the long-term, according to some theories of population dynamics.

Whether this distinction matters in reality depends, it seems, on a number of factors, most notably on the degree of density dependence within a population and the spatial concordance in fluctuations between populations (Hanski *et al.* 1996; Ripa & Lundberg 1996; Petchey *et al.* 1997). The response also depends on how fast the population can change density relative to how quickly the environment

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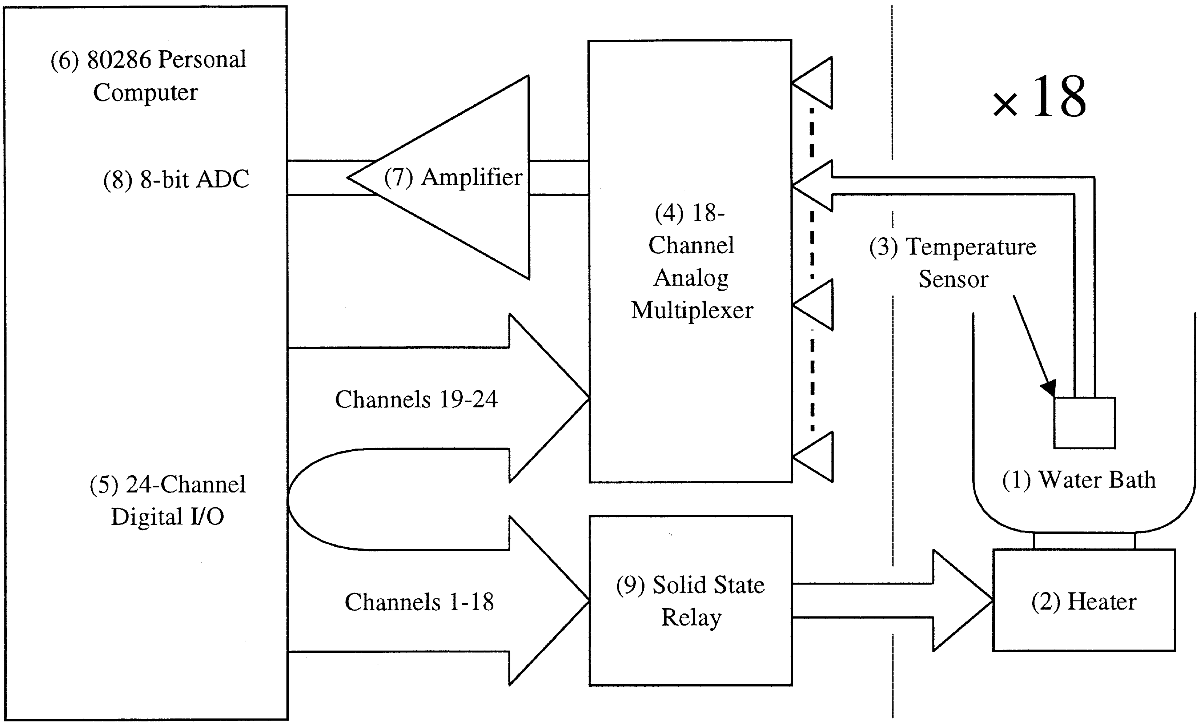

Figure 1. Schematic diagram of the temperature control system. Numbers in parentheses are referred to in the text.

changes (Hubbell 1973; Roughgarden 1975; Nisbet & Gurney 1982). However, until we know how environmental variability is filtered and translated by real populations, development of more realistic population models will remain an uncertain process.

To test the sensitivity of real populations to the colour of the noise they experience, we ideally need replicates of long time series of data from populations that have been exposed to distinctly different patterns of environmental noise. Such data do not exist because field studies cannot provide the necessary environmental control combined with sufficiently long time series. Here we describe a microcosm approach to this problem, in which we expose populations of freshwater protozoa to temperature fluctuations with different variance spectra. The short generation times of freshwater protozoa allow long time series to be collected quickly and temperature is a relatively easy environmental variable to control. The novel apparatus which allows replicated temperature control is described, together with the method used to synthesize noise with different colours, as input into the apparatus.

2. THE APPARATUS

The apparatus was designed to allow small replicated aquatic microcosms to experience accurate, complex temporal temperature fluctuations. The experimental design required 18 independent water baths. The apparatus is described in figure 1 and the text that follows; numbers in parentheses in the text refer to the parenthetical numbers in figure 1.

Microcosms were contained in covered water baths (1) (5 l aluminium pans with lids), which, in addition, contained a heating element (2) and a temperature sensor (3). The heating element was two 100 Ω aluminium clad resistors (RS Components, Northants, UK stock code 157–588) in parallel, mounted on a small aluminium heat sink. All electrical connections were insulated with adhesive lined heat shrink tubing and covered with epoxy resin. When on, the heating element was driven by a 60 V supply, and delivered 72 W of heating power. The water baths were housed in a 2 °C refrigerator which had a cooling power of approximately 35 W per water bath. Therefore, when the heating element was on, the baths were heated. When the heating element was off, the baths were cooled.

The temperature of each water bath was monitored by a LM35CZ temperature sensor (3) (RS Components, stock code 317–960) which provided an output of 10 mV $^{\circ}C^{-1}$. The initial accuracy of this item was ± 0.4 °C but sensor specific corrections were applied in software to improve this to ± 0.2 °C. A 'pulldown' resistor connected each sensor output to −12 V to maintain accuracy at lower temperatures. The sensor electrical connections were protected with adhesive lined heat shrink tubing, which was extended over part of the sensor body to prevent water ingress. The whole sensor was varnished for further protection.

The temperature sensor outputs were presented to the multiplexer system (4) as analogue inputs. The multiplexer system comprised two integrated circuits (I.C.). Since the experimental design required 18 channels and standard multiplexers come in eight or 16 channels, a 16-channel device (I.C. 4067B; RS Components, stock code 640-636) and an eight-channel device (I.C. 4051B; RS Components, stock code 640-585) were combined to perform the function of an 18-channel multiplexer. Sensor outputs 1–15 were connected to the 4067B I.C. and sensors 16–18 were connected to the 4051B I.C. The multiplexer 'address' lines (i.e. the digital signals which determine which input is to be selected) were controlled by a programmable digital input/output card (5) (digital I/O, Maplin Professional Supplies, Essex, UK stock code AM11M), which was fitted into a 80286 personal computer (6) (PC).

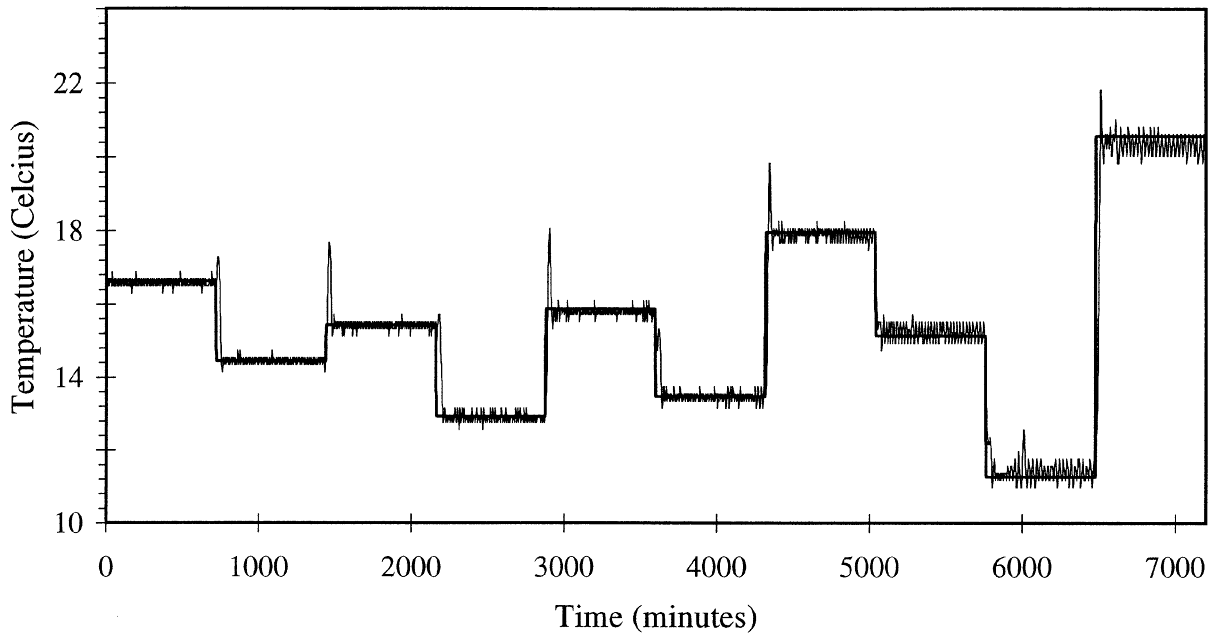

Figure 2. Performance of the temperature control system. The square wave (thicker line) is the control temperature, the thinner, fluctuating line is the actual temperature recorded by the temperature sensor in a representative culture vessel.

The address lines for the 4067B I.C. were driven by channels 19–22 of the digital I/O card, the 4051B had its address lines driven by channels 23 and 24. Thus the PC could monitor the temperature of each water bath in turn. Unused inputs of the multiplexer I.C.s were deliberately left unconnected to allow each multiplexer I.C.'s output to float while its partner was active: i.e. while the 4067B was active, the output of the 4051B was set to a floating input, and vice versa.

The multiplexer output (i.e. the bath temperature being monitored) was amplified (7) and applied to an analogue to digital convertor (8) (Pico Technologies Ltd—8-bit converter ADC10; supplied by Farnell Components, Leeds, UK stock code 256-122), which plugged directly into the parallel port of the PC.

Bath temperature was then compared with the setpoint temperature (as determined by the required temperature time series) and the digital I/O card channels 1–18 were used to turn the appropriate bath heater on or off as necessary. This was achieved by applying a digital signal to the control terminal of a 'solid state relay' (9) (CTX240D3Q quad units; Farnell Components, stock code 529-771), which controlled power to the appropriate heater element. To protect the digital I/O, its outputs were buffered into the solid state relays using 74LS244 I.C.s (Maplin Professional Supplies, stock code QQ56L).

The control software, written in QBasic, took as inputs the required temperature time series for each bath and the actual temperature of each bath. The software sequentially read the temperature in each bath (by connecting the temperature signal from each bath to the ADC via the multiplexer and amplifier). If the actual temperature in the bath was higher than the required temperature for that bath at that time, the corresponding heater was turned off. If the actual temperature was lower than the required temperature the heater was turned on. At user-selected intervals, the software moved to the next temperature value in all of the required temperature time series. The software also recorded to a file, at user-defined frequency, the actual temperature of each bath.

The apparatus performed as designed. Figure 2 shows actual bath temperature and required bath temperature and is typical of the results of other baths. The temperature control was not perfect: the actual temperature in the baths fluctuated around the desired temperature with an amplitude of 0.1–0.5 °C and variable period (up to 30 min). It is unlikely in theory (and preliminary results suggest) that the population dynamics of the aquatic organisms the apparatus was designed for will respond to fluctuations of this amplitude and period.

The difference between the mean actual bath temperature over time (12 h with temperature recorded every 5 min) and the required bath temperature was consistently less than 0.3 °C. The sign and magnitude of the difference between actual temperature averaged over time and required temperature seems to be bath-specific. This means that the cumulative temperature of baths over time will differ even if they have identical required temperatures. Correction of the bath-specific biases was achieved by measuring the bias over a short time (for example two weeks) and then adjusting the required temperature time series. The adjustment consisted of a permanent addition to, or subtraction from, the required temperature time series to prevent further biases, and a similar short-term correction to eliminate cumulative temperature differences that had already occurred. Regular monitoring of cumulative temperature during an experiment and continuous adjustment of control temperature series allowed bath-specific biases to be minimized. Numerical investigation of such manipulations of the required temperature time series has shown little effect on the colour of the time series.

3. SYNTHESIS OF TEMPERATURE SERIES

Time series synthesis allowed control of the spectral properties of the time series with all other statistical properties of the series held constant. The basis of the synthesis was the summation of sine waves and is described next.

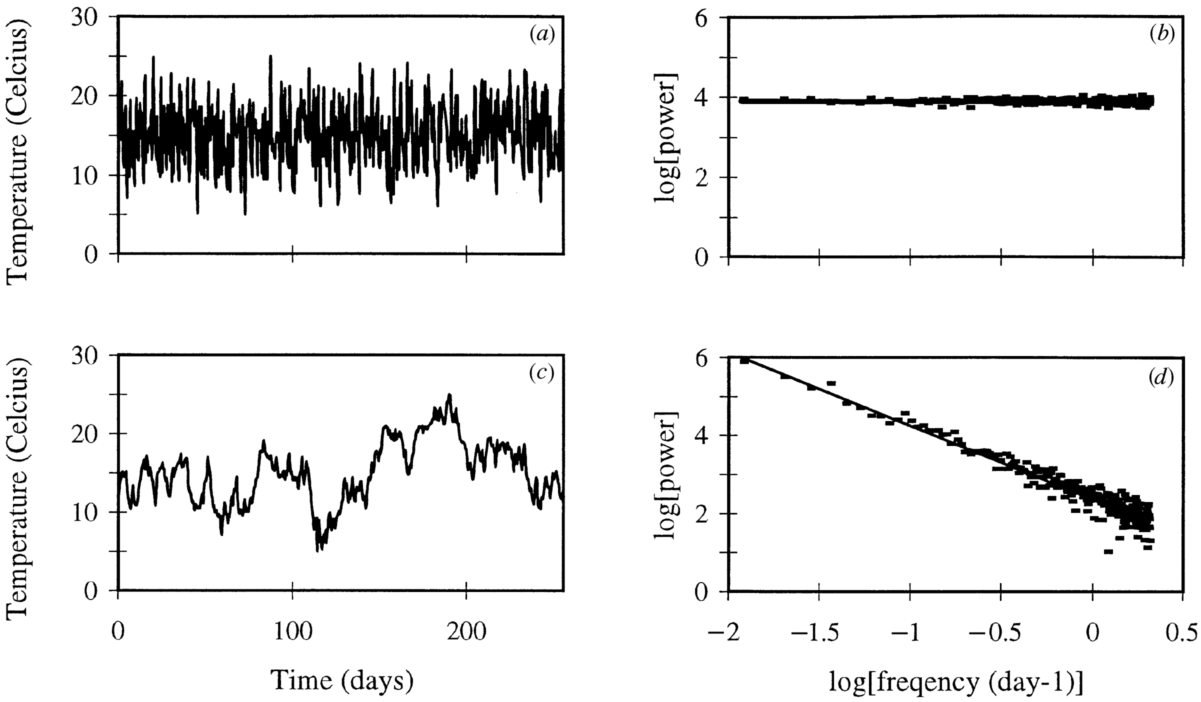

Figure 3. Control series synthesized as described in the text (*a*,*c*) and their power spectra (*b*,*d*). (*a*) Shows a white series ($\gamma = 0$), (*b*) its power spectra, showing $\gamma = 0.00225$ (—half the gradient of the least squares linear regression), $y = -0.0045x + 3.8831$, $R^2 = 0.001$. (*c*) Shows a $1/f$ series ($\gamma = 1$), (*d*) its power spectra showing $\gamma = 0.943$, $y = 1.8857x + 2.3648$, $R^2 = 0.9276$.

The required temperature time series, each of length n, where n is even, were synthesized by the addition of $n/2$ sine waves with phase randomly and uniformly distributed between 0 and 2π. The period of the longest sine wave was n (frequency 1 cycle per time series), the shortest period was 2 (frequency $n/2$ cycles per time series), and the remainder were $(n/2) - 2$ sine waves with frequencies equally distributed between $n/2$ cycles per time series and 1 cycle per time series. The relationship between the frequency, f, and amplitude $S(f)$ of the component sine waves defines the variance spectra (colour) of the fluctuations (Halley 1996):

$$S(f) \propto \frac{1}{f^{\gamma}}. \qquad (1)$$

To produce white noise, γ was set at 0: all frequencies had equal amplitude. To produce reddened ($1/f$) noise, γ was set at 1, i.e. amplitudes were the reciprocal of frequency.

Pairs of series thus produced, one red and one white, differed in variance and mean. To correct these differences one series was transformed to give the desired range and mean. The other untransformed time series was then mimicked (Cohen *et al.* 1998) to the transformed time series to ensure that both were composed of exactly the same numbers but in different orders. The order of the numbers defined the variance spectra of the time series.

Examples of time series produced using this method are given in figure 3*a*,*c*. This method of time series synthesis gives very good control over the variance spectra of the noise. To check this we calculated the Fourier transform of the series and retained only the first half of the output (due to the symmetry about its middle), and also discarded the first element. Each of the remaining elements of the transform was then multiplied by its complex conjugate to give the squared amplitude at the corresponding frequency (the power spectral density, psd). The relationship between the power and frequency of fluctuations in the time series is given by plotting log(psd) against log(frequency) (figure 3*b*,*d*). The slope of the linear regression of this plot is -2γ.

The advantages of this method of time series synthesis over other methods that control the variance spectra are that the variance and mean are exactly controlled, even in a time series of finite length. Further, when γ is set at 1, $1/f$ noise is produced (over a finite range of frequencies) and not a statistical analogue of $1/f$ noise such as is produced by an autoregressive process. That is, our method of synthesizing a $1/f$ noise yields a signal with a psd in which amplitude is exactly proportional to the inverse of frequency, whereas autoregressive noise yields a signal with a psd in which there is statistical fluctuation in amplitude around the reciprocal of frequency. The advantage of $1/f$ noise as a model of environmental variability is that it is more mechanistic. Autoregressive noise models the correlations between numbers in the time series and is therefore a phenomenological model. $1/f$ noise models many different processes that each have characteristic frequency and amplitude, the final signal being the sum of all these processes.

4. PRELIMINARY RESULTS

A pilot experiment was conducted to test whether cultures of protozoa behaved normally in the water baths and to check the reliability of the temperature control apparatus over several weeks. Six of the baths were set at a constant 15 °C and the temperature of the remaining 12 fluctuated between 5 °C and 25 °C, six baths with white and six baths with reddened ($1/f$) spectra. Each bath contained a 175 ml glass jar containing a 100 ml culture of *Paramecium tetraurelia*.

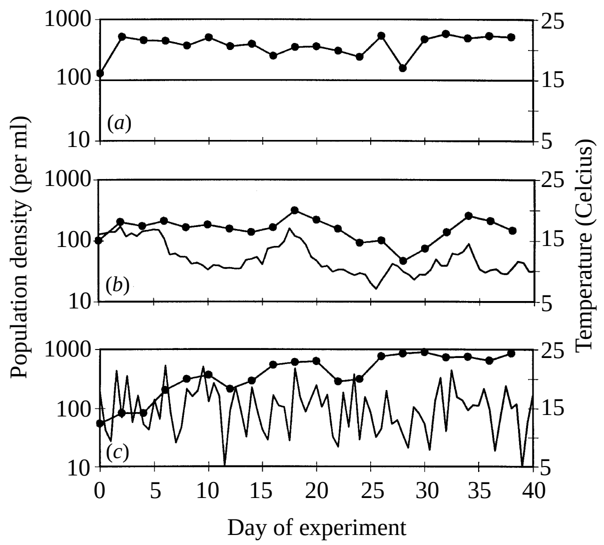

Figure 4. Results from a preliminary experiment in which population sizes of *P. tetraurelia* (solid lines with circles), were estimated every other day whilst temperature (solid lines with no circles) was held constant (*a*), or varied with reddened ($1/f$) spectra (*b*), or white spectra (*c*). The data are for one representative culture from each treatment.

Population density of the cultures was estimated every two days by measuring the density of *P. tetraurelia* in approximately 0.5 ml of culture media. At the same time 60% of the culture was removed and replenished with sterile media. Population densities of one culture from each of the temperature treatments are shown in figure 4. The cultures grew and persisted in the apparatus. Any further interpretation of these results will have low statistical power since the time series are relatively short. Much longer experiments (approximately 9–12 months) are required to test the sensitivity of these populations to temperature variations with different variance spectra.

5. CONCLUDING REMARKS

The new temperature control apparatus described above is a powerful experimental tool to study the effects of complex and varying patterns of temperature fluctuations on laboratory populations of protozoa and small aquatic invertebrates. Although it was designed with a specific study in mind, its generality and flexibility allow many potential uses. For example, the same principles could be applied to small terrestrial microcosms (when the baths contain no water, control of air temperature is good). It could also easily be adapted to control other environmental variables, such as light or precipitation.

Laboratory microcosms have played an important role in the development of population ecology (Kareiva 1989; Lawton 1995), but have almost invariably been run under constant conditions. We now have the means to extend the use of microcosms to study the population dynamics of organisms under precisely controlled, but variable, environmental conditions, simulating different types of environmental noise.

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